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Spatial and Temporal Activity of Migratory Bats at Landscape Features

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A thesis submitted in partial fulfillment of the requirements for the Master of Science degree in Biology

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SPATIAL AND TEMPORAL ACTIVITY OF MIGRATORY BATS AT LANDSCAPE FEATURES

(Spine title: Spatiotemporal Migratory Bat Activity at Landscape Features)
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by

Rachel M. Hamilton

Graduate Program in Biology

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science

School of Graduate and Postdoctoral Studies
The University of Western Ontario
London, Ontario, Canada

CERTIFICATE OF EXAMINATION

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The thesis by

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Spatial and temporal activity of migratory bats at landscape features

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Abstract

Geographical landmarks may be important features for navigation of migrating bats although spatial and temporal activity may depend on species-specific migration strategies. I predicted that latitudinal migrating bats would have higher activity along north-south oriented linear landscape features, especially during late-seasonal migration periods, compared to bat species that migrate within a regional area. I acoustically sampled four species of bats classified as latitudinal and regional migrants. I monitored twelve sites located in southwestern Ontario at four landscape features between May and October 2011. I found that specific landscape features may have greater importance to specific species rather than their migration strategy. Also, latitudinal migratory bat activity increased during the late-seasonal time period however all species activity increased in the mid-seasonal time period. Information, gained with acoustic monitoring, about seasonal relationships of species at landscape features may help identify critical areas used by migrating bats.

Keywords: migratory bats, landscape feature, acoustic monitoring, seasonal, ridge, shoreline, central

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1. Introduction

Migration is a biological phenomenon that spans across multiple animal taxa and across different environmental strata (air, water, and land). The definition of migration involves an undistracted, seasonally-timed movement spanning greater distances than typically covered in daily activity, between areas of seasonal residency and breeding grounds (Dingle and Drake 2007). Why animals migrate is often linked to spatiotemporal fluctuations in food resources, shelter, and climate conditions, but when and where migrants travel remains a constant area of research (e.g. Berthold 1993; Newton 2008). Flying animals, especially, can cover great distances in relatively short amounts of time. The migrations of birds are highly researched due to their conspicuous nature and impressive movements across multiple terrains and landscape barriers (Berthold 1993; Cox 1985; Newton 2008). Compared to bird migration, relatively little is known about the migrations of bats, although both groups of flying animals face similar challenges (i.e., weather, topography, resources) that influence temporal and spatial patterns of migratory movements (Fleming and Ebay 2003; Popa-Lisseanu and Voigt 2009).

The much smaller proportion of migrant bat species, compared to migrant birds, along with small body size, nocturnal nature, and rapid mobility make migratory bats difficult to capture and track. Knowledge of the routes and timing of migrating birds is largely attributed to extensive annual monitoring at banding stations located throughout the world (Dingle 1996), which are currently non-existent for bats. Early understanding of bat migration came from observational and collection studies where certain species were found to be absent in the winter (Dalquest 1943; Merriam 1887; Miller 1897). Since then, different techniques such as banding and re-capturing, (Ellison 2008; Hutterer et al.

2005), radio tracking (McGuire et al. 2012), wind turbine mortality counts (Fiedler et al. 2007; Johnson et al. 2004; Kunz et al. 2007), and stable isotope analysis (Cryan 2003; Fraser et al. 2012) have contributed to the understanding of temperate bat migratory movements by providing insight into specific locations migrant bats are found during the season.

Using acoustic monitoring to sample bat activity has increased in part because of the ability to easily record echolocation calls without actively capturing bats and the affordability of the equipment. Acoustic detectors record high-frequency sounds of echolocation calls, and calls are usually species-specific (Fenton and Bell 1981). Acoustic monitoring is useful for identifying critical areas of activity, but most studies focus on specific site locations and use a limited number of detectors (Baerwald and Barclay 2009; Barclay 1984; Serra-Cobo et al. 2000). However, sampling a large region using stationary acoustic monitors may allow us to determine important areas for migrating bat activity (Johnson et al. 2011).

1.1 Bat migration and landscape features

Bats may use many sensory cues to navigate during migration. Like birds, bats can recognize post sunset glows (Buchler and Childs 1982), the earth's magnetic field (Holland et al. 2006) and geographical landmarks (Baerwald and Barclay 2009). The combination of multiple sensory signals may contribute to a 'map and compass' strategy where perception of magnetic fields and celestial cues may provide a compass, and landscape features may provide a map (Holland 2007; Tsoar et al. 2011). The ability to use known, fixed reference points to navigate, typically by visual observation, is known as "piloting" (Dingle 1996). Bats' visual ranges extend farther than their echolocation ranges (Suthers 1970), thus it is likely that they navigate using visual cues (Suthers 1970; Timm 1989), in conjunction with echolocation. Prominent topographical features serve as fixed reference points, and may aid navigation by bats during migration.

Geographic landmarks with high concentrations of migratory bat activity indicate important areas for seasonal movements. For example, areas of land adjacent to barriers (such as expanses of water) are known as stopover sites where concentrations of migratory animals (e.g. birds) stop and, depending on the type of animal, refuel before continuing their journey. Sites adjacent to geographical barriers (e.g., The Great Lakes), like Long Point, ON, often serve as stopping sites for migratory bats and often have higher capture and activity rates during spring and late summer and fall than during other times of the year (Barclay 1984; Barclay et al. 1988; Dzal et al. 2009; McGuire et al. 2012; Hooton 2010). However, other geographical features, in relation to land and water, may focus migrating bats during moments to eventual final destinations (Baerwald and Barclay 2009; Furmankiewicz and Kucharska 2009).

Linear landscape features may be important to the migration of bats. Linear landscape features such as mountains (Baerwald and Barclay 2009) and rivers (Furmankiewicz and Kucharska 2009; Serra-Cobo et al. 2000) host heightened numbers of bats during migratory periods and may be used for seasonal or territorial directional flight. Shorelines (Ahlén et al. 2009; Barclay 1984; Serra-Cobo et. al. 1998) and forested ridges (Fiedler et al. 2007) are other possible concentrated areas for migration of bats.

Migrating bats appear to follow the coast of oceans (Ahlén et al. 2009; Cryan 2003, Jarzembowski 2003; Serra-Cobo et al. 2000) and large lakes (Barclay 1984; Timm 1989). Migrating bats have also been observed to fly over sea (Amengual et al. 2007), sometimes landing on oil rigs and ships (Ahlén et al. 2009; Czene et al. 2011; Griffin 1970) and on coastal islands (Cryan and Brown 2007; Johnson et al. 2011). Some nocturnally migrating birds follow coastlines to avoid crossing ecological barriers and navigate by landmarks (Alerstam 1990), and migratory bats may also use this strategy. For example, Timm (1989) suggested migrating bats "funnel" down the north-south oriented shore line of Lake Michigan, rather than cross open water. Likewise, Barclay (1984) observed bats flying along the shore of Lake Winnipeg, another north-south oriented shoreline, during migration rather than traversing the lake. These examples support Alerstam's (1990) barrier avoidance theory, however, migratory bats also cross large bodies of water (Ahlén et al. 2007; Amengual et al. 2007; McGuire et al. 2012). For example, McGuire et al. (2012) documented migratory bats crossing Lake Erie, an east-west oriented shoreline, during southward migration. The decision to cross water barriers or follow coastlines could depend on the land mass direction and the potential cost of energy to cross or to detour around a water barrier. Migrant bat species possibly use linear-like shorelines as a navigable tool if the coast is oriented in the direction of migratory flight.

Ridges are prominent linear-like landscape features that can span across long areas. Wind energy facilities located along ridgelines experience some of the highest bat mortalities in North America compared to other areas, suggesting that bats concentrate along ridges during migration (Fiedler et al. 2007; Johnson et al. 2004; Kunz et al. 2007). However, most research conducted on ridges is within areas where wind turbines are located (Arnett et al. 2008). There is little known about how migratory bats interact with ridge landscapes.

Migratory birds may migrate along topographical features during migration, but species can exhibit different movement patterns labeled as broad-front and narrow-front migration (Ralph 1981). Broad-front migration refers to migratory behavior moving in a constant direction regardless of topography while narrow front refers to concentrations of migration at topographical features (Berthold 1993; Ralph 1981) such as mountains, river valleys and shores. Migrating bats may also use particular geographic areas during migration; however migrant bat species have different migratory strategies often based on their life history. The importance of landscape features and movement patterns to migrant bats may be determined by their type of migration strategy.

1.2 Migration strategies and seasonal activity

In North America, bats display both latitudinal and regional migration strategies. Latitudinal migrants annually move across a north-south gradient and can travel greater than 1000 km between summer and winter grounds (Bisson et al. 2009; Fleming and Eby 2003). Latitudinal migrants, *Lasiurus borealis, Lasiurus cinererus* and *Lasionycteris noctivagans*, are considered "tree-dwelling" bats (Cryan and Veilleux 2007), with *Lasiuris* spp often roosting solitarily or in small family groups in tree foliage (Cryan and Veilleux 2007) and *L. noctivagans* in groups in cavities or solitarily under bark (Barclay and Kurta 2007; Campbell et al. 1996). However, roosting in trees in the winter increases body exposure to weather fluctuations and may cause *Lasiurus* and *Lasionycteris* spp to migrate long distances to southern latitudes that are less susceptible to freezing conditions (Cryan and Veilleux 2007). The summer ranges of *Lasiurus* and *Lasionycteris* spp ranges extend into Canada while the winter ranges, although still relatively unknown, are within the south-eastern United States, Mexico, and into South America (Cryan 2003; Shump and Shump 1982 a,b).

Regional migrants move in a multi-directional radiation from hibernacula to surrounding areas, approximately within a 600 km radius, in the spring and make return movements in fall (Fleming and Eby 2003). Presumed regional migrants, *Myotis lucifugus* and *Perimyotis subflavus*, hibernate in caves, abandoned mines, or rock crevices in the winter (Fenton 1969; Trombulak et al. 2001), but in the spring females form maternity colonies to rear young, while males remain solitary. Since temperatures in caves remain constant, regional migrants can hibernate throughout the winter in the same region that they breed, thus they do not make large migratory movements compared to those of latitudinal migrant species.

Latitudinal and regional migrants in North America have similar time frames for seasonal movement. Overall activity levels increase in the spring as latitudinal species move from southern to northern latitudes and regional species emerge from hibernation and move into surrounding areas. Sex-biased variations exist in the temporal patterns where female latitudinal and regional migrants arrive at summer grounds earlier than males and often make longer distance movements (Cryan 2003; Davis and Hitchcock 1965: Fleming and Eby 2003; Findley and Jones 1964; Humphrey and Cope 1976; Valdez and Cryan 2009). These sex differences may be driven by the energy demands and roost requirements of pregnancy and pup-rearing as theorized by Fleming and Eby (2003). During the summer months, increased activity occurs during periods of lactation, (June-July) and when young-of-year are volant and able to forage independently (Anthony and Kunz 1977). In late summer and fall, latitudinal migrants will mate and migrate south for the winter. Relatively little is known about migration rates for North American latitudinal migrants however activity at stopover sites adjacent to barriers indicate noticeable influxes of activity, sometimes in multiple waves, where individuals may only stay one to two days in the area (Barclay et al. 1988; Hooton 2010; McGuire et al. 2012). Within a similar time period, regional migrants make migratory movements to mating areas called swarming sites, which are typically also hibernation locations (Fenton 1969; Glover and Altringham 2008).

Although regional and latitudinal migrants have similar temporal activity, there is limited information about the spatial distribution of latitudinal and regional migrants during migration periods. Latitudinal migrants can be difficult to locate, capture, and track because they do not form large roost aggregations (Kunz and Lumsden 2003), and often fly above the forest canopy (Kalcounis et al. 1999; Menzel et al. 2005). Knowledge about latitudinal migration has increased in recent years with contributions from recording seasonal mortality at wind energy facilities (Arnett et al. 2008; Baerwald and Barclay 2009) and use of stable hydrogen isotope analysis to further understand seasonal distribution at a continental level (Cryan 2003, Fraser et al. 2012). Since latitudinal migrants partake in migrations outside of a regional summer area, it is possible that they adopt a narrow-front migration strategy and migrate according to landscape features to aid in navigation.

Most evidence of regional migration of bats in North America comes from banding projects where recoveries of bands and banded animals provide minimum straight-line distance between two locations of capture (Ellison 2008; Fenton 1969; Kurta and Murray 2002). Efforts have typically focused on *M. lucifugus* due to the ease of capture and relocation because they often congregate in large numbers (Fenton 1969). Although *M. lucifugus* and *P. subflavus* species are generally considered regional migrants (Bisson et al. 2009), recent research indicates that *P. subflavus* may make substantial migratory movements more similar to latitudinal migrants (Fraser et al. 2012). Thus, much remains unknown about migration of categorized regional migratory species and where they move across the landscape. However, landscape features may be less important to regional migrants, compared to latitudinal migrants, as a possible navigational tool during migration depending on hibernacula location in relation to summer roosting areas, and regional migrants may therefore have broad-front movement across an area instead of narrow-front migratory movement.

1.3 Statement of Purpose

The objective of my research was to determine the seasonal relationships between the occurrence and activity of four species of bats and prominent landscape features. I hypothesize that during different seasonal periods species categorized as latitudinal migrants, *L. cinereus* and *L. borealis*, would use landscape features similar to a narrow-front migration strategy, while species categorized as regional migrants, *M. lucifugus* and *P. subflavus*, would exhibit a broad-front migration strategy.

1) I predicted that *L. cinereus* and *L. borealis* activity would be greater at north-south oriented shoreline and ridge features than in flat regions since features may be used as navigational tools in north-south oriented migration to winter or summer roosting grounds.

2) I predicted that *M. lucifugus* and *P. subflavus* activity would be similar throughout the region, regardless of feature since hibernation sites can be located in any cardinal direction on the landscape.

3) I predicted that activity levels would increase in the mid-seasonal time period for all species because of foraging activity and increased populations due to volant juveniles. However, I predicted that *L. cinereus* and *L. borealis* will have higher activity in the late-seasonal time period compared to *M. lucifugus* and *P. subflavus* corresponding to portions of the population migrating through the area from northern latitudes.

2. Methods

2.1 Study Sites

I established study sites in the Southwestern region of Ontario, Canada along three main transects defined as: ridge, shore, and central features, and a fourth grouping at barrier adjacent features (Figure 1; Appendix II; Table A1). Ridge sites (n=4) were located on the Niagara Escarpment which is a largely forested ridge extending 725 km in a north-south oriented direction in Southwestern Ontario and reaching an elevation of 510 m at its highest point. Shore sites (n=2) were located along the Lake Huron shoreline which extends 328 km from the tip of the Bruce peninsula to Sarnia, Ontario on the west side of Southwestern Ontario and parallels the Niagara Escarpment. Central sites (n=3) were located between ridge and shore features in Southwestern Ontario where the landscape is mainly composed of flat, agricultural land. Barrier sites (n=3) were in areas located adjacent to a water barrier within my study area which is the first available land for migratory animals to encounter. All twelve field stations were situated at provincial and national parks and conservation areas due to the natural surroundings of the area, staff availability, equipment protection, and the presence of elevated platforms (i.e. towers, buildings).

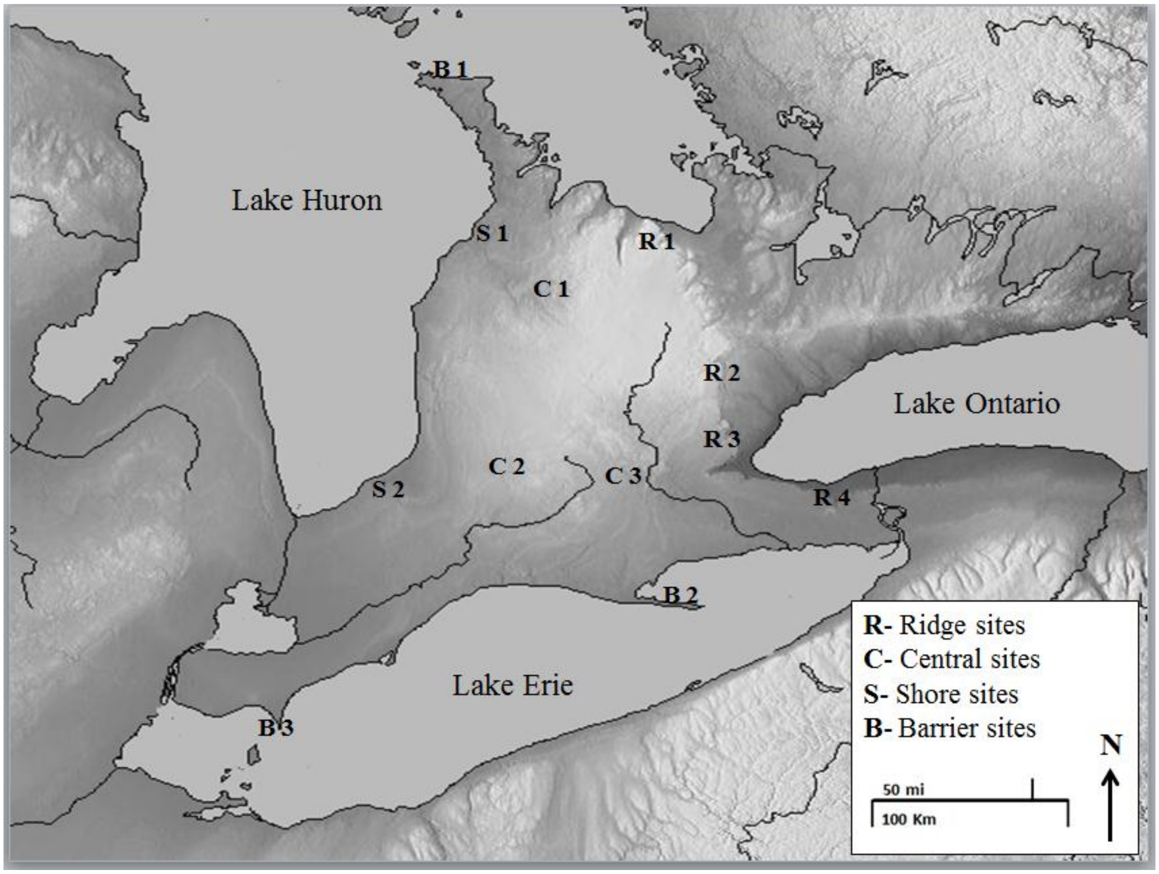


Figure 1: Location of twelve field sites at landscape features (ridge n=4, central n=3, shore n=2, barrier n=3) in Southwestern Ontario, Canada (Natural Earth 2012).

2.2 Data Collection

To assess bat activity at each of my sites, I recorded echolocation calls as a proxy for overall activity (Fenton 1970; Kuntz and Brock 1975; O'Farrell and Gannon 1999). I recorded echolocation calls using Song Meter SM2BAT (Wildlife Acoustics Inc., Concord, MA, USA) single microphone detectors, which are passive recording devices. The recording devices are programmable frequency-triggered ultrasonic detectors that record data on a secure digital high capacity (SDHC) memory card. Calls were recorded at a sampling frequency of 192 kHz with 16 bit sample resolution. Recordings were made in the presence of triggering noises that were within the range of set parameters that included upper and lower frequency cut-off, sound amplitude, post-trigger filter, and gain. Based on my parameters, a trigger event would occur if the noise was between 16 and 92 kHz also known as the upper and lower frequency cutoff. The sound amplitude of the noise was at least 18 dB in audible strength to trigger recording. The post-trigger began after 0.5 seconds of another detected call. The gain was set to 48, the second highest most sensitive setting available, to increase the detection of bats and to reduce recording poor-quality calls however this also may increase noise detection and power consumption. A file was a triggered event that was 1 minute in length.

I installed one SM2BAT at each site. The weatherproof, ultrasonic microphone was attached to an extendable 10 m cable connected to the recording box-shaped (20.3 x 20.3 x 5.1 cm) SM2BAT unit, which was placed within a security box. Findings suggest that some migratory bats may fly at higher altitudes than other bats (Baerwald and Barclay 2009; Reynolds 2006), so I placed microphones 5 m above ground to increase detection. I installed devices opportunistically on towers or poles to meet the 5 m height, habitat, and staff accessibility requirements. I oriented each microphone parallel to the ground, facing south, in an open area with the microphone pointed away from buildings or obstacles that might obscure a bat's flight path. Every week voluntary staff members changed batteries and downloaded data onto an external hard drive.

I recorded nightly activity every night from 13 May 2011 to 13 October 2011. I set the SM2BATs to begin recording at sunset and to stop recording at sunrise. Migratory activity may occur before or after these dates (Figure A3a; Figure A3b), but due to equipment and location availability I was unable to extend the sampling period. I used weather sensors located within the SM2BAT units to record temperature since lower temperature negatively affects bat activity (Erickson and West 2002). Each night, I collected average wind speed and temperature recorded by the closest Environment Canada weather station available (www.weatheroffice.gc.ca) from each site, as this was the only data available across all locations.

At each site I used land classifications based on the Ontario Ministry of Natural Resource's Southern Ontario Land Resource Information System (Version 1.2. OMNR 2008) in ArcGIS 10.0 (ERSI, Inc., 1999-2010) to measure the distance from the microphone to the closest forest (m), distance to the closest water source (m), and distance to the nearest building (m) (Appendix II; Table A1). To assess habitat type, I classified a 5 km radius surrounding the detector location into percentage of land type: forest (coniferous, deciduous, mixed), built-up (pervious e.g. playgrounds and impervious e.g. industrial areas), and water (open water, wetlands).

2.3 Call Analysis

The number and measured characteristics of bat calls were identified through an automated detection algorithm in a MATLAB based analysis program (callViewer, v18; Skowronski and Fenton 2008). The program identifies and measures recorded sounds based on detection parameters that include minimum and maximum frequency, frequency with most energy, and duration, which were written into an Excel file. The callViewer links-algorithm function detection parameters for identifying calls was set to a minimum link length of 10, a minimum energy of 14 dB, with an echo filter threshold at 10 dB, and the lower cutoff frequency at 15 kHz (Skowronski 2008; Skowronski and Fenton 2008). I manually analyzed 5% of my randomly selected files per site to ensure callViewer parameters were identifying bats calls correctly. A noise filter script was applied to the files in R (version 2.14.1; R development core team 2011), discarding any value less that .99 ms or greater than 30 ms, any frequency lower than 15 kHz or greater than 60 kHz, and harmonics greater than 1 to remove ambient noise. A quadratic discriminant function analysis (DFA) script (written by Amanda Adams, Ph.D Candidate at UWO) in R was used to automatically classify bat calls into four species, *L. cinereus*, *L. borealis*, *M. lucifugus*, and *P. subflavus* based on unique characteristic parameters of each Ontario bat species (Figure 2). Although putative latitudinal migrant *L. noctivagans*’s echolocation calls are recordable by acoustic detectors, it is difficult to distinguish these calls from those of the sympatric *Eptesicus fuscus*. Therefore, I did not include the calls of these species in my final analysis. Classification accuracy by the DFA using a jack-knife leave one out validation was: *M. lucifugus* 90.0 %, *L. cinereus* 90.4 %, *L. borealis* 87.9 %, *P.subflavus* 90.5 %. I used species-specific post filter parameters to eliminate any misclassified calls detected in callVeiwer and classified by the DFA (Table 1). I checked 20 files each for each of the 12 sites (240 files) to assess accuracy of classification to species. Each file that I checked was typically comprised of a series of calls from a single bat. In cases where the DFA mistakenly identified multiple species within a file, the most common species identification was applied and only counted the calls identified for that species.

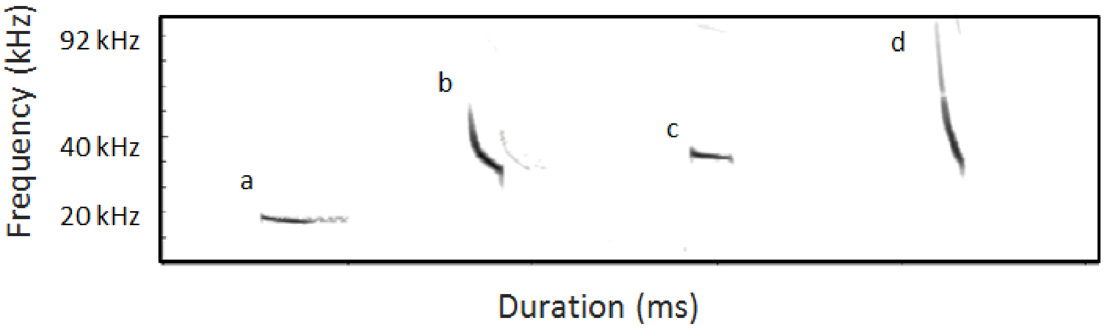


Figure 2. A typical image of an echolocation call produced by species: a) *Lasiurus cinereus* b) *Lasiurus borealis* c) *Perimyotis subflavus* and d) *Myotis lucifugus*. The characteristic of the echolocation call differs by frequency and duration for each species.

Table 1: Species-specific post filter parameters for call classification in Discriminant Function Analysis.

Species	Call Duration (ms)	Minimum Frequency Range (kHz)
Lasiurus cinereus	<8, >30	<15, >29
Lasiurus borealis	<5, >30	<28, >40
Perimyotis subflavus	<5, >15	<36, >46
Myotis lucifugus	<3, >12	<33, >42

2.4 Statistical Analyses

To test my hypothesis that latitudinal migratory bats use linear landscape features during migration, I analyzed bat activity (number of bat calls per night for each species) at each feature (shoreline, ridge, central, barrier) in relation to date. I conducted all statistical analysis in R. After initial data exploration, I chose not to remove any outliers due to the nature of my investigation where outliers may be indicative of migratory activity. I used a factorial ANOVA to determine if overall activity levels per species differed among landscape features and a Tukey's post hoc test to determine the relationship between features and season.

My final data set included number of calls per species, temperature, wind speed, feature, site, distance to water, distance to building, and distance to forest. Before data modeling, the distribution of calls was right skewed, so I applied a data transformation. *Lasiurus cinereus* data was transformed by ln(x + 1) and all other species were transformed as ln(x + 0.5). Wind speed, distance to buildings, and distance to water were also transformed due to right-skewed non-normality. I applied an ln(x+1) transformation to wind speed, a ln(x+0.5) transformation to distance to buildings, and a square root transformation to distance from water.

Generalized Additive Mixed Modeling

My data followed a non-linear pattern thus I applied statistical models that were not based on linear assumptions. A generalized additive mixed model allows for non-linearity and the ability to use smoothing curves by plotting moving averages. It also allows for hierarchical data and includes fixed and random variables (Zuur et al. 2009). I set site as a random variable to reduce the between site variability which is also considered nested within feature. Within my statistical model, I tested and controlled for explanatory variables of feature (ridge, shore, central), habitat (distance from water, distance from building, distance from forest), latitude, and weather (temperature, wind speed). Date was treated as repeated measure. I used ANOVAs to identify significance of multiple variables. I used backward stepwise selection, to remove the least significant variable one at a time until only significant variables ($p < 0.05$) remained. After plotting the results, I used a Plot Digitizer (free Software, Inc., Boston, MA) to identify high activity on the plotted output graphs.

Latitude and peak activity

I identified activity peaks as data points that were three standard deviations higher than the mean of the number of calls at each site. I defined late-seasonal period from 1 August to 1 October based on literature review (Table 2). I used a Pearson's correlation to examine the relationship of peak activity at latitude and date for each feature for each species. I used an exact poisson test to compare the frequency of peaks per species and per feature in two month periods which I defined as mid-seasonal period (1 June to 30 July) and late-seasonal period (1 August to 1 October). The early-seasonal time period refers to 1 April to 31 May.

Table 2: A literature review documenting the month(s) with the highest latitudinal and regional bat species activity within the study sampling period by location, indicative of migratory activity.

State/Province	Increased activity	Source
Alberta	August (mid); September (early)	Baerwald and Barclay 2009
Alberta	August to October	Brown and Hamilton 2006
Arkansas	August(mid) to September (mid)	Perry et al. 2010
California	September(mid)	Cryan and Brown 2007
California	August to September	Dalquest 1943
Illinois	August (mid) to October (mid)	Timm 1989
Iowa	July; August; September	Arnett et al. 2008
Manitoba	September (early)	Barclay 1984
Maryland	September (early) to November	Johnson et al. 2011
Massachusetts	August (late) to September (mid)	Miller 1897
Minnesota	July (mid) to September (mid)	Johnson et al. 2004
Nebraska	September(late)- October(mid)	Damm and Gelosuo 2008
New Mexico	August	Findley and Jones 1964
New York	July (mid) to August (mid)	Jain et al. 2007
Ontario	August (mid)	Dzal et al. 2009
Ontario	August; September	Fenton 1969
Ontario	August to September	Hooton 2010
Ontario	August(late) to September (mid)	McGuire et al. 2012
Pennsylvania; Maryland	August; September	Agosta et al. 2005
Tennessee	August to September(mid)	Fiedler et al. 2007
West Virginia	August(mid) to October (early)	Kerns and Kerlinger 2004
West Virginia/ Pennsylvania	August (early) to September (mid)	Kerns et al. 2005

Categorizing late-seasonal peak activity at each site and feature

Activity for each species was variable among sites and it was sometimes difficult to discern potential migration activity (Appendix; Figure A4:A7). To summarize late-seasonal period (1 August to 1 October) migratory activity levels, I used a set of criteria to score if the peaks of activity in the late-seasonal period more closely resembled migration activity (yes), were questionable (maybe), or likely not (no). An example of raw data and corresponding label according to criteria is shown in Figure 3. After testing and discarding other thresholds, I only considered peaks that were three standard deviations above the mean within site which was able to capture all outlier peaks. First, I assessed and marked each site by species with eight different categories to determine if the peak was: the same peak, within the late-seasonal period, within 1st week of the late-seasonal period, lone, high, near foraging activity, and near summer activity.

The same peak: Some sites had multiple peaks and if they were within two days of each other I considered it one peak. Each peak was taken into account and assessed in relation to all other peaks.

Within the late-seasonal period: I assessed if peaks were located within the determined late-seasonal migration period of 1 August to 1 October.

Within 1st week of the late-seasonal period: I determined if the peak was within seven days of 1 August. Since bats possibly migrate outside of my defined late-seasonal guidelines, I considered peaks in the first week of August to possibly be continued foraging or mid-seasonal activity determined by other categories.

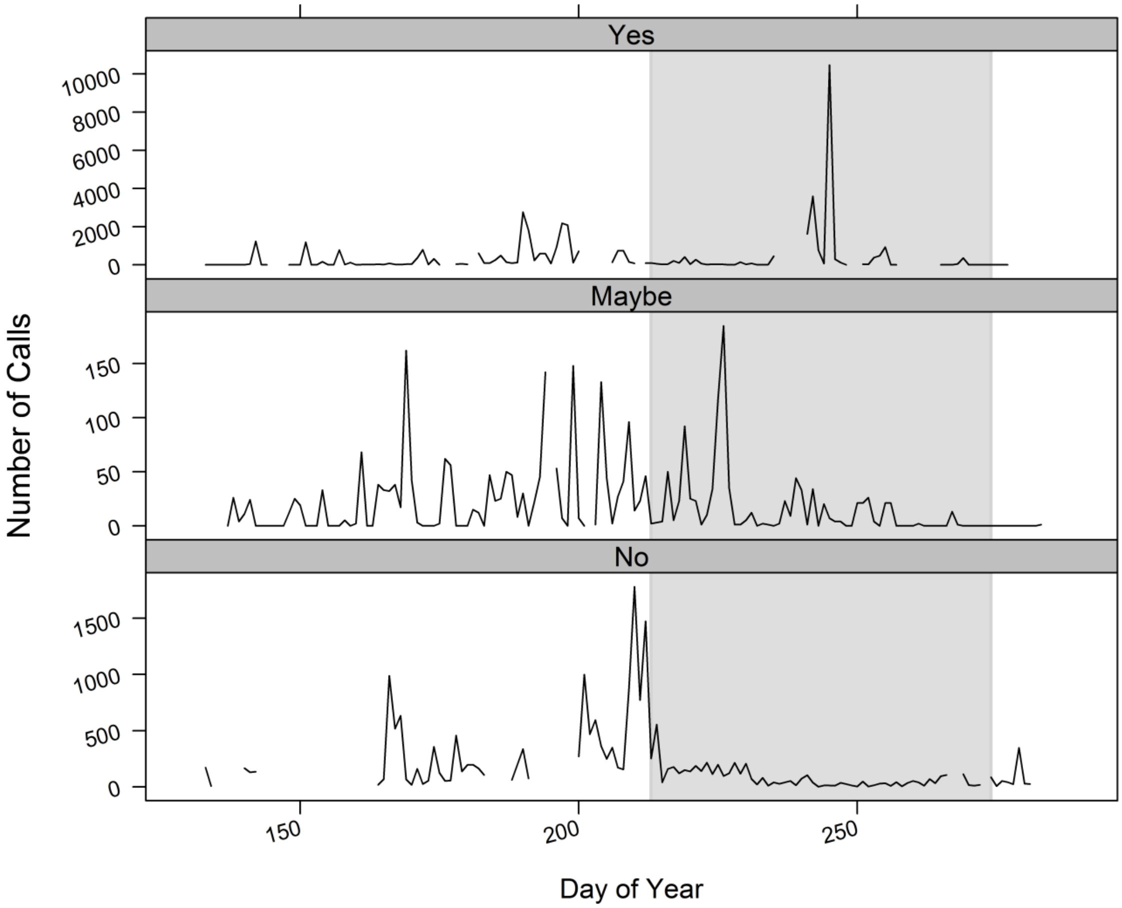


Figure 3: Examples of raw call data across day of year at three sites for *Lasiurus borealis* with labels (Yes, Maybe, No) of possible migration activity based on categorization criteria. The gray box indicates potential late-seasonal migration time period defined as 1 August (213) to 1 October (274).

Lone: I determined if peaks were lone, which I defined as either constituting the only peak at the site or being ten days or more from other identified peaks and not considered part of other foraging or mid-seasonal activity.

High: I identified peaks that were four standard deviations above the mean to determine if there was a large difference of activity comparable to the other identified peaks.

Near foraging activity: If the site had high constant levels of activity spanning most of the mid-seasonal period, I classified it as foraging-like activity. Typically, this category corresponded with peaks within the first week of August.

Mid-seasonal activity: I determined if the peak was attached to increased activity within the last week of July, usually in relation to peaks located within the first week of August.

After taking into account specific categories and the relation to the overall seasonal activity I then gave each site for each species a yes, maybe, or no for late-seasonal migration (Figure 3). For example, a definite yes would be a peak that was later than the first week in August, was lone and high, and there was no connection to mid-seasonal or foraging activity. A no typically was within the first week of August, had connection to foraging and/or mid-seasonal activity, and was not lone or high. A maybe was a peak that had some aspects of a combination of the criteria such as where multiple peaks were classified as one peak, was at the end of the first week in August but within the late-seasonal period, was high and lone, not near foraging, but may represent migration or a late mid-seasonal period activity peak.

I then used a scoring system to determine a numerical classification of overall possibility of migratory activity at each feature. For example, if the site scored a yes I would assign a numerical 3, maybe I would assign a numerical 2, and no I would assign a numerical 1. I added together the site scores of the yes, no, and maybe status labels to get an overall score for feature (Table 3). I created an index to classify the activity level during the late-seasonal time period at each feature based on the possible numerical scores. I created 5 activity level categories labeled as very low, low, medium, high and very high (Table 4). I first determined what the overall lowest and highest numerical score could be for each feature based on the sample size (Table 3) and assigned labels of very low or very high to those scores. For example, if the lowest possible score for the shore was 2 then the corresponding label was very low (Table 4). Only the shore feature had 5 possible scores that paired evenly with the 5 activity labels. The other features had more potential numerical scores than the 5 activity labels so I only assigned one possible score to very low, high, and very high labels to have a conservative ranking for those categorizes and then evenly distributed number scores in the low and medium labels as defined as term distribution (Table 4). Based on the overall score (Table 3), I assigned an activity label (Table 4). For example, *P. subflavus* received an overall score of 4 (Yes=3 + No=1) at the shore (Table 3), so its' activity label at the shore was Medium (Table 4) for late-seasonal migratory activity.

Table 3: The sum of numerical scores by species and feature that corresponded to an assigned status (Yes=3, Maybe=2, No=1) applied to each species at individual sites based on a set of peak assessing criteria that determined the level of possible migratory activity within the late-seasonal period (1 August to 1 October). The lowest number possible was the lowest score that could be assigned to a species at a site multiplied by the sample size at each feature while the highest number possible was the highest score that could be assigned to a species at a site multiplied by the sample size at each feature.

	Feature			
Species	Shore (n=2)	Central (n=3)	Ridge (n=4)	Barrier (n=3)
Perimyotis subflavus	4	6	10	7
Myotis lucifugus	4	8	10	5
Lasiurus cinereus	3	9	7	6
Lasiurus borealis	4	7	10	5
Lowest number possible	2	3	4	3
Highest number possible	6	9	12	9

Table 4: The distribution of the possible sum of site scores a species could have received based on a numerical score that corresponded to a status (Yes, No, Maybe) that was given to each species at each site based on a set of peak assessing criteria that determined the level of possible migratory activity within the late-seasonal period (1 August to 1 October) and a corresponding activity label that indicates the level of overall possible migratory activity during the late-seasonal period (1 August to 1 October) at a feature that could be assigned to each species. The term distribution indicates how many numbers or groups of numbers that are allowed in the activity label row. The numbers that are possible sum of scores are determined by the sample size of each site.

	Feature				
Activity Label	Shore (n=2)	Central (n=3)	Ridge (n=4)	Barrier (n=3)	Term distribution
Very Low	2	3	4	3	1
Low	3	4,5	5,6,7	4,5	Even
Medium	4	6,7	8,9,10	6,7	Even
High	5	8	11	8	1
Very High	6	9	12	9	1

3. Results

3.1 Mean activity for feature and season by species

I recorded data on 153 nights, for a total of 1173 microphone nights across sites and detected all four species. *Lasiurus cinereus* calls made up half of the total recordings (Table 5). Comparing within species, *L. cinereus* had the greatest activity at the ridge during the mid-seasonal time period but had greater activity at the central feature during the late-seasonal time period ($F_{2,920}$ = 33.72, $p < 0.0001$; Figure 4) which increased significantly from the mid-seasonal time period ($F_{2,920}$ =29.72, $p < 0.0001$). *Lasiurus borealis* had the highest activity at the ridge and shore features during the late-seasonal time period with a significant increase of activity at the ridge feature from the mid-seasonal time period ($F_{2,920}$ =3.07, $p < 0.047$). *Myotis lucifugus* had the greatest activity at the shore for both seasons ($F_{2,920}$ =39.26, $p < 0.001$). Within the late-seasonal time period, *P. subflavus* had the greatest activity at the ridge and shore features ($F_{2,920}$ =2.23, $p < 0.0002$).

3.2 Activity patterns across landscape features

Lasiurus cinereus activity at the ridge transect increased at 19 June (Day of Year = 160) and remained consistently high until gradually decreasing beginning at approximately 7 August (219; $F_{7,8}$=10.177, $p < 0.001$; Figure 5). At the central transect, peak activity levels correspond to 1 June (152), 18 August (230) and 27 September (270; $F_{9,11}$ = 10.820, $p < 0.001$), the last two dates occurring within the putative late-seasonal migration time period from 1 August (213) to 1 October (274). There was no distinguishing, non-linear activity at the shore transect ($F_{2,3}$ = 1.772, $p = 0.157$).

Table 5: The total number of calls and percent of total recordings of each species at each site and feature.

		Species								
		Lasiurus cinereus		*Lasiurus borealis*		*Myotis lucifugus*		*Perimyotis subflavus*		
Feature	**Site label**	N	%	N	%	N	%	N	%	**Site Total**
Ridge	R1	9991	36	2775	10	14266	51.5	692	2.5	27724
	R2	119103	89.6	1793	1.3	8577	6.5	3435	2.6	132908
	R3	21030	71.6	568	1.9	6382	21.7	1382	4.7	29362
	R4	131826	35.1	131012	34.9	38579	10.3	73773	19.7	375190
	Total Ridge	281950	49.9	136148	24.1	67804	12	79282	14	565184
Central	C1	41452	68.2	1753	2.9	16790	27.6	773	1.3	60768
	C2	157098	96.4	2138	1.3	2541	1.6	1260	0.8	163037
	C3	95776	66.7	4526	3.2	31049	21.6	12282	8.6	143633
	Total Central	294326	80.1	8417	2.3	50380	13.7	14315	3.9	367438
Shore	S1	26119	6.8	42831	11.1	307059	79.4	10614	2.7	386623
	S2	3633	52.4	1672	24.1	848	12.2	777	11.2	6930
	Total Shore	29752	7.6	44503	11.3	307907	78.2	11391	2.9	393553
Barrier	B1	16133	22.1	2417	3.3	54182	74.3	224	0.3	72956
	B2	157605	57.7	19528	7.2	19518	7.2	76267	27.9	272918
	B3	158197	81	14602	7.5	14258	7.3	8193	4.2	195250
	Total Barrier	331935	61.3	36547	6.8	87958	16.3	84684	15.6	541124
	Species Total	937963	50.2	225615	12.1	514049	27.5	189672	10.1	1867299

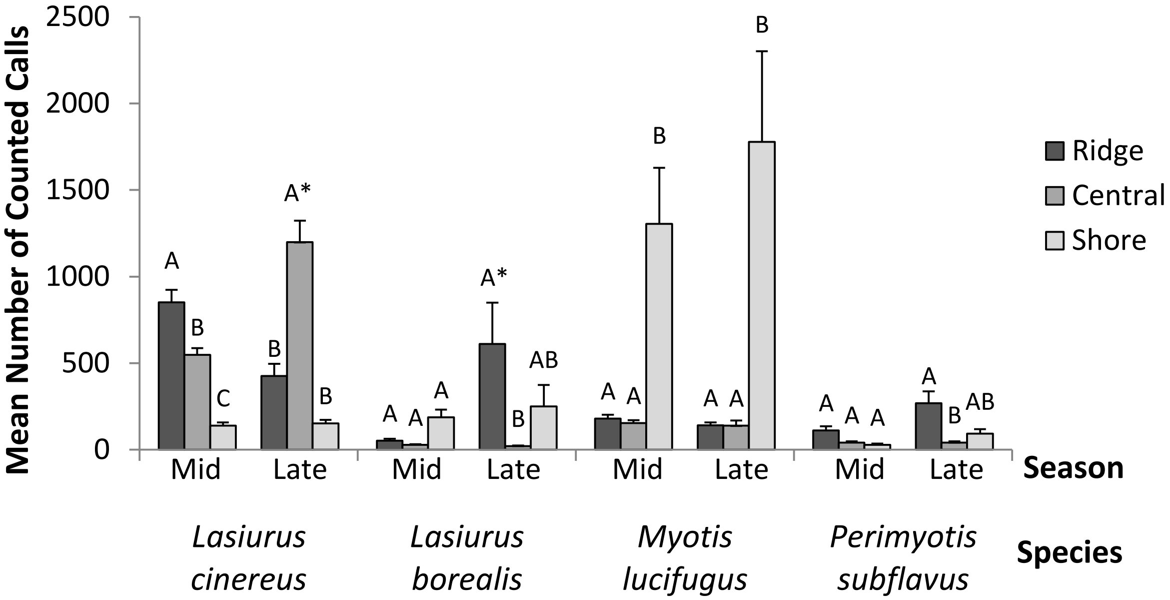


Figure 4: Mean activity levels for each species at ridge (n=4), central (n=3), and shore (n=2) features within Mid (1 June to 31 July) and Late (1 August to 31 September) seasonal time periods (N=926 recording nights). Error bars represent S.E. from the mean. Differences of activity were compared within species; not among species. Upper case letters (e.g. A,B,C) compare activity at feature (ridge, central, shore) within the same time period while asterisks (*) indicate significant differences of the same feature between seasons (Mid, Late).

Lasiurus borealis activity gradually increased in the mid-seasonal period and decreased in the late-seasonal period at ridge ($F_{5,5}$,= 20.637; $p < 0.001$) and central ($F_{5,5}$,=14.140; $p < 0.001$) features (Figure 5). At the shore feature, *L. borealis* activity peaked on 24 July (205) and slightly peaked at 7 September (250; $F_{7,7}$=10.505, $p < 0.001$).

Myotis lucifugus activity increased overall near 27 July (208) at ridge ($F_{6,6}$ = 50.662, $p < 0.001$), central ($F_{5,5}$= 30.859, $p < 0.001$), and shore ($F_{7,7}$ = 16.967, $p < 0.001$) sites with no strong peaks in early or late-seasonal periods at any of the features (Figure 5a).

Perimyotis subflavus had a noticeable increase of activity between 2 August (214) and 13 August (225), at all three landscape features (Figure 6) but no other dominant peaks.

No habitat variables had significant influences on activity for any of the species (GAMM $p > 0.05$).

3.3 Temperature and wind speed

Activity for all species significantly increased with rising temperature to an upper limit of approximately 25 degrees Celsius (Figure 7, GAMM $p < 0.001$; or approximately 20 degrees Celsius adjusted Appendix III; Figure A2) then activity decreased. The mean temperature across the sampling period was 22.8 °C ± 4. Bat activity increased at low to mid wind speeds (Figure 8; GAMM $p < 0.01$) for all species except for *P. subflavus*.

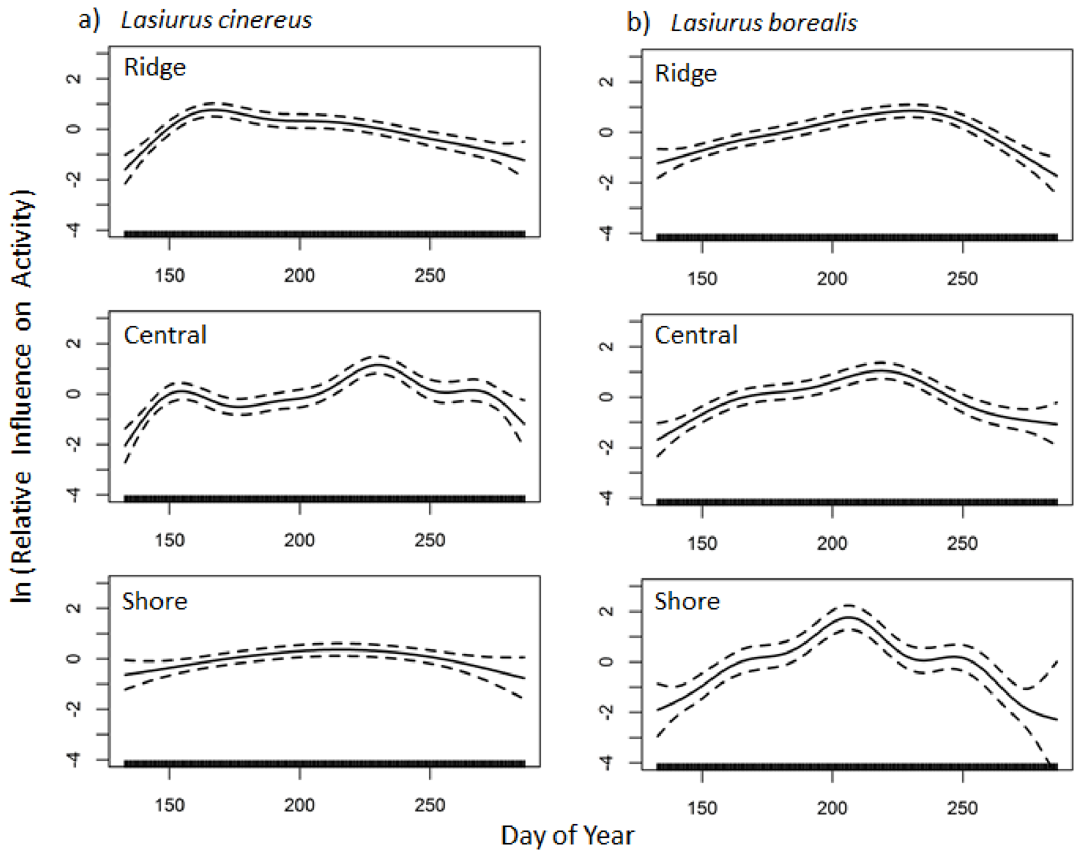


Figure 5: The relative activity levels for categorized latitudinal migrants a) *Lasiurus cinereus* and b) *Lasiurus borealis* over recording nights (n=1703) from 13 May (day of year 133) to 13 October (day of year 286) across three landscape features, ridge (n=4), central (n=3), and shore (n=2). The graphs show a fitted line for activity trends across sites (solid line) ± SD 1 (dotted line) based on generalized additive mixed models. The y-axis shows relative activity, after controlling for other variables, where activity changes positively or negatively by date.

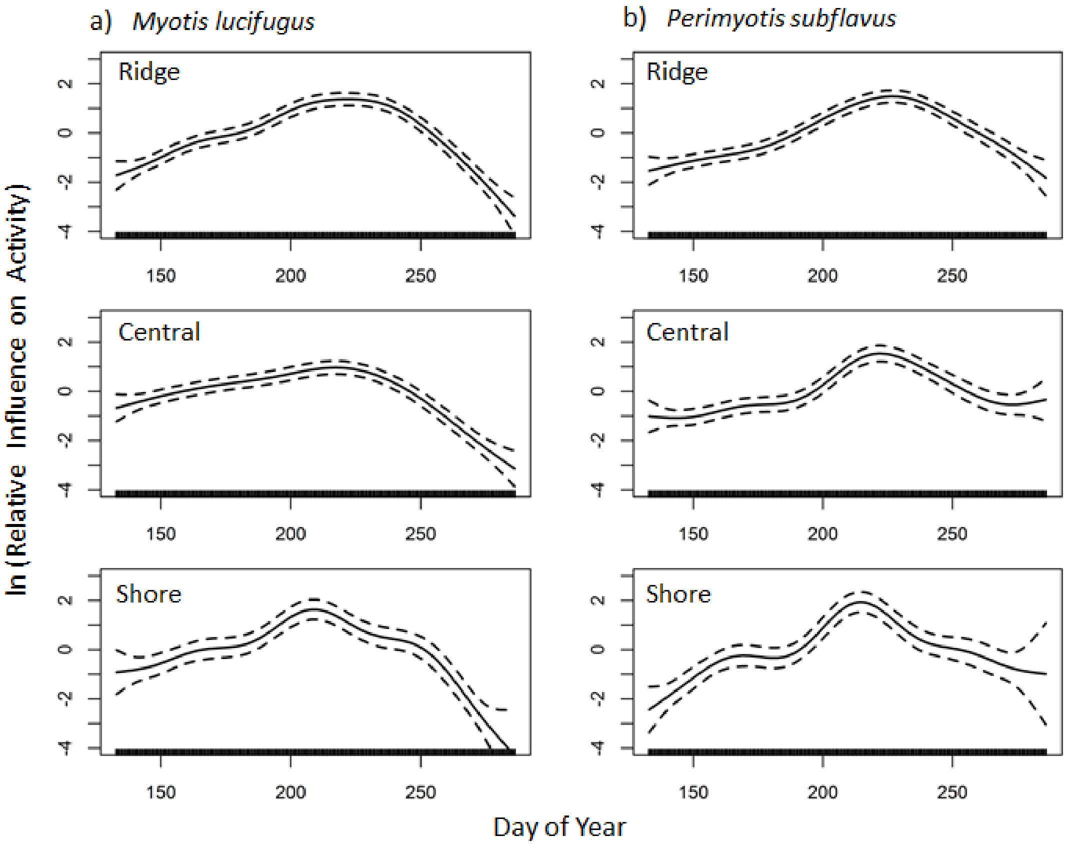


Figure 6: The relative activity levels for categorized regional migrants a) *Myotis lucifugus* and b) *Perimyotis subflavus* of recording nights (n=1703) from 13 May (day of year 133) to 13 October (day of year 286) across three landscape features, ridge (n=4), central (n=3), and shore (n=2). The graphs show a fitted line for activity trends across sites (solid line) ± SD 1 (dotted line) based on generalized additive mixed models. The y-axis shows relative activity, after controlling for other variables, where activity changes positively or negatively by date.

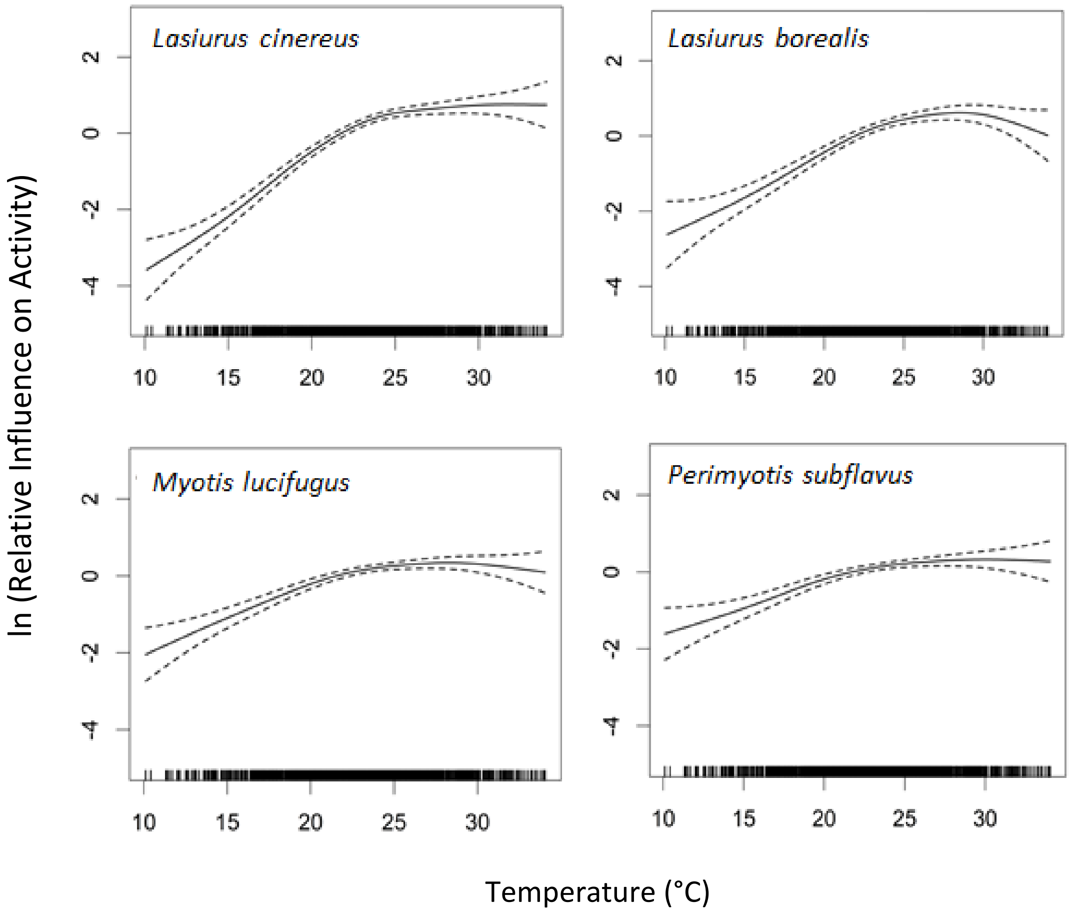


Figure 7: Activity levels in relation to temperature for each species. The graphs show a fitted line (solid line) ± SD 1 (dotted line) based on generalized additive mixed models. The y-axis shows relative activity, after controlling for other variables, where activity changes positively or negatively by temperature.

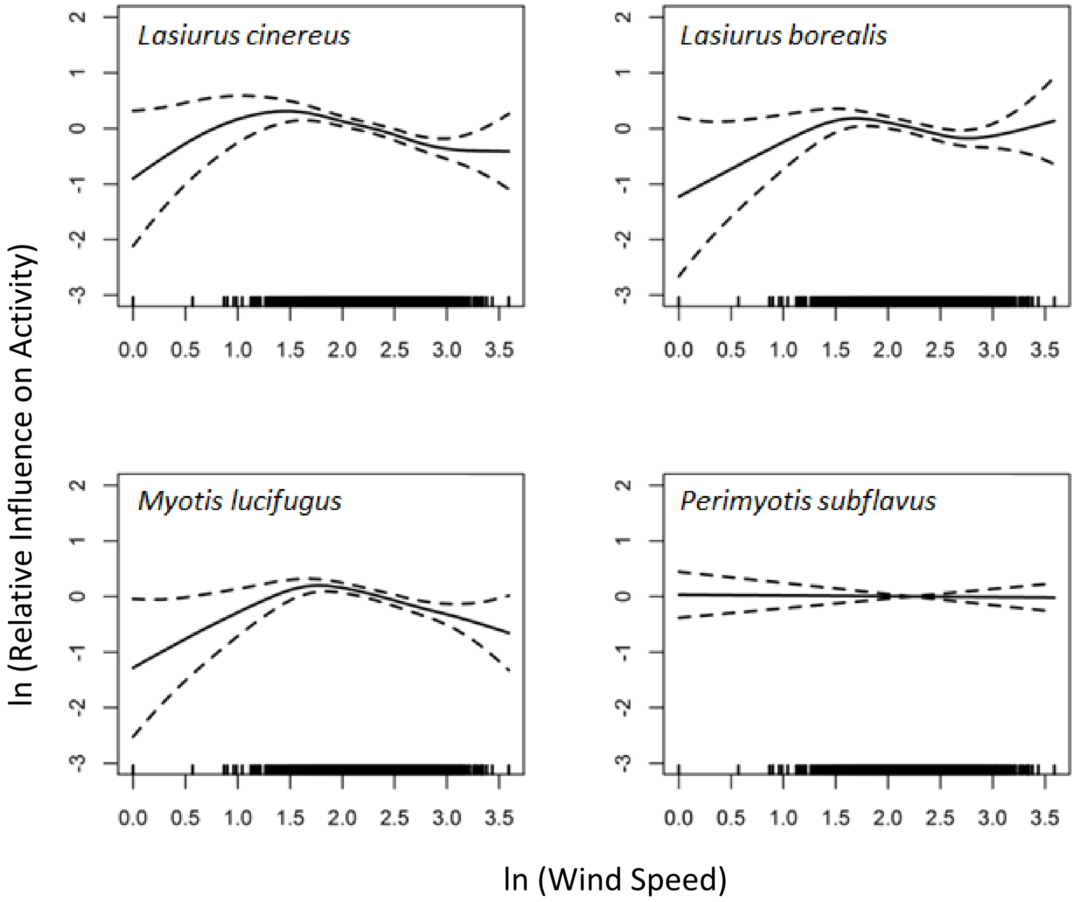


Figure 8: Influence of log wind speed on activity levels by species. The graphs show a fitted line (solid line) ± SD 1 (dotted line) based on generalized additive mixed models. The y-axis shows relative activity, after controlling for other variables, where activity changes positively or negatively by wind speed.

3.4 Temporal and spatial patterns of peak activity

Overall, late-seasonal peak activity had a marginally negative but non-significant relationship with latitude (Pearson's Correlation t_{128} = -0.126, *p* = 0.155). There was no significant linear relationship between latitude and day for any species at any feature (Pearson's Correlation *p* > 0.1103), however late seasonal activity peaks for *P. subflavus* at the ridge feature had a marginally negative linear relationship with latitude (Pearson's Correlation t_9 = -2.186, *p* = 0.057). The overall frequency of peak activity for *P. subflavus* increased in the late-seasonal period compared to the mid-seasonal period (Exact Poisson Test r_{60} = 0.40, *p* = 0.017) while all other species did not have a significant difference of peak activity between periods (Exact Poisson Test *p* > 0.2). Comparing frequency of peak activity by species at each feature, *P. subflavus's* peak activity significantly increased from mid-seasonal period to late-seasonal period at the ridge feature (Exact Poisson Test $r_{60,13}$ = 0.182, p = 0.022).

Trends in peak activity varied across species (Figure 9). *Lasiurus cinereus* had the earliest occurring peaks, at 21 May (141) at two lower latitudes for ridge and barrier sites (B2: 42°58 N; R3: 43°47 N). *Lasiurus borealis* activity peaked at 18 June (169) at the higher latitudinal located sites for ridge (R1: 44°52 N) and barrier (B1: 45°26 N) features. Increased frequency of activity peaks across all species occurred between 12 July (193) and 1 August (213). The majority of peak activity for *P. subflavus* occurred early within the late-seasonal period clustering around 6 August (218) across latitudes and all landscape feature types. *Lasiurus cinereus* had no clustering but rather, was randomly spread across time and latitude (Figure 9). In contrast, *P. subflavus*, *M. lucifugus*, and *L. borealis* had clustering of activity around 2 September (245) across multiple landscape features and latitudinal locations. *Lasiurus borealis* had no more peak activity after 6 September (249) while all other species had later peak activity. *M. lucifugus* had the latest peak in activity at one barrier site (B2: 42°58 N) at 5 October (278).

The highest clustering of peak activity across species occurred on two dates, 6 August and 2 September, which were both located within the late-seasonal migratory period. The average temperature was 23 degrees Celsius (28 degrees Celsius internal sensors) and average wind speed was 7 km/h on peak days across all species.

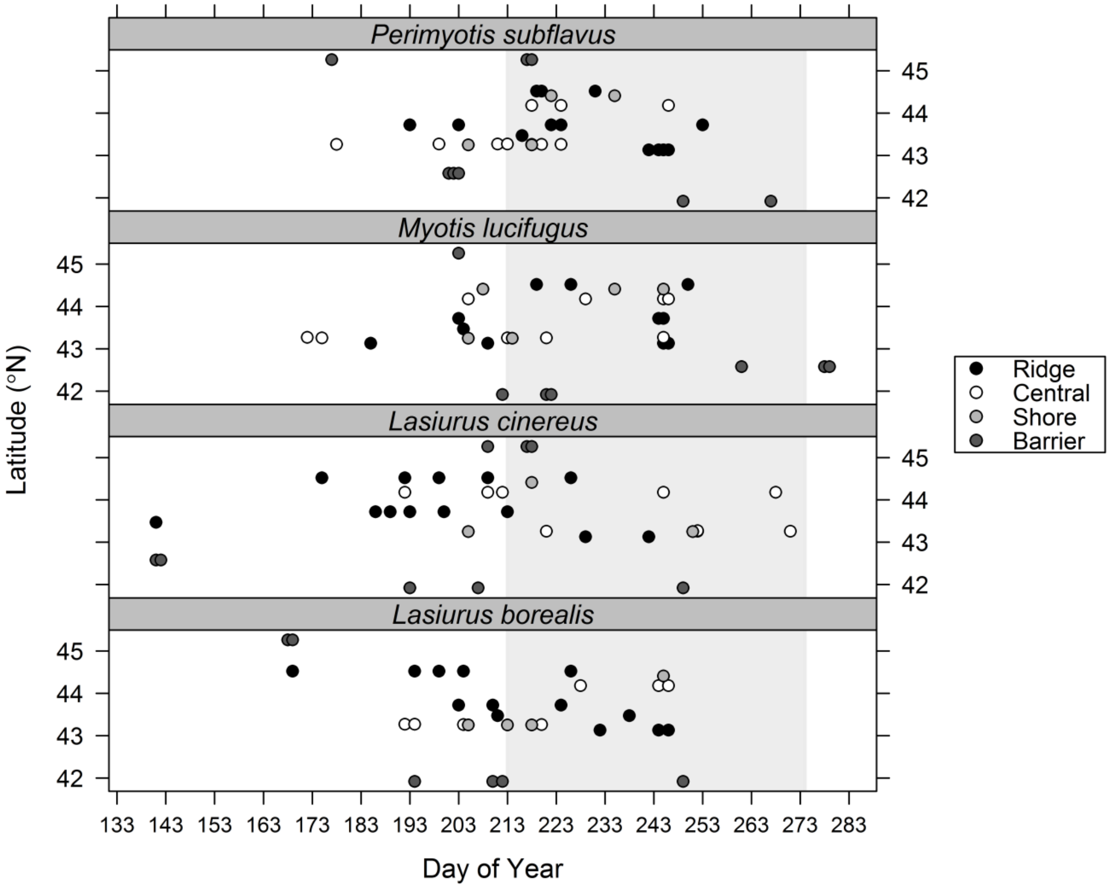


Figure 9: Latitudinal site locations of peak activity, defined as three standard deviations above the mean, color coded by feature and separated by species within the sampling period of 13 May (133) to 13 October (287). The gray box indicates the potential late-seasonal migration time period defined as 1 August (213) to 1 October (274).

3.5 Categorizing peak activity in the late-seasonal period for sites and feature

According to the criteria, late-seasonal migratory activity occurred for all species at central site C1 and ridge site R4 (Figure 10). At the shore sites, migratory activity for all species except for *L. cinereus* was present at site S1, while S2 had little to no indication of late-seasonal migratory activity for any species (Figure 10), thus all species scored a medium level of late-seasonal migratory activity at the shore feature except *L. cinereus,* which had an overall low late-seasonal migratory activity score (Table 6). Late-seasonal migratory activity occurred at all central sites for *L. cinereus* (Figure 10), and this species received an overall very high late-seasonal migratory activity level score for the central feature (Table 6). *Myotis lucifugus* also scored a high level for late-seasonal migratory activity at central sites (Table 6). Central site, C3, had no late-seasonal migratory activity for either *P. subflavus* or *L. borealis* (Figure 10). At the ridge feature, all species, except for *L. cinereus*, indicated positive medium late-seasonal migratory activity (Table 8), but there were no uniform presence, possible, or absent activity trends across any sites or species except for R4 (Figure 10). All species scored medium to low late-seasonal migratory activity levels at barrier sites with B2 having the lowest presence of activity during the late-seasonal migratory period for any species (Figure 10).

3.6 Summary of species activity at feature

Lasiurus cinereus was the only species with strong late-seasonal activity associations at the central featureless landscape across multiple analysis methods (Table 7). *Myotis lucifugus* activity received a high level score for late-seasonal migratory activity at the central feature in one analysis, but overall seemed to have no strong preference at any landscape feature (Table 7). Late-seasonal migratory activity at linear landscape features was weakly associated with *L. borealis* at the shore and *P. subflavus* at the ridge feature but overall had no strong relation with any landscape feature (Table 7).

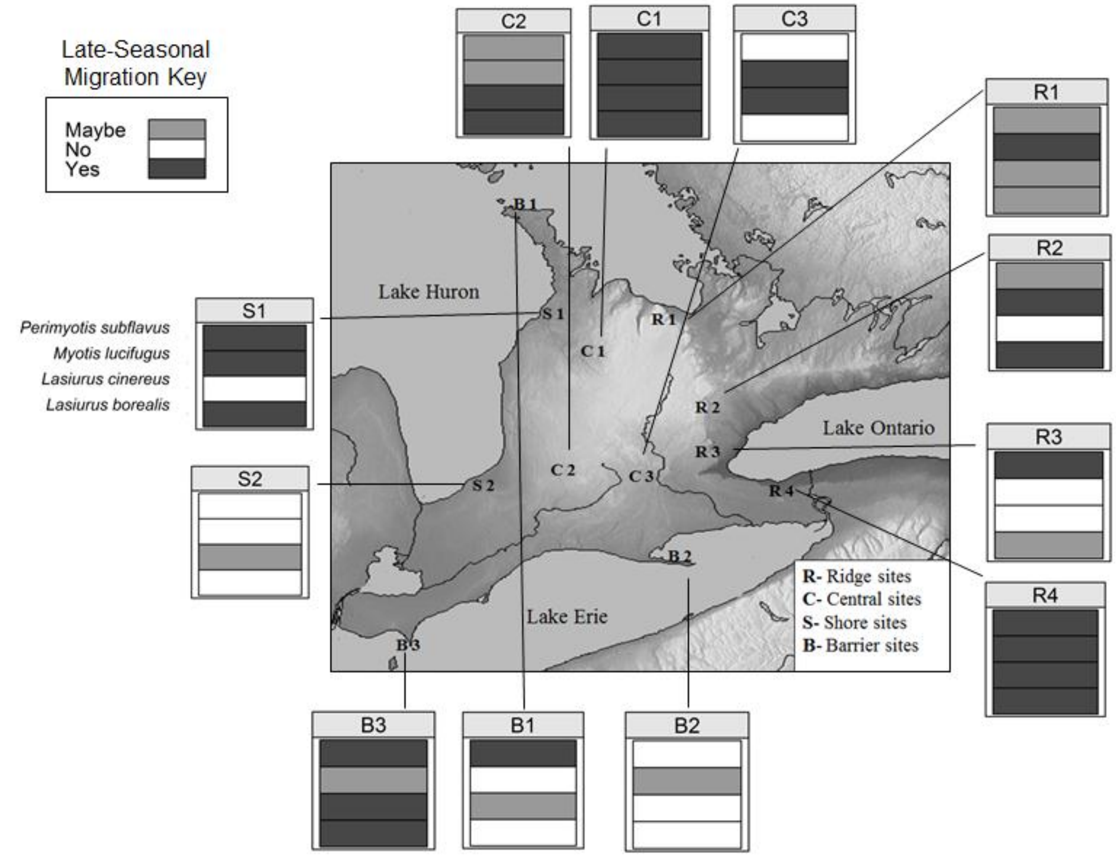


Figure 10: A status of yes (black), maybe (grey), and no (white) with respect to potential migratory activity in the late-seasonal period (1 August to 1 October) by species at each site located on the map. The status was determined based on a set of peak assessing criteria within the late-seasonal period.

Table 6: Activity labels that indicates the level of possible migratory activity during the late-seasonal period (1 August to 1 October) at a feature for each species. The assigned activity label corresponds to a site score sum by feature for a species that was based on a status that was given to each species at each site determined by a set of peak assessing criteria that assessed the level of possible migratory activity within the late-seasonal period (1 August to 1 October).

	Feature			
Species	Shore (n=2)	Central (n=3)	Ridge (n=4)	Barrier (n=3)
Perimyotis subflavus	Medium	Medium	Medium	Medium
Myotis lucifugus	Medium	High	Medium	Low
Lasiurus cinereus	Low	Very High	Low	Medium
Lasiurus borealis	Medium	Medium	Medium	Low

Table 7: Summary of results of each analysis method indicating greatest overall or migratory activity at a feature for each species.

	Species			
Analysis Method	*Lasiurus cinereus*	*Lasiurus borealis*	*Myotis lucifugus*	*Perimyotis subflavus*
Seasonal activity using ANOVA (Figure 3)	Central	Ridge, Shore	Shore	Ridge, Shore
Late-seasonal migration using GAMM (Figure 4; Figure 5)	Central	Shore	-	-
Activity peaks at latitude and between seasons (Figure 8)	-	-	-	Ridge
Indication of late-seasonal migration using criteria (Figure 9)*	Central (Very High) / Shore, Ridge (Low)	Ridge, Central, Shore (Medium)	Central (High) / Shore, Ridge (Medium)	Ridge, Central, Shore (Medium)

* Status in parenthesis () indicating the probability of late-seasonal migratory activity at a feature.

4. Discussion

I predicted that *L. cinereus* and *L. borealis*, categorized as latitudinal migrants, would have greater late-seasonal activity at ridge and shore landscape features during seasonal transitional periods than *M. lucifigus* and *P. subflavus*, presumed regional migrants. I found that seasonal activity at landscape features differed by species rather than according to categorized migration strategy depending on the analysis. I also predicted that activity would increase in the mid-seasonal time period for all species, since bats increase in foraging activity and have increased populations due to volant juveniles, but migratory peaks of activity at late-seasonal time periods would be more defined for *L. cinereus* and *L. borealis* which was supported in my results. Bat species may not have the same relationship to prominent landscape features based on shared putative migration strategy. Understanding the interactions of migratory bats with landscape features depends on the overall perception of landmarks based on location, seasonal timing, analysis, and sampling methods.

4.1 Species activity at landscape features

What a migratory bat perceives as a prominent landscape feature could depend on the species-specific behavior, regional location, and the magnitude of geographical features. For example, some bat species may perceive “featureless” areas as a “prominent” feature depending on species-specific characteristics and behavior. *Lasiurus cinereus* is thought to forage in open habitats rather than closed forested areas (Fenton 1990; Ford et al. 2005; Jantzen 2012) based on wing morphology and call characteristics (Norberg and Rayner 1987; Orbrist 1995). In addition, *L. cinereus* fatalities at wind turbines, often situated in open areas, occur in higher proportions compared to other species (Arnett et al. 2008). Open, agricultural habitat surrounds the area of central sites which may be better suited for open habitat foraging and migration by *L. cinereus.* My study showed little evidence that *L. cinereus* use coastlines during migration in spite of previous documentation of migratory activity at the Pacific Ocean and northern Atlantic Ocean coastlines (Cryan 2003, Dalquest 1943, Findley and Jones 1964, Miller 1897, Tenaza 1966). Species may use different coastlines disproportionately depending on species range and winter destinations. Since *L. cinereus*'s range spans across both east and west North America, from *L. cinereus*'s perspective, ocean shores, especially in west coast areas, may be better for migratory navigation than the lakes like the Lake Huron shoreline.

Other species like *L. borealis*, may perceive prominent landscape features, like shorelines, as important for navigation during migration depending on the type of coastline and the continental location. *Lasiurus borealis* has often been associated with shorelines (Cryan 2003; Griffin 1970; Mackiewicz and Backus 1956; Miller 1897), typically described on the Atlantic Ocean (Cryan 2003; Mackiewicz and Backus) due to its eastern range in North America; however, geographical features in relation to lake shorelines could also influence migration. For example, Lake Manitoba, located in central North America (Winnipeg, Canada), receives high migration activity of *L. borealis* at specific times of the year (Barclay 1984). As well, after collecting forty-three *L. borealis* compared to one *L. cinereus* and *M. lucifugus* during the fall season on the west coast of the north-south oriented Lake Michigan, Timm (1989) suggested that *L. borealis* migrates along lake shorelines. Compared to Lake Michigan and Lake Manitoba, Lake Huron's eastern shoreline leads into the east-west oriented Lake Erie, which is perhaps not as easily navigated, compared to other types of lake shore locations. Ridge features may also be important for *L. borealis* during migration. Eastern forested sites with wind turbines had increased mortality of *L. borealis* than other habitat types (Arnett et al. 2008). Forested ridges may provide suitable roosting habitat as this species roosts in trees (Mager and Nelson 2001) and more active foragers at forested locations than at aquatic areas in Ontario (Furlonger et al. 1987). During the migratory season, *L. borealis* may follow portions of a coast and/or ridge before turning inland, thus migratory activity spreads across other landscape features within the study area. However no study has determined the magnitude of directional change of migrating bats.

Some species may perceive different features as important depending on the season. *Myotis lucifugus* is historically abundant across Southwestern Ontario (Fenton 1980) and hibernates within its summer range (Fenton 1969). Across the non-hibernation period, *M. lucifugus* often forages over water and wetlands (Anthony and Kunz 1977; Belwood and Fenton 1976; Buchler 1976) possibly contributing to the overall higher activity at shoreline areas. During June and July, female *M. lucifugus* form maternity colonies often in buildings. An area with high agricultural abundance and with suitable roosting structures available, like the central feature, may have greater roosting populations of *M. lucifugus*. High influxes of migrants at central locations may account for adults and young of year leaving roosting areas for swarming and hibernation locations. However, directionality of departure to winter sites is unknown for summer residents of *M. lucifugus* in southwestern Ontario but may be inferred with reference to known existing hibernacula (Fenton 1969; Furlonger et al. 1987). No linear landscape feature was associated with high migratory activity possibly due to the radial movement within the regional area rather than using landscape features for navigational direction.

Similar to *M. lucifugus*, *P. subflavus* may use different landscape features depending on the season. Compared to open areas characteristic of shore and central features, rocky outcroppings and forested areas define the ridge feature. Evidence of migratory activity of *P. subflavus* at ridges include studies where proportionally greater *P. subflavus* fatalities occurred at wind turbines located at forested ridge locations (Arnett et al. 2008; Fiedler 2004). Important habitat requirements of *P. subflavus* include forested areas as it typically roosts in foliage of trees during the reproductive season and forages in forest areas (Broders et al. 2003; Fujita and Kuntz 1984; Perry and Thrill 2007; Veilleux et al. 2003). Rock crevices at ridges may also provide hibernacula for *P. subflavus* (Barbour and Davis 1969; Fiedler 2004). The negative latitudinal trend within the late-seasonal period at the ridge feature for *P. subflavus* could further support the idea that this species makes larger southern migration movements than previously thought (Fraser et al. 2012). However, *P. subflavus* migratory activity across other landscape features within the late-seasonal time period indicates a wider dispersal of movement not located at one specific landscape feature.

Although in some cases latitudinal migrant species have been known to use linear landscape features like mountains (Baerwald and Barclay 2009), neither *L. cinereus* nor *L. borealis* had any migratory association with the ridge feature in my study. Geographical location and magnitude of the landscape feature may determine the distribution of migratory activity. For example, Baerwald and Barclay (2009) suggest that the Rocky Mountains, a large geographical barrier next to flat, open prairie, funnels migratory activity. However I did not find similar evidence at the Niagara Escarpment for latitudinal migrants. In addition, wind turbines located on forested ridges have among the highest bat mortality especially for latitudinal migrant species (Arnett et al. 2008), typically at forested ridge sites located in the Eastern United States of America often on the Appalachian mountain range (Arnett et al. 2008). *Lasiurus cinereus* and *L. borealis* emigration may start from southwestern Ontario, part of the northern extent of these species' range, thus migratory concentration at landscape features could occur at more southward locations, like the mid-Atlantic section of the Appalachian Mountains (Johnson et al. 2011). In addition, putative latitudinal migrating bats may use sensory cues such as magnetic fields (Holland et al. 2006), and post sunset glows (Buchler and Childs 1982), relying on topography as a secondary cue during migration. Latitudinal migratory species may depend on prominent linear landscape features on a finer scale when homing into winter roost areas (Williams et al. 1966). Other landscape features such as streams and rivers might have greater importance as migration routes on the landscape (Furmankiewicz and Kucharska 2009; Seidman and Zabel 2001; Serra-Cobo et al. 2000). Determining relationships with habitat variables might indicate areas of importance for migratory bats. A comparison among sites shows that some differed from others in levels of activity, none of them explained by habitat variables of water, built-up, and forest amounts in the area or distance from each. Identifying potential quality of foraging or roosting habitat or locations of maternity colonies may be more indicative of activity levels and potential migration areas.

4.2 Seasonal activity of migratory species

The increase in mid-seasonal activity levels for *L.cinereus*, *L.borealis*, *M. lucifugus*, and *P. subflavus* could indicate movements of young of the year (Anthony and Kunz 1977) occurring within the similar time of the season. Also, increased activity occurs on days with warm ambient temperatures and low wind speeds (Baerwald and Barclay 2011; Cryan and Brown 2007) in accordance with my study.

Peak migratory movement of presumed latitudinal migratory species across features occurred from August to October as identified at other barrier adjacent site locations (e.g., Barclay 1984; Hooton 2010; McGuire et al. 2012), wind energy facilities (e.g. Arnett et al. 2008; Fiedler et al. 2007), and other types of landscape features (e.g. Dalquest 1943; Timm 1989). The absence of peaks in activity for species categorized as regional migrants, according to the GAMM analysis, indicates a more general pattern of movement rather than orientation to specific features. Differences in individual patterns of migratory activity indicate that some species migrate faster than others or have different timing of departure. For example, *P. subflavus* migrate to hibernation and swarming sites earlier than *M. lucifugus* (Vincent and Whitaker 2007) possibly associated with earlier clustering activity of *P. subflavus* and late peaks for *M. lucifugus*. Timing of migration for *L. borealis* and *L. cinereus* often occurs at similar time periods in the late seasonal period (Table 2); however, indication of which species migrate earlier has not been well documented.

4.3 Interpretation of analysis

Species relationships to landscape features differed depending on the analysis. Each analysis used had different strengths and weaknesses (Table 8). Recognizing limitations can improve interpretation about species relationships with landscape features.

Table 8: Comparison of the strengths and weaknesses of four different methods of analysis.

Analysis Method	Strength	Weakness
Seasonal activity using factorial ANOVA (Figure 4)	• Compares differences of mid and late seasonal activity for each species at each feature	• Influenced by individual site variation and sample size
Late-seasonal migration using GAMM (Figure 5; Figure 6)	• Incorporates significant variables that affects activity levels • Displays general activity patterns at each feature by species	• Reduces strength of individual peaks indicative of high migratory activity at sites
Activity peaks at latitude and between seasons (Figure 9)	• Easy to identify commonalities and differences across feature and species	• Statistical tests (Exact poisson test and Pearson’s Correlation) influenced by sample size • Does not account for any relationships between activity peaks and non-peak activity
Indication of late-seasonal migration using criteria (Figure 10:Table 6)	• Flexibility in describing complicated data sets • Descriptive of site variability	• No statistical test

4.4 Acoustic Detection

The detectability of bat activity using acoustic monitoring has multiple limitations and assumptions (Hayes 2000). Acoustic monitoring can allow detection of seasonal differences in activity of bat species, but recordings of calls do not provide information about the actual number of bats (Kunz and Brock 1975). Call characteristics of different bat species also affects detectability. *Lasiurus cinereus* has a low frequency but high intensity call much less vulnerable to atmospheric attenuation compared to other species with higher frequency, low intensity calls (Lawrence and Simmons 1982). This may explain why *L. cinereus* was detected over 50% of the time. Also the detection range and location of the microphone will determine the amount of activity recorded (Adams et al. 2012). Placing microphones 5 m above ground was an effort to increase the range over which bats' calls were detected (Baerwald and Barclay 2009; Menzell et al. 2005; Reynolds 2006; Valdez and Cryan 2009). But a typical bat detector in ideal conditions (e.g. reduced clutter) is only likely to detect the calls of *L. cinereus* at up to 40 m, and somewhat less for the calls of other species (Adams et al. 2012). The specific location variables like water (Menzel et al. 2005), forest edges (Gehrt and Chelsvig 2003; Jantzen 2012; Müller et al. 2012), amount of clutter (Brooks 2009), and light sources (Hickey and Fenton 1989) may account for the variability in number of calls detected at each site.

My study determined seasonal changes of bat activity over time at one specific location per site. However, multiple detectors across a smaller sampling space may better describe activity at individual sites (Hayes 2000; Skalak et al. 2012). Pairing acoustic monitoring with other capture techniques could increase accuracy of behavior and timing during migration. The importance of including capture data as well as the location of the acoustic detector became apparent with the analysis of barrier sites, particularly at Long Point Bird Observatory (LPBO) or site label B2. LPBO is known as an important stopover site for bird migration and a location for also catching migratory bats (Dzal et al. 2009; Hooton 2010; McGuire et al. 2012). However, the results from my study indicate that LPBO has low migratory activity in the late-seasonal period. The acoustic detector location at this site might not have been placed in the most ideal area that receives high migratory activity of bats. Although acoustic monitoring has limitations, overall it has the ability to detect activity of species across the landscape over long periods of time without undue stress to the animals.

4.5 Management and Implications

Acoustic monitoring can identify sites and areas that are important for echolocating bats. This method is applicable to habitat and site assessments to determine species presences, relative activity levels, and temporal activity changes (e.g. Barclay 1984; Vaughn et al. 1997). However, my research showed that seasonal activity for species could be identified across specific regional areas. Although activity at individual sites can be extrapolated to overall landscape features, this should be used in conjunction with other tracking techniques such as radio tagging or radar (Fenton 1997; Williams et al. 1973). Stationary acoustic monitoring stations could identify annual seasonal patterns of activity across multiple locations, similar to banding stations for birds. With new emergences of disease such as white-nose syndrome which is devastatingly affecting populations of hibernating bats like *M. lucifugus* (Blehert et al. 2009), tracking relative activity levels may be informative to overall estimates of population activity over seasons and years within areas.

Wind energy facilities, a source of renewable energy, are growing in number in North America but cause high mortality of bats and birds (e.g., Arnett et al. 2008; Baerwald and Barclay 2009; Cryan and Barclay 2009). At a landscape level, my research indicated significant areas of species-specific migratory movement. Identifying areas heavily used by bats can inform the placement of new wind turbines as well as mitigation and pre and post construction activity monitoring. In addition, wind energy facilities could reduce the operation of wind turbines during seasonal periods of high migratory movement activity to reduce mortality caused to migrating bats.

5. Conclusions

1) The use of landscape features for migration differs by species of bat rather than categorized migratory strategy and can be used to understand important areas for migration by species.

i) *Lasiurus cinereus,* a putative latitudinal migrant, had a strong association of migratory activity at the central feature, while *Lasiurus borealis* had some associated migratory activity at the shore feature.

ii) *Myotis lucifugus* a putative regional migrant had high late-seasonal migratory activity within the central area but overall had the greatest activity at the shore feature. *Perimyotis subflavus* had some associated migratory activity at the ridge feature.

2) Seasonal activity differed by species and may indicate time periods associated with differences in seasonal behavior. Activity increased in the mid-seasonal time period, associated with mid-summer for all species. Late-seasonal activity indicative of fall migration was evident for putative latitudinal migratory species *Lasiurus cinereus* and *Lasiurus borealis* at one feature while putative regional migrants *Myotis lucifugus* and *Perimyotis subflavus* had no late-seasonal activity overall but specific sites by species had evidence of migratory activity.

3) Acoustic monitoring allows detection of seasonal changes in the activity of echolocating bats within a specified area.

References

Adams, A.A., M.K. Jantzen, R.M. Hamilton, M.B. Fenton. 2010. Do you hear what I hear? Implications of detector selection for acoustic monitoring of bats. Methods in Ecology and Evolution doi: 10.1111/j.2041-210X.2012.00244.x.

Agosta, S.J., D. Morton, B.D. Marsh, and K.M. Kuhn. 2005. Nightly, seasonal, and yearly patterns of bat activity at night roosts in the central Appalachians. Journal of Mammalogy 86: 1210-1219.

Ahlén, I., H.J. Baagøe, and L. Bach. 2009. Behavior of Scandinavian bats during migration and foraging at sea. Journal of Mammalogy 90: 1318-1323.

Ahlén, I., L. Bach, H.J. Baagøe, and J. Pettersson. 2007. Bats and offshore wind turbines studied in southern Scandinavia. Swedish Environmental Agency, Stockholm, Sweden, Report 5571:1-36.

Amengual, B, M. López-Roig, and J. Serra-Cobo. 2007. First record of over sea migration of *Miniopterus schreibersii* and *Myotis capaccinii* between Balearic Islands (Spain). Acta Chiropterlogica 9: 319-322.

Anthony, E.L.P., and T.H. Kunz. 1977. Feeding strategies of the little brown bat, *Myotis lucifugus*, in southern New Hampshire. Ecology 58:775-786.

Alerstam, T. 1990. Ecological causes and consequences of bird orientation. Experientia 46: 405-415.

Arnett, E. B., K. Brown, W. P. Erickson, J. Fiedler, T. H. Henry, G. D. Johnson, J. Kerns, R. R. Kolford, C. P. Nicholson, T. O'Connell, M. Piorkowski, and R. Tankersley, Jr. 2008. Patterns of fatality of bats at wind energy facilities in North America. Journal of Wildlife Management 72: 61–78.

Barbour, R.W. and W.D. Davis. 1969. Bats of America. The University of Kentucky Press. Lexington, Kentucky, USA.

Barclay, R.M.R. 1984. Observations on the migration, ecology and behaviour of bats at Delta Marsh, Manitoba. Canadian Field Naturalist 98:331-336.

Barclay, R.M.R, P.A. Faure, and D. R. Farr. 1988. Roosting behavior and roost selection by migrating silver-haired bats (*Lasionycteris noctivagans*). Journal of Mammalogy. 69:821-825.

Barclay, R.M.R. and A. Kurta. 2007. Ecology and behavior of bats roosting in tree cavities and under bark. In Bats in Forests: Conservation and Management. The John Hopkins University Press, Baltimore.

Baerwald, E.F. and R.M.R. Barclay. 2009. Geographical variation in activity and fatality of migratory bats at wind energy facilities. Journal of Mammalogy 90:1341-1349.

Baerwald, E.F. and R.M.R. Barclay. 2011. Patterns of activity and fatality of migratory bats at a wind energy facility in Alberta, Canada. Journal of Wildlife Management 90:1341-1349.

Belwood, J.J. and M.B. Fenton. 1976. Variation in the diet of *Myotis lucifugus* (Chiroptera: Vespertilionidae). Canadian Journal of Zoology 54:1674-1678.

Berthold, P. 1993. Bird Migration: A General Survey, 2nd ed. Oxford University Press, Oxford.

Bisson, I. -A., K. Safi, R.A. Holland. 2009. Evidence of repeated independent evolution of migration in the largest family of bats. PLoS One 4:e7504.

Blehert, D.S., A.C. Hicks, M. Behr, C.U. Meteyer, B.M. Berlowski-Zier, E.L. Buckles, J.T.H. Coleman, S.R. Darling, A. Gargas, R. Niver, J.C. Okoniewski, R.J. Rudd, and W.B. Stone. 2009. Bat white-nose syndrome: An emerging fungal pathogen? Science 323: 227.

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

Brooks, R.T. 2009. Habitat-associated and temporal patterns of bat activity in a diverse forest landscape of southern New England, USA. Biodiversity Conservation 18: 529-545.

Brown, W. K., and B.L. Hamilton. 2006. Bird and bat monitoring at the McBride Lake Wind Farm, Alberta, 2003–2004. Report for Vision Quest Windelectric, Inc., Calgary, Alberta, Canada., http://www.batcon.org/windliterature. Accessed 1 Aug 2012.

Buchler, E.R. 1976. Prey selection by *Myotis lucifugus* (Chiroptera: Vespertilionidae). The American Naturalist 110:619-628.

Buchlar, E.R. and S.B. Childs. 1982. Use of the post-sunset glow as an orientation cues by big brown bats (*Eptesicus fuscus*). Journal of Mammalogy 63: 243-247.

Cox, G.W. 1985. The evolution of avian migration systems between temperate an tropical regions of the new world. The American Naturalist 126: 451-474.

Cryan, P.M. 2003. Seasonal distribution of migratory tree bats (*Lasiurus* and *Lasionycteris*) in North America. Journal of Mammalogy 84: 579-593.

Cryan, P.M. and R.M.R. Barclay. 2009. Causes of bat fatalities at wind turbines: hypothesis and predictions. Journal of Mammalogy 90: 1330-1340.

Cryan, P.M. and A.C. Brown. 2007. Migration of bats past a remote island offers clues to the problem of bat fatalities and wind turbines. Biological Conservation 139: 1-11.

Cryan, P.M. and J.P. Veilleux. 2007. Migration and use of autumn, winter, and spring roosts by tree bats. In Bats in Forests: Conservation and Management. The John Hopkins University Press, Baltimore.

Czene, Z., S.N.P. Wong, and C.K.R. Willis. 2011. Observations of Eastern Red Bats (*Lasiurus borealis*) 160 kilometers from the coast of Nova Scotia. Bat Research News. 52:28-30.

Dalquest, W.W.1943. Seasonal distribution of the hoary bat along the Pacific coast. Murrelet 24:21–24.

Damm, J.P. and K. Geluso. 2008. Use of a mine by eastern pipistrelles (*Perimyotis subflavus*) in east central Nebraska. Western North American Naturalist. 68:382-389.

Davis, W.H. and H.B. Hitchcock. 1965. Biology and migration of the bat, *Myotis lucifugus*, in New England. Journal of Mammalogy 46:296-313.

Dingle, H. 1996. Migration: The biology of life on the move. Oxford University Press Inc: New York.

Dingle, H. and V.A. Drake. 2007. What is migration? BioScience 57:113-121.

Dzal, Y., L.A. Hooton, E.L. Clare, and M.B. Fenton. 2009. Bat activity and genetic diversity at Long Point, Ontario, an important bird stopover site. Acta Chiropterologica 11:307-315.

Ellison, L.E. 2008. Summary and analysis of the U.S. government bat banding program. U.S. Geological Survey Open-File Report 2008:1363.

Environmental Canada Weather Office.2011 March 15. *Retrieved* March 18, 2011 from http://www.weatheroffice.gc.ca.

Erickson, J.L and S.D. West. 2002. The influence of regional climate and nightly weather conditions on activity patterns of insectivorous bats. Acta Chiropterologica 4:17-24.

ESRI, Inc. (1999-2010). ArcMAP: GIS and Mapping Software. USA. Available http://www.esri.com.

Fenton, M. B. 1969. Summer activity of *Myotis lucifugus* (Chiroptera:Vespertilionidae) at hibernacula in Ontario and Quebec. Canadian Journal of Zoology 47:597-602.

Fenton, M.B. 1970. A technique for monitoring bat activity with results obtained from different environments in southern Ontario. Canadian Journal of Zoology 48:847-851.

Fenton, M.B. and R.M.R. Barclay. 1980. *Myotis lucifugus*. Mammalian Species no. 142:1-8.

Fenton, M.B. and G.P. Bell. 1981. Recognition of species of insectivorous bats by their echolocation calls. Journal of Mammalogy 62: 233-243.

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

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

Fiedler. J.K. 2004. Assessment of bat mortality and activity at Buffalo Mountain windfarm, eastern Tennessee. [dissertation].[Knoxville, (TN)]: Department of Wildlife and Fisheries Science, University of Tennessee.

Fiedler, J.K., T.H. Henry, C.P Nicholson, and R.D. Tankersley. 2007. Results of bat and bird mortality monitoring at the expanded Buffalo Mountain windfarm, 2005. Tennessee Valley Authority, Knoxville, Tennessee, USA.

Findley, J. S., and C. Jones. 1964. Seasonal distribution of the hoary bat. Journal of Mammalogy 45:461-470.

Fleming, T.H. and P. Eby. 2003. Ecology of bat migration. Pp 156-208 in Bat ecology (T.H. Kunz and and M.B. Fenton, eds.). University of Chicago Press, Chicago, Illinois.

Ford, W. M., M. A. Menzel, J. L. Rodrigue, J. M. Menzel, and J. B. Johnson. 2005. Relating bat species presence to simple habitat measures in a central Appalachian forest. Biological Conservation 126:528–39.

Fraser, E.E., L.P McGuire, J.L. Eger, F.J. Longstaffe, and M.B. Fenton. 2012. Evidence of latitudinal migration in tri-colored bats, *Perimyotis subflavus*. PlosOne 7:1-9.

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

Furlonger, C.L., H.J. Dewar, and M.B. Fenton. 1987. Habitat use by foraging insectivorous bats. Canadian Journal of Zoology 65:284-288.

Furmankiewicz, J. and M. Kucharska. 2009. Migration of bats along a large river valley in southwestern Poland. Journal of Mammalogy 90:1310-1317.

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

Griffin, D.R. 1970. Migrations and homing of bats. Biology of Bats: Volume I. (W.A. Wimsatt ed.). Academic Press: New York and London.

Hayes, J.P. 2000. Assumptions and practical considerations in the design and interpretation of echolocation-monitoring studies. Acta Chiropterologica. 2:225-236.

Hickey, M.B.C. and M.B. Fenton. 1989. Foraging by red bats (*Lasiurus borealis*): do intraspecific chases mean territoriality? Canadian Journal of Zoology 68:2477-2482.

Holland, R. A. 2007. Orientation and navigation in bats: known unknowns or unknown unknowns? Behavioral Ecology and Sociobiology 61:653–660.

Holland, R. A., K. Thotup, M. J. Vonhof, W. W. Cochran, and M. Wikelski. 2006. Bat orientation using Earth’s magnetic field. Nature 444:702.

Hooton, L.A. 2010. Identifying critical stopover sites for migratory bats. [dissertation] [London, (ON)]: The University of Western Ontario.

Humphrey, S.R. and J.B. Cope. 1976. Population ecology of the little brown bat, *Myotis lucifugus*, in Indiana and north-central Kentucky. American Society of Mammalogists 4:81.

Hutterer, R., T. Ivanova, C. Meyer-Cords, and L. Rodrigues. 2005. Bat migrations in Europe- A review of banding data and literature. Federal Agency for Nature Conservation, Bonn, Germany.

Jain, A., P. Kerlinger, R. Curry, and L. Slobodnik. 2007. Annual report for the Maple Ridge wind power project post-construction bird and bat fatality study-2006. Annual report prepared for PPM Energy and Horizon Energy, Curry and Kerlinger LLC, Cape May Point, New Jersey, USA.

Jantzen, M.K. Bats and the landscape: the influence of edge effects and forest cover on bat activity.[dissertation].[London, (ON)]: The University of Western Ontario:2012.

Jarzembowski, T. 2003. Migration of the Nathusius’ pipistrelle *Pipistrellus nathusii* (Vespertilionide) along the Vistuala Split. Acta Theriologica 48:301-308.

Johnson, G.D., M.K. Perlik, W.P. Erickson, and M.D. Strickland. 2004. Bat activity, composition, and collision mortality at a large wind plant in Minnesota. Wildlife Society Bulletin 32:1278-1288.

Johnson, J.B., J.E. Gates, and N.P. Zegre. 2011. Monitoring seasonal bat activity on a coastal barrier island in Maryland, USA. Environmental Monitoring Assessment 173: 685-699.

Johnson, J.S., K.S. Watrous, G.J. Giumarro, T. S. Peterson, S.A. Boyden, and M.J. Lack. 2011. Seasonal and geographical trends in acoustic detection of tree-roosting bats. Acta Chiropterlogica 13: 157-168.

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

Kerns, J, W. P. Erickson, and E. B. Arnett. 2005. Bat and bird fatality at wind energy facilities in Pennsylvania and West Virginia. (E. B. Arnett eds.). Relationships between bats and wind turbines in Pennsylvania and West Virginia: an assessment of bat fatality search protocols, patterns of fatality, and behavioral interactions with wind turbines. A final report submitted to the Bats and Wind Energy Cooperative.

Kerns, J. and P. Kerlinger. 2004. A study of bird and bat collision fatalities at the Mountaineer Wind Energy Center, Tucker County, West Virginia. Annual report for 2003. Curry and Kerlinger, LLC, McLean, Virginia, USA.

Kunz, T.H., E.B. Arnett, W.P. Erickson, A.R. Hoar, G.D. Johnson, R.P. Larkin, M.D. Strickland, R.W. Thresher, and M.D. Tuttle. 2007. Ecological impacts of wind energy development on bats: questions, research needs, and hypotheses. Frontiers in Ecology and the Environment 5:315–324.

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

Kunz, T. H., and L. F. Lumsden. 2003. Ecology of cavity and foliage roosting bats. Bat ecology (T. H. Kunz and M. B. Fenton eds.). University of Chicago Press, Chicago, Illinois.

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

Lawrence, B.D. and J.A. Simmons. 1982. Measurements of atmospheric attenuation at ultrasonic frequencies and the significance for echolocation by bats. Journal of Acoustic Society of America 71:585-590.

Mackiewicz, J., and R.H. Backus. 1956. Oceanic records of *Lasionycteris noctivagans* and *Lasiurus borealis*. Journal of Mammalogy 37:442-443.

Mager, K.J. and T.A. Nelson. 2001. Roost-site selection by eastern red bat (*Lasiurus borealis*). American Midland Naturalist 145: 120-126.

McGuire, L.P., C.G. Guglielmo, S.A. Mackenzie, and P.D. Taylor. 2012. Migratory stopover in the long-distance migrant silver-haired bat, *Lasionycteris noctivagans*. Journal of Animal Ecology 81:377-385.

Menzel, J. M., M. A. Menzel, J. C. Kilgo, W. M. Ford, J. W. Edwards, and G. F. McCracken. 2005. Effects of habitat and foraging height on bat activity in the southeastern coastal plain. Journal of Wildlife Management 69:235–45.

Merriam, C.H. 1887. Do any Canadian bats migrate? Evidence in the affirmative. Transactions of the Royal Society of Canada. 4: 85 – 87.

Miller, G.S. 1897. Migration of bats on Cape Cod, Massachusetts. Science 5:541–543.

Müller, J., M. Mehr, C. Bässler, M.B. Fenton, T. Hothorn, H. Pretzsch, H-J. Klemmt, and R. Brandl. 2012. Aggregative response in bats: prey abundance versus habitat. Oecologia. doi: 10.1007/s00442-011-2247-y.

Natural Earth. Retrieved 19 October, 2012 from www.naturalearthdata.com.

Newton, Ian. 2008. The Migration Ecology of Birds. Academic Press, London, UK.

Norberg,V.M. and J.M.V. Rayner.1987. Ecological morphology and flight in bats (Mammalia; Chiroptera): Wing adaptations, flight performance, foraging strategy, and echolocation. Philosophical Transactions of the Royal Society Bulletin 316: 335-427.

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

Orbrist, M.K. 1995. Flexible bat echolocation: the influence of individual habitat structure and conspecifics on sonar design. Behavior and ecology of Sociobiology 36: 207-219.

Perry, R.W. and R. Thill. 2007. Tree roosting by male and female eastern pipistrelles in a forested landscape. Journal of Mammalogy 88:974–981.

Perry, R.W., S.A. Carter, and R.E. Thill. 2010. Temporal patterns in capture rate and sex ratio of forest bats in Arkansas. American Midland Naturalist 164:270-282.

Popa-Lisseanu, A.G. and C.C. Voigt. 2009. Bats on the move. Journal of Mammalogy 90:1283-1289.

R Development Core Team. 2011. R: A language and environment for statistical computing. R foundation for statistical computing, Vienna.

Ralph, J.C. 1981. Age ratios and their possible use in determining autumn routes of passerine migrants. The Wilson Bulletin 93:164-188.

Reynolds, S.D. 2006. Monitoring the potential impact of a wind development site on bats in the northeast. The Journal of Wildlife Management 70:1219-1227.

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

Serra-Cobo J., V. Sanz-Trullén, and J.P. Martínez-Rica. 1998. Migratory movements of *Minopterus schreibersii* in the north-east of Spain. Acta Theriologica 43:271-283.

Serra-Cobo, J., J.M. Lopez-Roig, T. Marques-Bonet, and E. Lahuerta. 2000. Rivers as possible landmarks in the orientation of flight of *Miniopterus schreibersii*, Acta Theriologica 45:347-352.

Shump, K.A., JR., and A.U. Shump. 1982a. *Lasiurus borealis*. Mammalian Species 183:1–6.

Shump, K.A., JR., and A.U. Shump. 1982b. *Lasiurus cinereus*. Mammalian Species 185:1–5.

Skalak, S.L., R.E. Sherwin, and R.M. Brigham. 2012. Sampling period, size, and duration influence measures of bat species richness from acoustic surveys. Methods in Ecology and Evolution 3: 490-502.

Skowronski, M.D. 2008. callViewer version 18 User's Manuel. 1-19.

Skowronski, M.D. and M.B Fenton. 2008. Model-based automated detection of echolocation calls using the link detector. Journal of Acoustical Society of America. 124:328-336.

Southern Ontario Land Resource Information System (SOLRIS) Land Classification Data. Version 1.2. Peterborough, Ontario: The Ontario Ministry of Natural Resources, 2008.

Suthers, R.A. 1970. Vision, olfaction, taste. Biology of Bats: Volume II (W.A. Wimsatt, ed). Academic Press: New York and London.

Tenaza, R.R. 1966. Migration of hoary bats on South Farallon Island, California. Journal of Mammalogy 4:533-535.

Timm, R.M. 1989. Migration and molt patterns of red bats, *Lasiurus borealis* (Chiroptera: Vespertilionidae), in Illinois. Bulletin of the Chicago Academy of Sciences 14:1-7.

Trombulak, S.C., P.E. Higura, and M. DesMeules. 2001. Population trends of wintering bats in Vermont. Northeastern Naturalist 8:51-62.

Tsoar, A., R. Nathan, Y. Bartan, A. Vyssotski, G. Dell'Omo, and N. Ulanovsky. 2011 Large scale navigational map in a mammal. Proceeds of the National Academy of Science. 108: E718-E724.

Valdez, E.W. and P.M. Cryan. 2009. Food habits of the hoary bat (*Lasiurus cinereus*) during spring migration through New Mexico. The Southwestern Naturalist. 54: 195-200.

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

Veilleux, J.P., J.O. Whitaker Jr., and S.L. Veilleux. 2003. Tree-roosting ecology of reproductive female eastern pipistrellus, *Pipistrellus subflavus*, in Indiana. Journal of Mammalogy 84:1068-1075.

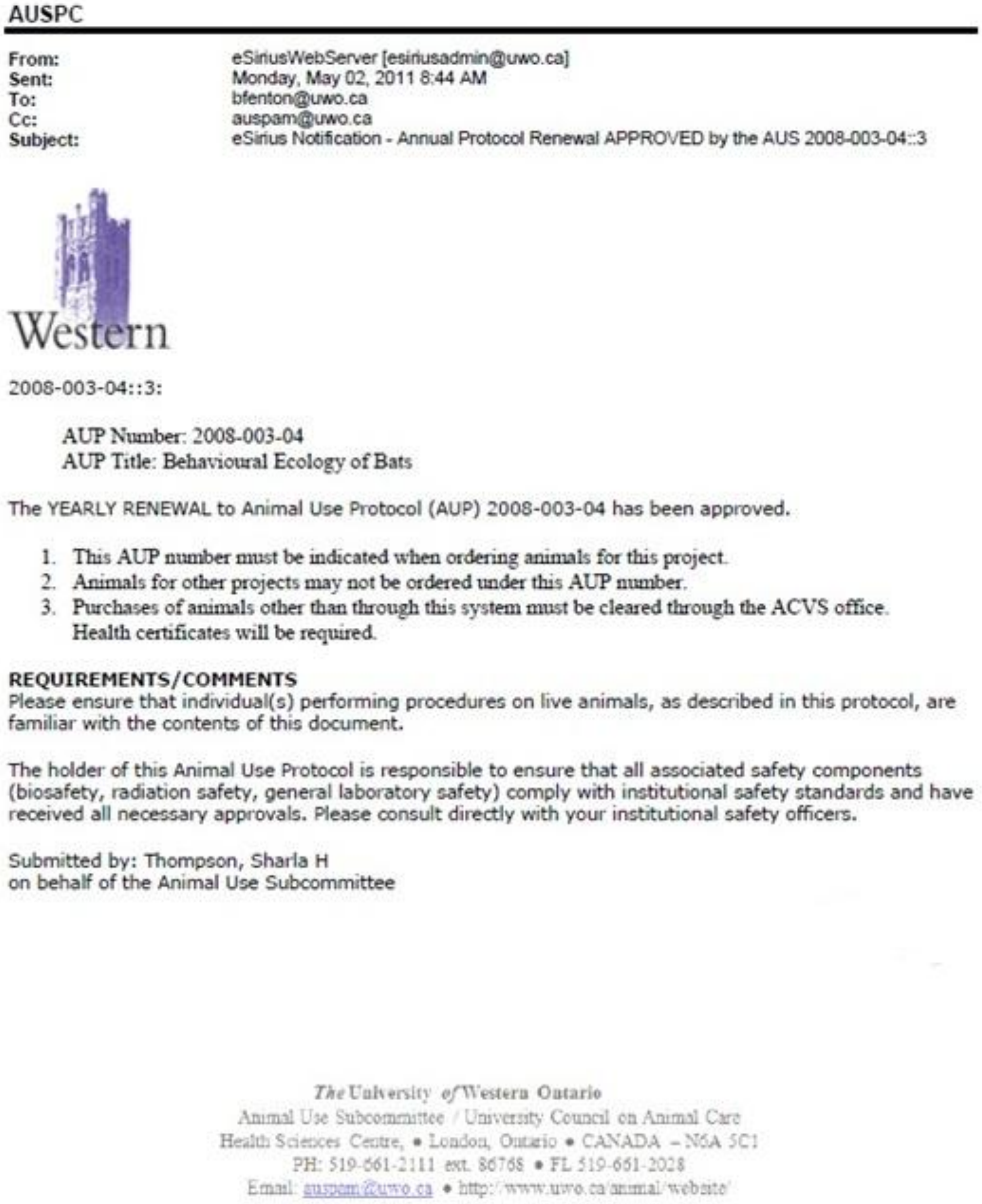
Vincent, E.A. and J.O. Whitaker Jr. 2007. Hibernation of the eastern pipistrelle, *Perimyotis subflavus*,in an abandoned mine in Vermillion County, Indiana, with some information on *Myotis lucifugus*. Proceedings of the Indiana Acedemy of Science 16:58-65.

Williams, T.C., J.M. Williams, and D.R. Griffin. 1966. The homing ability of the neotropical bat *Phyollostomas hastatas,* with evidence for visual orientation. Animal Behavior 1:468-473.

Williams, T.C., L.C. Ireland, and J.M. Williams. 1973. High altitude flight of the free-tailed bat, *Tadarida brasiliensis,* observed with radar. Journal of Mammalogy 54:807-821.

Zuur, A.F., E.N. Ieno, N.J. Walker, A.A. Saveliev, and G.M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York.

Appendix I: Approval letter from the Animal Use Subcommittee of the University of Western Ontario



AUSPC

From: eSiriusWebServer [esiriusadmin@uwo.ca]
Sent: Monday, May 02, 2011 8:44 AM
To: bfenton@uwo.ca
Cc: auspam@uwo.ca
Subject: eSirius Notification - Annual Protocol Renewal APPROVED by the AUS 2008-003-04::3

Western

2008-003-04::3:

AUP Number: 2008-003-04
AUP Title: Behavioural Ecology of Bats

The YEARLY RENEWAL to Animal Use Protocol (AUP) 2008-003-04 has been approved.

1. This AUP number must be indicated when ordering animals for this project.
2. Animals for other projects may not be ordered under this AUP number.
3. Purchases of animals other than through this system must be cleared through the ACVS office. Health certificates will be required.

REQUIREMENTS/COMMENTS
Please ensure that individual(s) performing procedures on live animals, as described in this protocol, are familiar with the contents of this document.

The holder of this Animal Use Protocol is responsible to ensure that all associated safety components (biosafety, radiation safety, general laboratory safety) comply with institutional safety standards and have received all necessary approvals. Please consult directly with your institutional safety officers.

Submitted by: Thompson, Sharla H
on behalf of the Animal Use Subcommittee

The University *of* Western Ontario
Animal Use Subcommittee / University Council on Animal Care
Health Sciences Centre, • London, Ontario • CANADA – N6A 5C1
PH: 519-661-2111 ext. 86768 • FL 519-661-2028
Email: auspam@uwo.ca • http://www.uwo.ca/animal/website/

Appendix II: Name, coordinates, and measured habitat variables at each site.

Table A1: The site names with accompanying identity for each feature and the corresponding coordinates and measured habitat variables.

Feature	I.D.	Site Name	Coordinates	Distance to Forest (m)	Distance to Water (m)	Distance to Building (m)	Forest in 5 km radius (%)	Water in 5 km radius (%)	Built-up in 5 km radius (%)
Shore	S1	MacGregor Point Provincial Park	44°41 N, 81°45 W	<10	1366	2	10	38	3
	S2	The Pinery Provincial Park	43°25 N, 81°83 W	<10	638	85	17	25	4
Central	C1	Durham Conservation Area	44°18 N, 80°80 W	<10	153	17	15	15	6
	C2	Wildwood Conservation Area	43°26 N, 81°07 W	>10	70	15	8	6	4
	C3	Pinehurst Lake Conservation Area	43°27 N, 80°39 W	<10	164	3	10	13	4
Ridge	R1	Craigleith Provincial Park	44°52 N, 80°37 W	<10	396	367	14	27	5
	R2	Terra Cotta Conservation Area	43°72 N, 79°96 W	<10	434	178	25	8	5
	R3	Rattlesnake Point Conservation Area	43°47 N, 79°91 W	<10	634	0	18	6	8
	R4	Balls Falls Conservation Area	43°13 N, 79°39 W	<10	180	20	10	4	9
Barrier	B1	Bruce Peninsula National Park	45°26 N 81°66 W	<10	367	62	25	46	3
	B2	Long Point Bird Observatory	42°58 N, 80°39 W	>10	4	1	0.3	39	1
	B3	Point Pelee National Park	41°92 N, 82°50 W	<10	268	4	2	76	0.2

Appendix III: Habitat Variables

Although the ridge feature averaged the highest percent of forest and built-up area (Figure A1), the ridge, central, and shore features did not significantly differ in the amounts of percent forest (ANOVA $F_{2,7} = 1.9$, $p = 0.22$) or built-up area (ANOVA $F_{2,7} = 2.9$, $p = 0.122$) within a 5 km radius. Shore sites had a significantly greater percent of water (ANOVA $F_{2,7} = 5.0$, $p = 0.05$; Figure A.1) area compared to central feature.

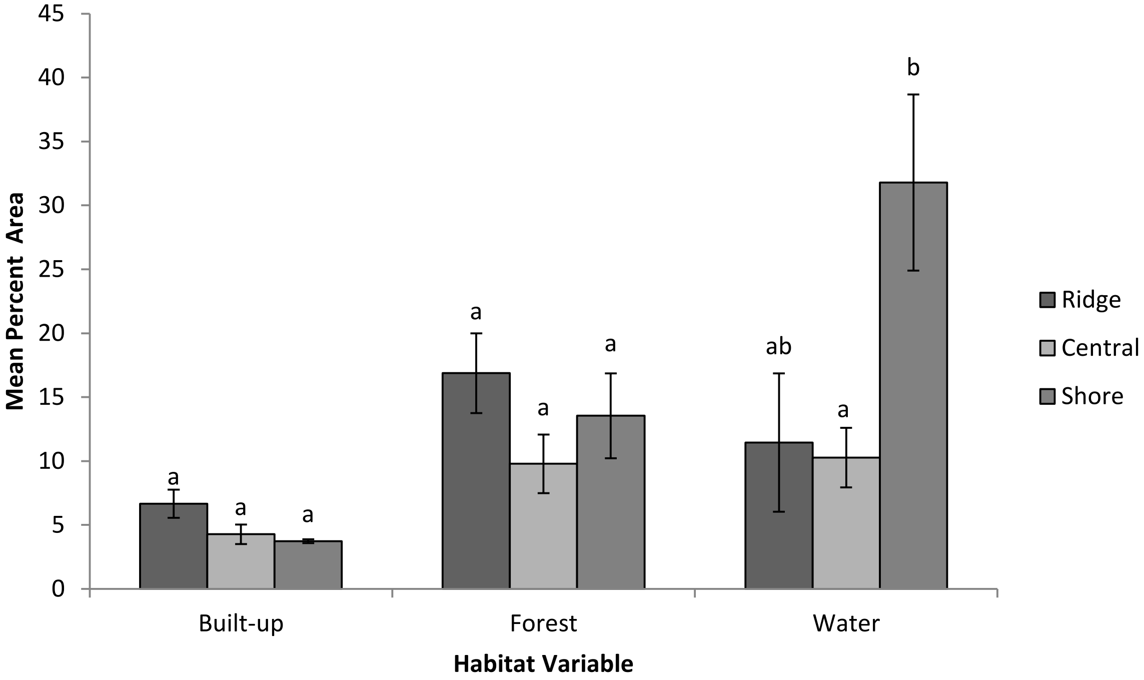


Figure A1: Mean amount of forest, built-up, and water percent area within a 5 km radius at each feature. Values shown are mean ± SE.

Appendix IV: Temperature Comparison

I collected temperature from SM2 internal sensors which were placed inside an enclosed box. I also collected data from the closest Environmental Canada stations to my sites. SM2 BAT internal sensors recorded on average 5 degrees higher than the Environmental Canada stations.

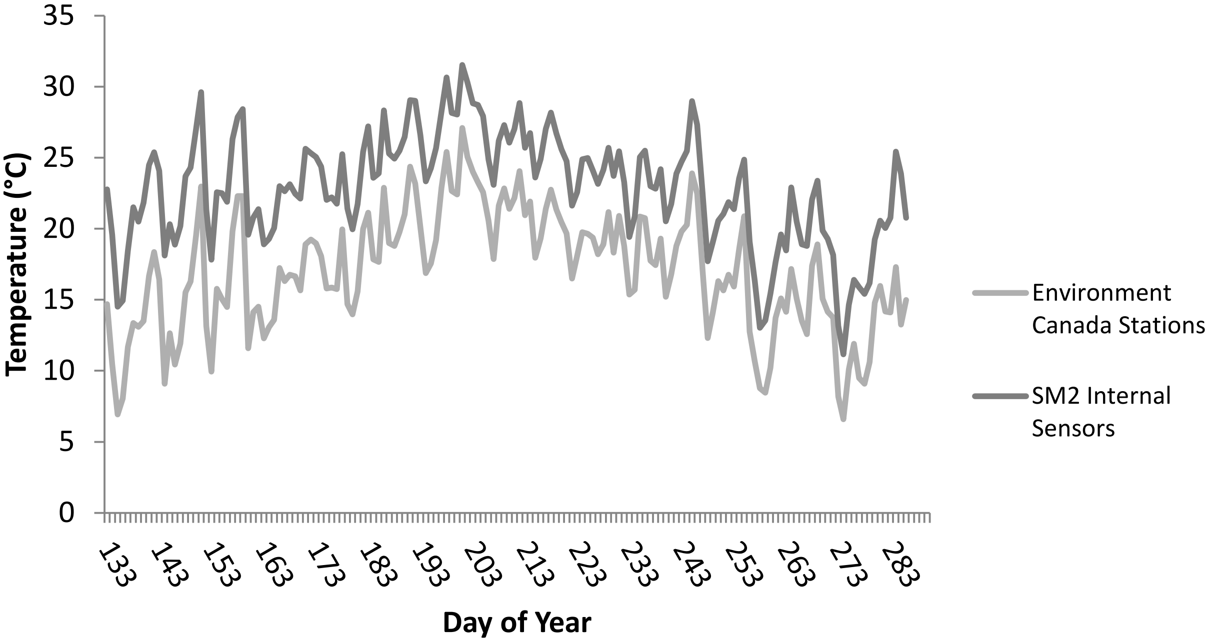


Figure A2: Mean temperature at each day of year from 13 May (133) to 13 October (287) for Song Meter internal sensors and environmental Canada weather stations collected from closest tower to each site.

Appendix V: Timing of Early-Seasonal Migration

Equipment at MacGregor Point Provincial Park was actively recording by of 28 April 2011 but the official start date occurred on 13 May 2011. I assessed if migratory activity had occurred before my official start date. I plotted the number of calls for both migratory species before and after the official start date. *Lasiurus cinereus* showed heighted activity before the official start date. This is indicative of possible migration activity that was not captured within my sampling period. However, *L. boreali*s activity was consistently low before the official start date, possibly indicating that *L. borealis* has a later spring migration period than *L. cinereus*. MacGregor Point Provincial Park is also at the more northern range of my study area so it might take longer for migrant species to arrive in that area. Early arrivals might have occurred before the sampling period began at the more southern sites.

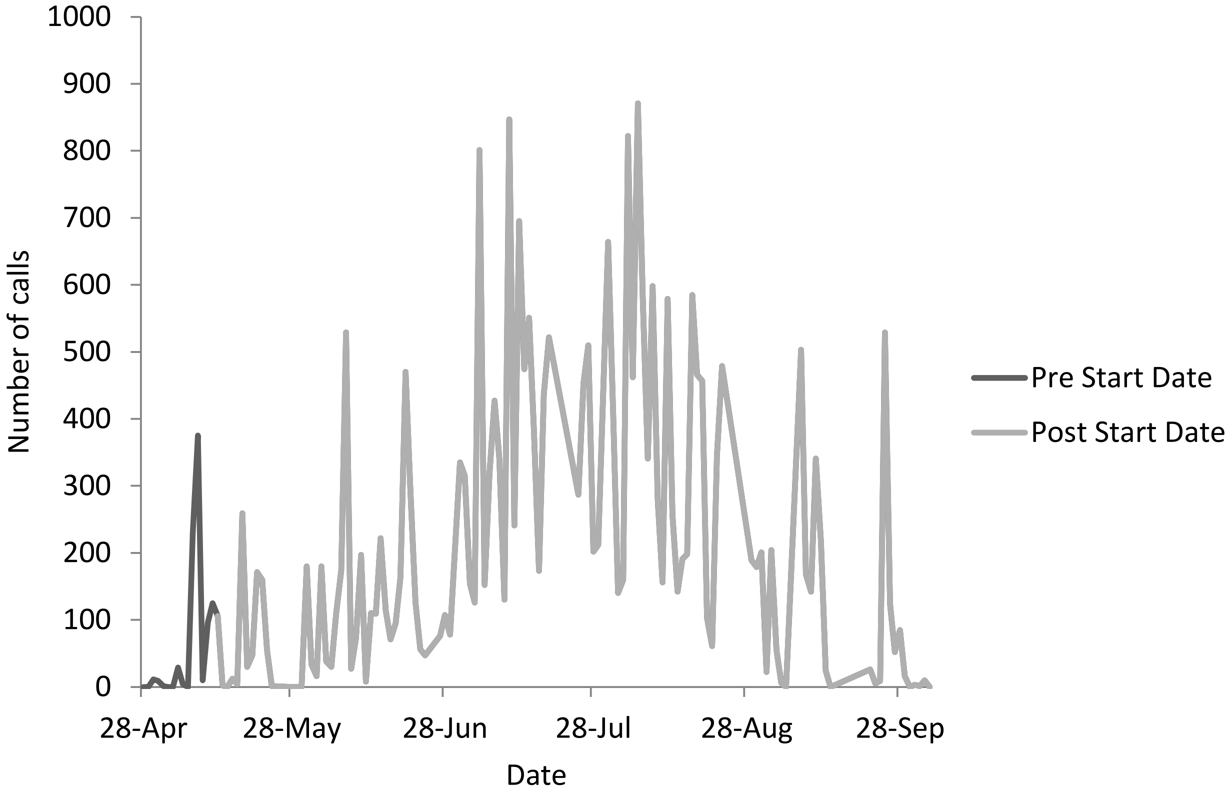


Figure A3a: Activity levels of *Lasiurus cinereus* pre and post official start date at 13 May during the sampling period at MacGregor Point Provincial Park.

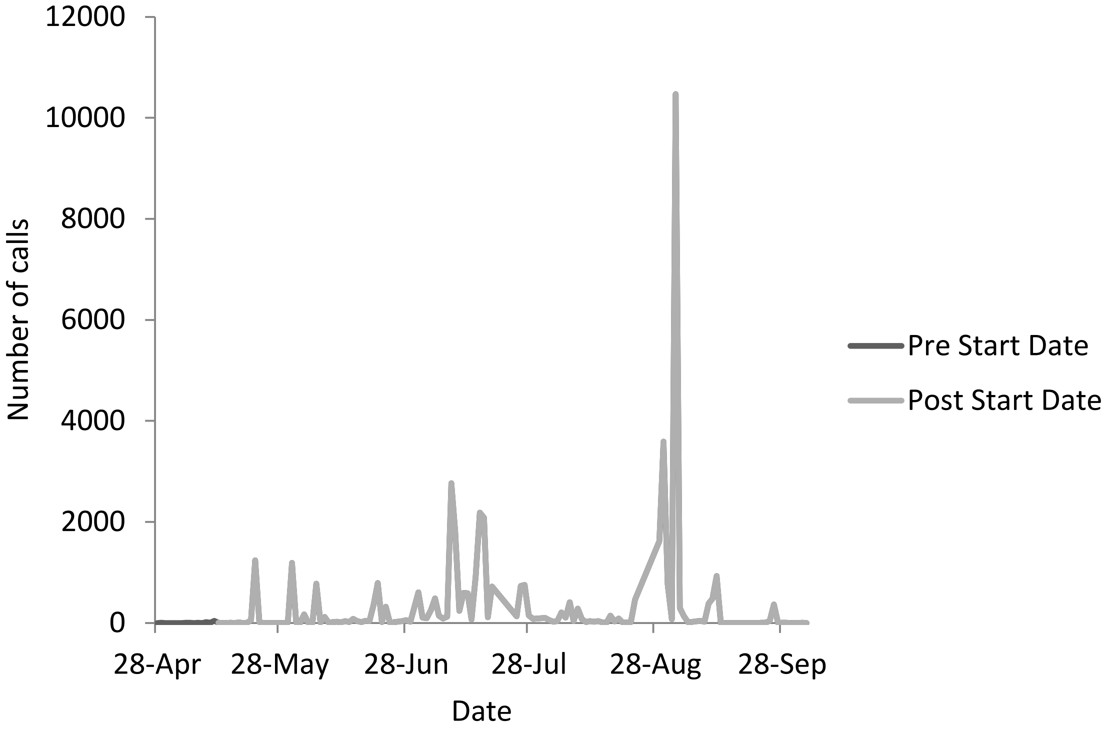


Figure A3b: Activity levels of *Lasiurus borealis* pre and post official start date 13 May during the sampling period at MacGregor Point Provincial Park.

Appendix VI: Plots of raw data by species

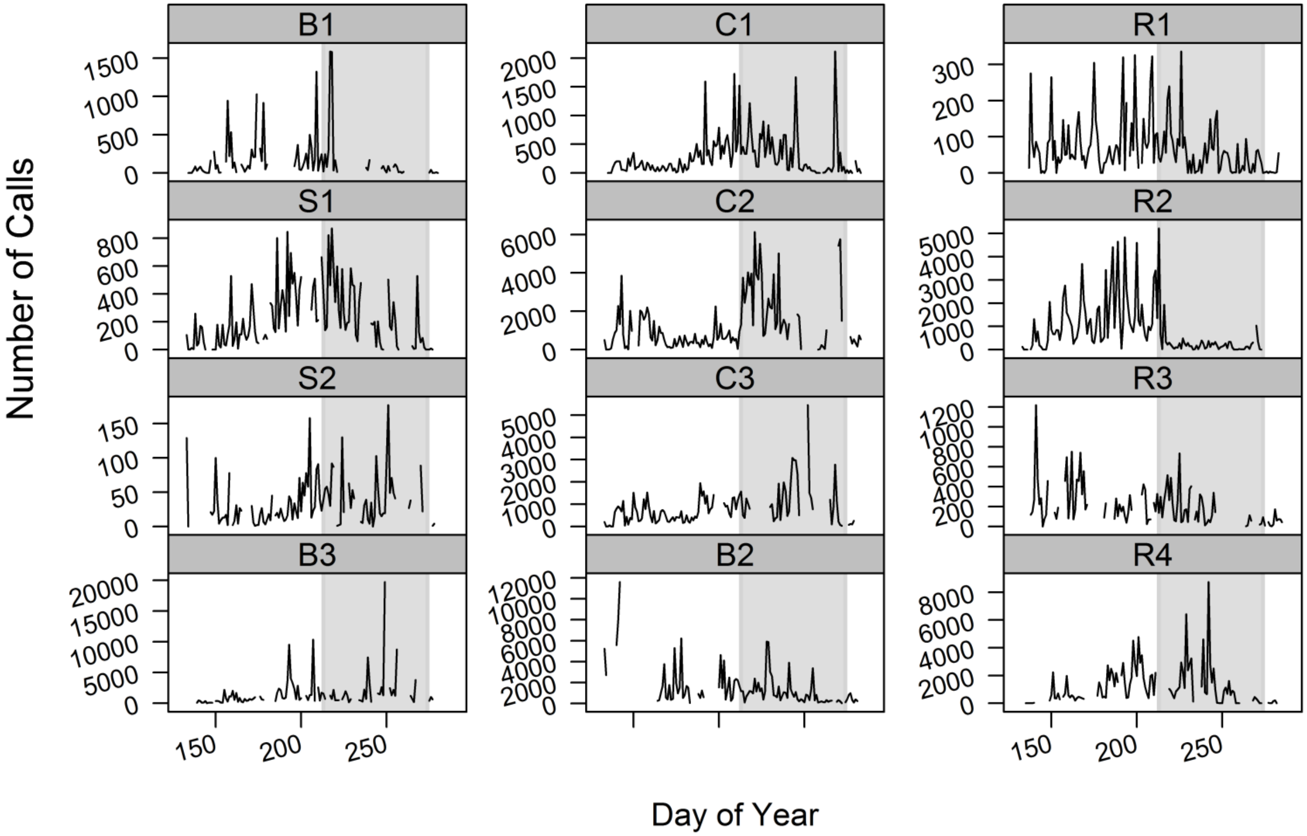


Figure A4: Activity of *Lasiurus cinereus* at twelve field sites collected from 13 May (133) to 13 October (287). The gray box indicates the potential late-seasonal migration time period defined as 1 August (213) to 1 October (274).

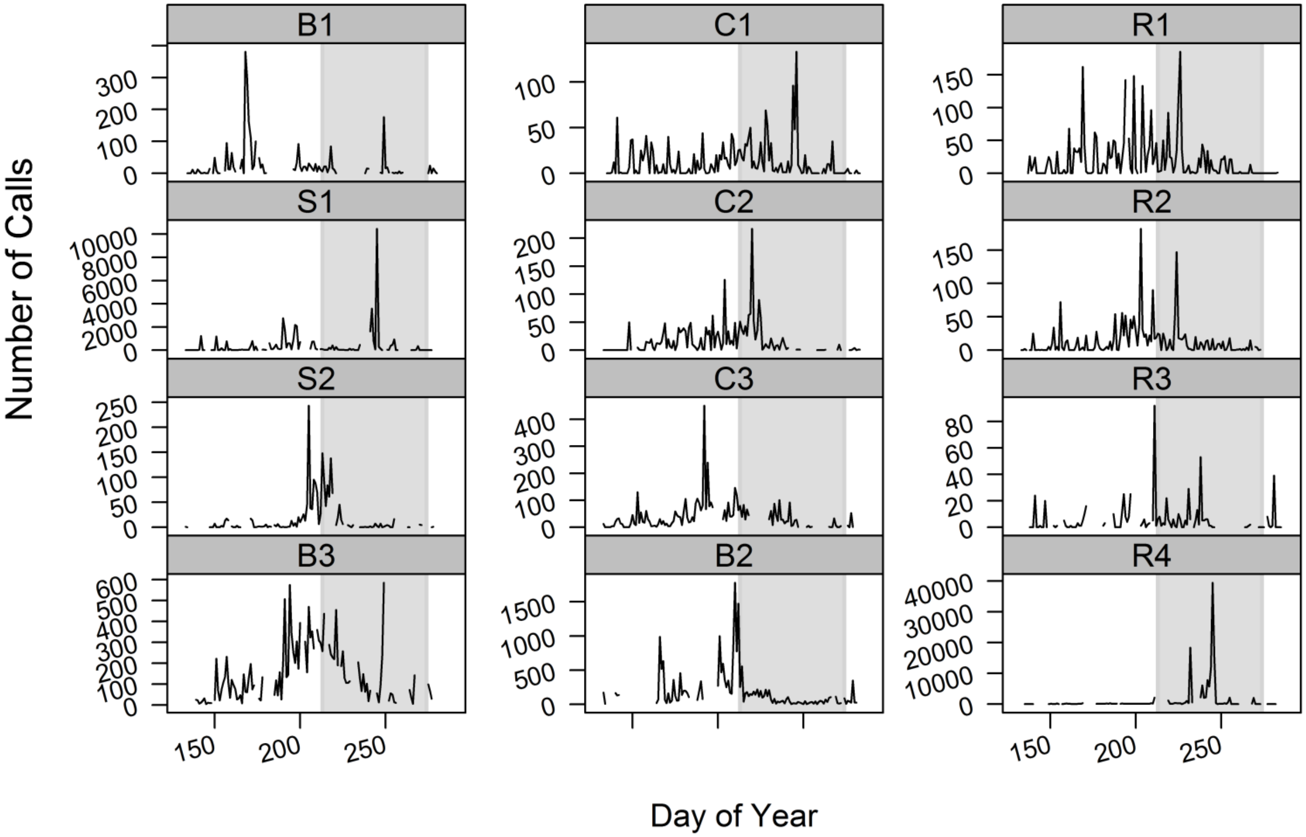


Figure A5: Activity of *Lasiurus borealis* at twelve field sites collected from 13 May (133) to 13 October (287). The gray box indicates the potential late-seasonal migration time period defined as 1 August (213) to 1 October (274).

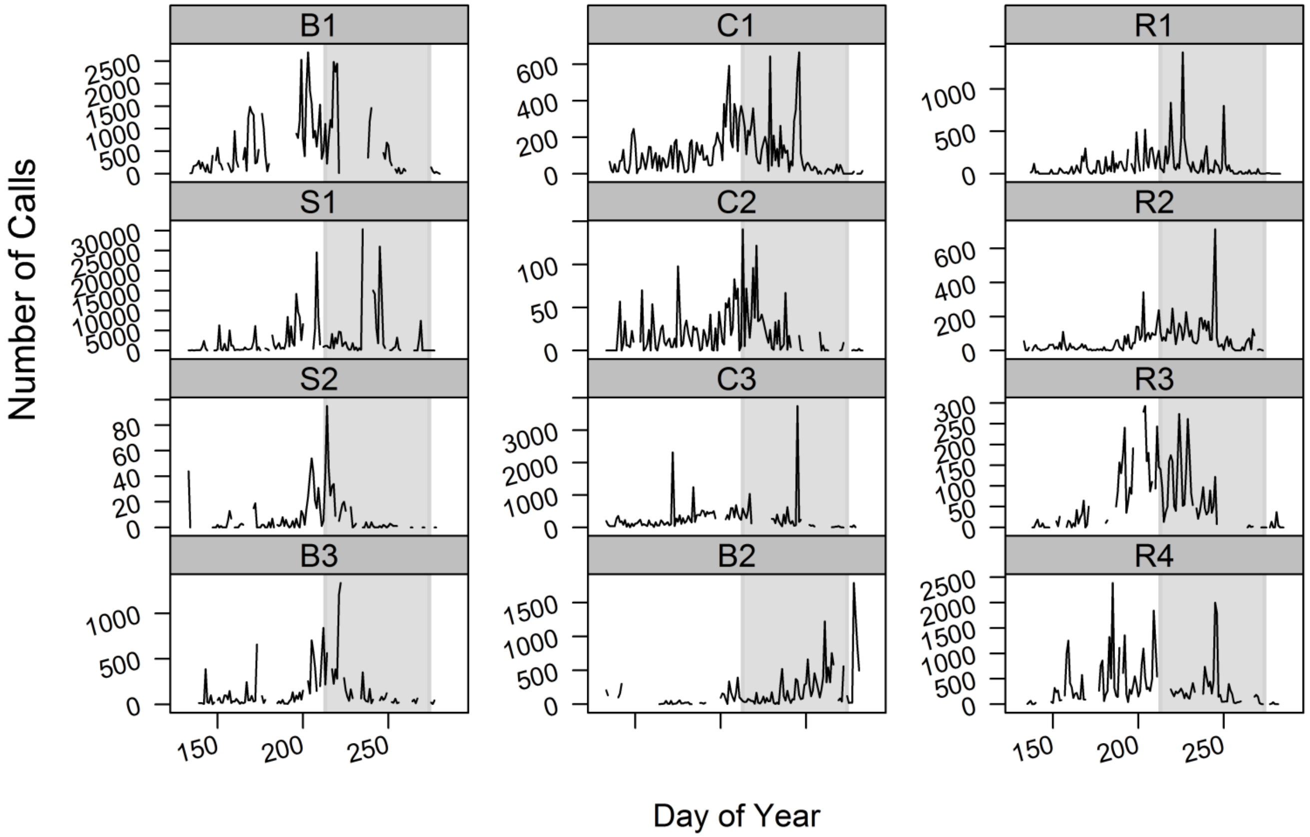


Figure A6: Activity of *Myotis lucifugus* at twelve field sites collected from 13 May (133) to 13 October (287). The gray box indicates the potential late-seasonal migration time period defined as 1 August (213) to 1 October (274).

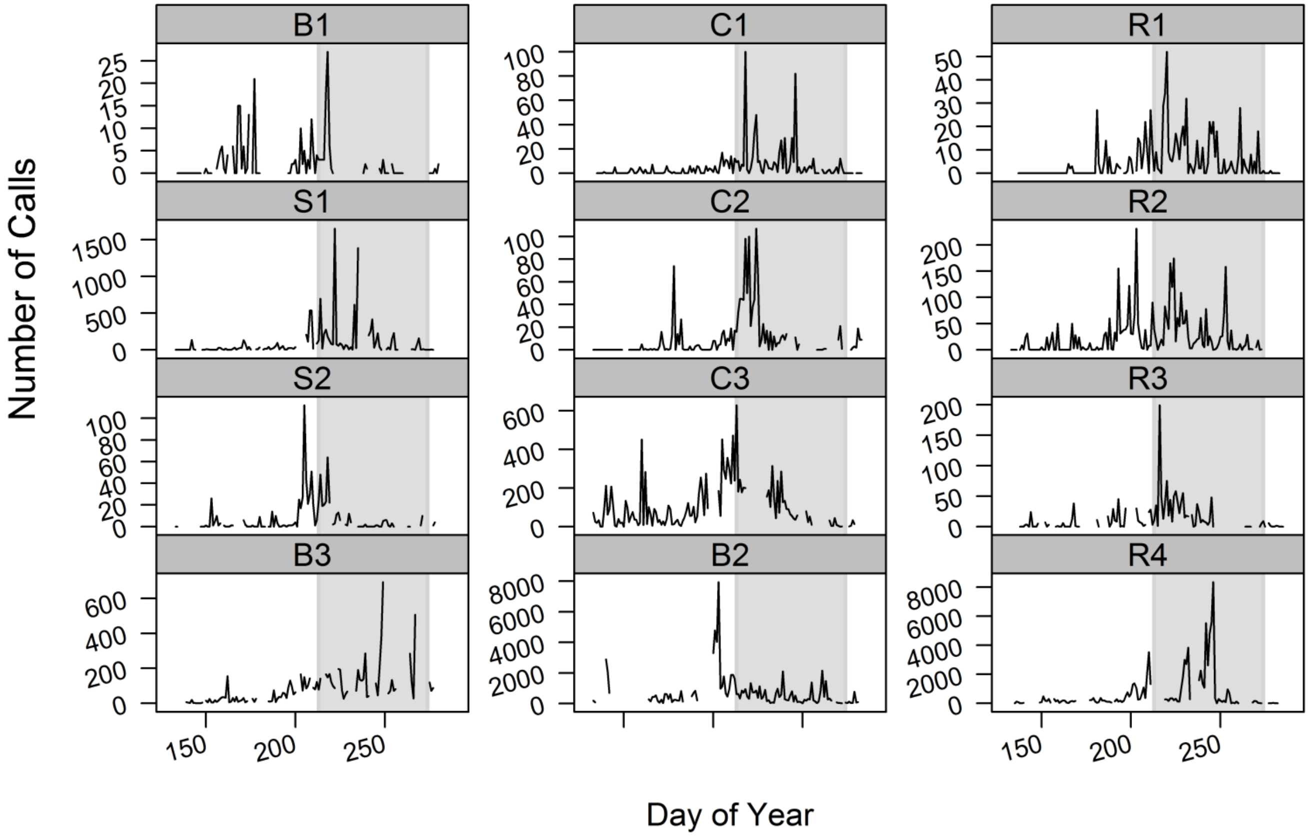


Figure A7: Activity of *Perimyotis subflavus* at twelve field sites collected from 13 May (133) to 13 October (287). The gray box indicates the potential late-seasonal migration time period defined as 1 August (213) to 1 October (274).

Curriculum Vitae

EDUCATION

2010-2012	Masters of Science in Biology, The University of Western Ontario, Advisor: M. Brock Fenton
2005-2009	Bachelor of Science in Wildlife Science with Natural Resource Recreation and Biology minors, Virginia Polytechnic and State University (Virginia Tech), *magna cum laude*

RESEARCH EXPERIENCE

2010-2012	Graduate Research Assistant, Fenton lab, University of Western Ontario
2010	Wildlife Intern, United States Fish and Wildlife Service at Okefenokee National Wildlife Refuge, Folkston, GA, USA
2009	Ecology Technician, Smithsonian Institute Conservation and Research Center, Front Royal, VA, USA
2008	Environmental Education Interpretation Intern, James Madison's Montpelier, Orange County, VA, USA
2007	Ecology Technician Intern, Wetland Studies and Solutions Inc., Gainesville, VA, USA
2006-2009	Volunteer, The Wildlife Society (Virginia Tech Chapter), Blacksburg, VA, USA

PRESENTATIONS

2012	Hamilton RM. Monitoring bat migration across landscape features. Bat Research Meeting Cuba-Canada, Havana, Cuba
2011	Hamilton RM. Monitoring bat migration across landscape features. 41st North American symposium on bat research, Toronto, Canada.
2010	Hamilton RM. Seasonal activity of migratory bats along coastal and ridged landscape features. 40th North American symposium on bat research, Denver, Colorado, USA.

POSTERS

2011	Adams AM, Jantzen MK, Hamilton RM. Bat detector comparison with synthetic playback and free-flying bats. 41st North American symposium on bat research, Toronto, Canada.
2009	Hamilton, RM. Prospective scope of forest management education at James Madison's Montpelier. 7th Annual Undergraduate Research and Prospective Graduate Student Conference, Blacksburg, VA, USA

PUBLICATIONS

2012	Adams AA, Jantzen MK, Hamilton RM, Fenton MB. Do you hear what I hear? Implications of detector selection for acoustic monitoring of bats. Methods in Ecology and Evolution. doi: 10.1111/j.2041-210X.2012.00244.x
2009	Munsell JF, Hamilton RM, Downing AK. Prospective Scope of Forest Management Education at James Madison's Montpelier. Journal of Natural Resources and Life Sciences Education 38: 198-203.

TEACHING EXPERIENCE

2012	Teaching Assistant, Scientific Methods in Biology Intersession
2012	Teaching Assistant, General Biology II/ Biology for Science II: Tutorial
2010-2011	Teaching Assistant, General Biology/ Biology for Science I and II: Lab
2010	Teaching Assistant, Physiology of Organisms: Lab

LEADERSHIP AND OUTREACH

2012	Assistant, Bats and Abandoned Mines Workshop, Sudbury, Ontario, Canada.
2012	Presenter and Training Assistant, Acoustic Monitoring Training Workshop, Credit Valley Conservation Authority, Mississauga, Ontario, Canada.
2011-2012	Educational Presenter, The Mysterious World of Bats, various locations in southwestern Ontario, Canada.