12-15-2014 12:00 AM

The Role of Islands in the Migration of Bats Across Lake Erie and Lake Ontario: Lasiurus borealis, Lasiurus cinereus and Perimyotis subflavus

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

Recommended Citation

Thorne, Toby J., "The Role of Islands in the Migration of Bats Across Lake Erie and Lake Ontario: Lasiurus borealis, Lasiurus cinereus and Perimyotis subflavus" (2014). *Electronic Thesis and Dissertation Repository*. 2602.
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THE ROLE OF ISLANDS IN THE MIGRATION OF BATS ACROSS LAKE ERIE AND LAKE ONTARIO: *LASIURUS BOREALIS*, *LASIURUS CINEREUS* AND *PERIMYOTIS SUBFLAVUS*

(Thesis format: Monograph)

by

Toby J. Thorne

Graduate Program in Biology

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

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Abstract

Large bodies of water, such as the Great Lakes in North America, are potential barriers to migrating bats. Islands may be used as stopover sites by bats crossing the Great Lakes as stopover sites, or included in crossing routes to reduce the distance flown over open water. I predicted that stopover use by migrating bats would result in higher activity on Great Lakes islands during late-season migration than at mainland sites. I monitored acoustic activity at 11 sites across four locations in Ontario: Amherst and Pelee islands, Kingston and Pinery Provincial Park during the summer (June and July), and during the putative late-season migration period (August and September). I found some evidence of migration by *Lasiurus borealis* and *Perimyotis subflavus* at Amherst Island, and by *Perimyotis subflavus* at Pelee Island. Islands may have occasional roles as stopover sites for migrating bats.

Keywords

bats, migration, acoustic monitoring, seasonal, islands, Great Lakes, shoreline,

Acknowledgments

Many people allowed me to locate bat recorders on their properties, and many also helped to keep the recorders running through the regular tasks of changing batteries and downloading data. I am indebted to Alistair MacKenzie, Tanya Berkers and other staff at Pinery Provincial Park; Christopher and Suzie Grooms, Peter Good, William Bradford and Kurt Hennige at Kingston Ontario; Connor Ryersee, Kim Gardener, Jay Nageleisen, Graeme Gibson, Onishi Sumiko, Mhairi McFarlane and Nature Conservation Canada on Pelee Island and Bill Barratt, Cherry Allen and many landowners on Amherst Island. I offer particular thanks to Cherry, whose interest in my project and perceptive questioning was always a pertinent reminder of the high standard to which I should hold my efforts.

I would like to thank my lab mates past and present, Amada Adams, Matthew Emrich, Colin Hayward, Meghan Murphy, Leslie Reynolds and Benoit Talbot for their friendship and help. I am particularly grateful to Benoit and Meghan for their repeated willingness to drive me to distant field sites. I also thank my "honorary lab mate" Julie Faure-Lacroix, for always answering my stupid questions about call analysis and being an excellent partner in crime on our Engineering Thursdays.

I am grateful to my advisory committee: Hugh Henry and Jack Millar for their friendly support and encouragement. I am especially grateful to my co-supervisor Jeremy McNeil for his support advice and very helpful editorial comments on my thesis draft (despite having to send them from a different continent).

Perhaps most of all I would like to thank my supervisor, Dr. Brock Fenton, for taking me as a student and helping me through the course of this degree. I feel both lucky and honoured to have spent the past two years working full time on bats, my passion in life, under the guidance of an international authority. It has been a pleasure.

Finally I thank my family for always encouraging me, even when I decided to go and study on the other side of the world; I thank all of the friends I have made since arriving in Canada, who have made the past two years one of the best times of my life; and I thank my wonderful girlfriend Jenna Siu, for her support, for believing in me and for picking me up every time I fell down.

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Chapter 1

1 Introduction

Migration presents a challenge to the human imagination, with the mystery and marvel of many long-distance journeys lending a sense of enigma to the organisms that undertake them. Given that observational data are important to scientific investigations, the difficulty of observing animals during long-distance movements has historically presented a challenge for biologists studying migration. However, technological advances have allowed us to uncover many of the secrets of migration (Diehl et al., 2003; Dingle, 1996; Richter and Cumming, 2008), although these new data often generate new questions. Migration by bats – the order Chiroptera – has been relatively understudied although recent studies are beginning to shed light on the phenomenon (Fleming and Eby, 2003; Popa-Lisseanu and Voigt, 2009).

When habitat suitability declines, due to spatiotemporal patterns in climate and resource availability (Alerstam et al., 2003) or to varying habitat requirements during different periods of an animal's life history (Dingle, 1996), there are two possible responses: wait for it to become suitable again – 'here later', or to move to a suitable habitat – 'there now' (Solbreck, 1978; Southwood, 1977). The effectiveness of these strategies depends upon the costs and risks of staying in a sub-optimal habitat relative to those of moving. The costs of 'here later' are highly variable and are a combination of the costs of remaining in a sub-optimal habitat and of any adaptations or strategies necessary for survival, and the risks if habitat remains sub-optimal for a longer period than expected. Upfront costs of 'there-now' include the energetic demands of moving, time required to gather the energy and to undertake migration (Alerstam et al., 2003), as well as risks of mortality during migration (Giavi et al., 2014). Physiological and morphological optimisations related to migration can also be considered costly when they involve trade-offs between migration and reproduction (e.g. Prop, Black, & Shimmings, 2003). The tenuous evolutionary balance between migration and staying put is illustrated by the degree of behavioural flexibility associated with it; migration can occur or be suppressed over a short timescale (Alerstam et al., 2003). Migratory behaviour can also vary within species, occurring in some populations or demographic groups and not in others (Alerstam et al., 2003; Lack, 1968).

Migration in response to changes in habitat suitability has been reported in a wide variety of taxa and thus, not surprisingly there are a number of scenarios and/or author specific definitions of the phenomenon (Dingle, 1996). Here I use the broad, non-specific, definition of Dingle and Drake (2007), whose definition of migration can be summarised as a persistent, directed movement at greater spatial and temporal scale than the animals' usual daily movements, which may occur once or repeatedly.

1.1 Migration in bats

While non-migratory behaviour is the ancestral state, migration occurs in a minority of bat species (Fleming and Eby, 2003). Bisson et al. (2009) noted that < 3% of known bat species have seasonal movements > 50 km, with < 0.02% travelling distances over 1000 km. However, such figures are probably underestimates given the scarcity of year-round data for most bat species. Fleming and Eby (2003) suggest that widespread sedentary behaviour occurs, in part, because a large proportion of bat species live in tropical environments that are relatively stable throughout the year (Levey, 1988; Findley, 1993). However, the bat species that migrate are distributed through multiple families (McGuire and Ratcliffe, 2011), suggesting multiple evolutionary events (Fleming and Eby, 2003). For example, detailed investigation of migratory bat species in the family Vespertilionidae showed that genetic evidence, combined with the absence of intermediary forms in the lineage, is most parsimoniously explained by independent evolutions of migratory behaviour (Bisson et al., 2009).

Although relatively few cases of bat migration have been documented in detail, they typically are related to the same variations in habitat suitability and cost benefit relationships reported for migration in other animals. Many bat species respond to temporary declines in habitat suitability by hibernation, building up energy reserves in advance of a period of sub-optimality, during which they survive by lowering their metabolic rate in a deep torpor (Kunz and Fenton, 2006; Lyman et al., 1982). Costs and risks of hibernation appear low, although the apparent anthropogenic introduction of the fungus *Pseudogymnoascus destructans* to North America is currently causing high mortality of hibernating bats (Blehert et al., 2009). Although species hibernating in Ontario are not thought to undertake long-distance movements, the rapid spread of *P. destructans* suggests a high rate of movement and mixing of individuals between hibernation sites.

Data on the costs and risks of migration by bats are sparse, although estimates of the survival rate of *Nyctalus leisleri* based on capture-recapture suggests that mortality rates are low (Giavi et al., 2014). However, numerous studies have recorded high mortality rates for migratory bats at wind turbines in North America (Baerwald and Barclay, 2011; Kunz et al., 2007; Ryan, 2011). Bats flying close to wind turbines are killed either through direct collision or by barotrauma resulting from areas of low air pressure around the blades (Cryan and Barclay, 2009). A variety of reasons have been proposed to explain why bat mortality at wind turbines includes a disproportionate number of putative long-distance migrant species, however none has yet proved conclusive (reviewed by Cryan and Barclay, 2009). Increased understanding bat migration, the routes followed and factors affecting its occurrence, is necessary to design and manage future and current turbine development to reduce the ecological impact on bats (Baerwald and Edworthy, 2009; Kunz et al., 2007).

Some temperate bat species cope with the decline of habitat suitability (Lyman et al., 1982) by using a combination of ‘here later’ and ‘there later’ strategies because they hibernate at overwintering sites have highly specific characteristics not usually found in their summer home ranges (Glover and Altringham, 2008). Consequently, they have a seasonal migration and may travel several hundred kilometres to and from their summer ranges to overwintering sites (Barbour and Davis, 1969; Kerth et al., 2011; Perry, 2011). For example, banding recoveries of *Myotis lucifugus* in Ontario demonstrated individuals moving between 120 and 800 km between hibernation sites during autumn swarming, prior to hibernation (Fenton, 1969). Partial migration occurs in many migratory bat species (Fleming and Eby, 2003). For example, populations of *Tadarida brasiliensis* in Texas and New Mexico migrate, while those in California do not (Bernardo and Cockrum, 1962). Other examples of partial migrants include *Nyctalus noctula* (Dietz and

Helversen, 2006), *Pteropus poliocephalus* (Fleming and Eby, 2003) and *Leptonycteris yerbabuenae* (Rojas-Martínez, 1999).

Detailed track information for individuals of many larger animal species has been obtained through radio-telemetry (Kenward, 2001). However, the low body weight of most bat species limits the size of transmitter one can attach to an individual. Thus, only short-range transmitters can be used, which is of limited use as they are only detectable over a few kilometres, although McGuire et al. (2012) monitored the movements of *L. noctivagans* around Lake Erie (Ontario, Canada) using coded tags and automated receiving towers. Heavier satellite transmitters have also been deployed with moderate success with larger bat species (Richter and Cumming, 2008; Smith et al., 2011; Tidemann and Nelson, 2004).

Due to the difficulty of directly studying migrating bats much of our understanding of their migration is based on secondary evidence. Banding (Ellison, 2008) and isotopic analysis (Cryan et al., 2004; Fraser et al., 2012) provide post facto information on the distance moved based on the location of the capture site relative to the site of banding or by comparing the isotopic profiles respectively. Radar can be used to track large scale movement by bats (Cryan and Diehl, 2009) but not at an individual level and confirmed identification of target species can be problematic. Temporal (Dzal, Hooton, Clare, & Fenton, 2009; Furmankiewicz & Kucharska, 2009; Ibáñez, Guillén, & Agirre-Mendi, 2009; Reynolds, 2006) and spatial (Baerwald and Barclay, 2009; Hooton, 2010) patterns of activity and capture rate (Cryan, 2003; Geluso, 2006; Geluso et al., 2004; Hooton, 2010) may provide further insight into migration.

Activity of bats is commonly assessed acoustically by monitoring the echolocation calls they produce for orientation (Adams, 2013). The rate of production, and volume of calls varies between species, affecting their detectability, however changes in the number of calls recorded in a given time period can be used to indicate relative change in bat activity (Adams, 2013). The structure of echolocation calls results from the primary function of echo based orientation, and thus may not always differ sufficiently between species to allow identification (Barclay, 1999). However, in many cases sufficient differences occur between the calls of different species to allow reliable identification. In Ontario the calls of *Lasiurus borealis*, *L. cinereus Myotis lucifugus*, *M. septentrionalis* and *Perimyotis subflavus* can be reliably distinguished from other species using high-quality full spectrum recordings (Amanda Adams, personal communication).

1.2 Migration by *Lasiurus borealis*, *Lasiurus cinereus* and *Perimyotis subflavus* in Ontario

Lasiurus borealis and *L. cinereus* are summer residents of Ontario (Dzal et al., 2011, 2009; Hooton, 2010; Van Zyll de Jong, 1985) and appear to roost in foliage of trees and vines throughout the year, although there are few data about their overwintering habits (Cryan and Veilleux, 2007; Griffin, 1970; Van Zyll de Jong, 1985). Patterns of acoustic activity suggest that all three species migrate south in the fall (Barclay, 1984; Barclay et al., 1988; Cryan, 2003; Geluso et al., 2004), possibly travelling distances > 1000 km or more (Fleming and Eby, 2003). There is no direct evidence to confirm such regular long-distance movements, but indirect evidence based on seasonal distribution patterns and isotopic evidence (Cryan, 2003; Cryan et al., 2004) supports this hypothesis.

Perimyotis subflavus roosts in foliage in summer (Veilleux et al., 2003) and is believed to migrate short distances to swarming and hibernation sites in caves, although the species' seasonal movements are poorly understood (Cryan and Barclay, 2009). Isotopic evidence suggests that some individuals, more commonly males, make longer migrations, probably because their behaviour during hibernation, roosting individually or in small clusters, is poorly adapted to cold temperatures (Fraser et al., 2012).

All three species roost in foliage (Van Zyll de Jong, 1985), a widely available habitat. To date, no published data confirms the southwards migration of *L. borealis*, *L. cinereus* or *P. subflavus* in Ontario, although seasonal patterns of *L. cinereus* activity at Long Point in Lake Erie suggests migration by this species at this site. However, evidence from through the full ranges of each species suggests they migrate and so it is possible that populations in Ontario also do so. If this is the case, the Great Lakes are likely to be encountered during any southwards movement.

1.3 Bat migrations around water

Water is not an absolute barrier for bats; they have been recorded flying 40 km among islands in the Mediterranean Sea (Amengual et al., 2007) and multiple studies report bats flying offshore (e.g. Ahlén et al., 2007; Hatch et al., 2013; Peterson and Pelletier, 2014; Rydell et al., 2014). Studies of bat physiology indicate that most bats are capable of flying at sufficient speed with sufficient duration to travel > 100 km in a single flight (McGuire, 2012). However, high levels of bat activity are regularly recorded along shorelines, suggesting that in some situations bats follow the shore rather than crossing the water (Barclay, 1984; Barclay et al., 1988; Hamilton, 2012; Timm, 1989). Bats may avoid water crossings due to the lack of landmarks for navigation (Fleming and Eby, 2003; Hamilton, 2012) and to avoid the risk of being caught at sunrise without access to suitable roosts. Furthermore, when bats make long water crossings they may halt at stopover sites at the shoreline to rest and feed, prior to departure to cross during darkness (McGuire et al., 2012; Rydell et al., 2014).

The most detailed study of stopover site use by bats was conducted at Long Point Ontario, a spit extending into Lake Erie. Using radio telemetry, McGuire et al. (2012) showed that most *L. noctivagans* captured during late-season migration only stopped for a day, with longer stopovers typically associated with unfavourable weather conditions. The short time spent at stopover sites suggests that feeding is not a priority, but diurnal roosting and timing the crossing to occur during darkness are. Acoustic and mist-net capture data suggest that Long Point is an important site for other species of bat because activity of *L. noctivagans*, *L. borealis* and *L. cinereus* was highest during putative migratory periods (Dzal et al., 2009; Hooton, 2010). The geography of Long Point may serve to funnel bats to the south of the spit, where the crossing distance over open water is shorter than the surrounding area (~30 km vs. 50-80 km).

The evidence obtained at Long Point suggests that bats may minimise the distance of water crossings, and may respond to geographical barriers by stopping initially before crossing. In addition to shorelines, the presence of islands could be relevant to these behaviours. Observations from Southeast Farallon Island (Cryan and Brown, 2007; Tenaza, 1966) and Assateague Island (Johnson et al., 2011), on the west and east coasts of North America respectively, included increases in activity of *L. borealis* and *L. cinereus* during putative late season migration. The geographical isolation of the islands makes migration a compelling explanation for the patterns observed. These examples all pertain to coastal islands; no data are currently available relating to bat migration at islands within smaller water bodies.

The southern extent of Ontario borders several of the Great Lakes, potentially representing a significant barrier to the possible southwards migration of *P. subflavus*, *L. noctivagans*, *L. borealis* and *L. cinereus*. A number of islands with varying characteristics are present in the Great Lakes that migrating bats could use as stopover sites.

1.4 Statement of purpose

I hypothesised that if bats minimise the distance they fly over open water, and use stopover sites in relation to water crossings, then they will make use of islands in the Great Lakes during crossings. I investigated activity of *L. borealis*, *L. cinereus*, *Myotis* species and *P. subflavus*, which can be identified acoustically. I tested my hypothesis by comparing seasonal bat activity on islands to mainland control sites not associated with lake crossings, and made the following predictions:

1) There would be increased activity on islands during the putative late-season migration (August and September) compared to the middle of the season (June and July).

2) There would be greater activity of possible long-distance migrants (*L. borealis*, *L. cinereus* and *P. subflavus*) at island sites relative to mainland sites. This is because if those species migrate southwards to overwinter I expect a greater proportion to cross the lakes, unlike *Myotis* species that migrate within Ontario.

Chapter 2

2 Materials and Methods

2.1 Study locations

I monitored bat activity at two mainland and two island locations in southwestern Ontario. The mainland locations were rural areas south of Kingston, Ontario and Pinery Provincial Park on the north shore of Lake Ontario and the south shore of Lake Huron, respectively. Amherst Island (70 km^2) is located approximately 2-3 km from the shore in northeastern Lake Ontario while Pelee Island (42 km^2) is about 14 km and 20 km respectively from the north and south shores of Lake Erie (Figure 1). Pinery Provincial Park had high woodland coverage, while the other sites were comprised of open farmland, hedgerows and small patches of woodland.

Figure 1: Map of field locations in southwestern Ontario, Canada. I monitored bat activity on Amherst Island in 2013, and at all four locations in 2014 (Google Earth, 2014a).

2.2 Recorder sites

In addition to differences among sites located far apart, local landscape features may affect temperature, rain, wind and light intensity, which in turn could influence bat activity (Adams, 2013). Consequently, at each study location I set up several bat recorders between 1 and 10 km apart, in different open habitats close to edges, field boundaries or woodland edges where bat activity is high (Jantzen and Fenton, 2013). The use of multiple simultaneous recorders increases the accuracy of estimated activity levels (Adams, 2013) In 2013 I installed 8 recorders on Amherst Island (A1-A8; Figure A1) while in 2014 I had four recorders on Amherst Island (A2, A3, A4, A7; Figure A1), Kingston (BB, CG, LM, PG; Figure A2), Pelee Island (JN, KG, NC, SR; Figure A3) and the Pinery Provincial Park (BB, NB, SH, VC; Figure A4).

2.3 Data collection

In both years I monitored activity in June and July when bats forage locally (Barbour and Davis, 1969), as well as from August through September (2014) or October (2013) (Table 1), a period when migrant species of bats in Ontario are thought to migrate (Dzal et al., 2009; Hooton, 2010; McGuire et al., 2012). In 2014 I also monitored bat activity in April and May at Amherst Island and Kingston, but I was not able to do so at Pelee Island or the Pinery Provincial Park, or at Pinery Provincial Park after July (Table 1) due to delays in the return of equipment sent to the manufacturers to be recalibrated and difficulties recruiting local volunteers to maintain recorders.

I recorded echolocation calls using two types of automated recorder, batcorders (ecoObs, 2008, Nürnberg, Germany) and Song Meter SM2BATs (Wildlife Acoustics, 2009, Massachusetts, U.S.A.). Both record sounds as 16 bit full spectrum recordings and have maximum frequencies of 250 kHz and 98 kHz, respectively. A comparative study found no significant difference in call detection between the two recorders, although the lower maximum frequency of the SM2s affected the identification of *Myotis* species, which are closer to the upper cut-off (Adams et al., 2012).

Table 1: The time periods during which the acoustic activity of bats was monitored at study locations in southwest Ontario.

Site	2013		2014	
	Start	**End**	**Start**	**End**
Amherst Island	19 June	31 October	14 April	30 September
Pelee Island	Not sampled		25 June	
Kingston			14 April	
Pinery Provincial Park			30 May	31 July

In 2013 I only used batcorders, but in 2014 I used two batcorders and two SM2s at each of the sites. All recorders were placed approximately 2 m above ground, with the microphones oriented in accordance with the manufacturers instructions to maximise detection. SM2s were positioned with microphones perpendicular to the ground and batcorder microphones were pointed upwards, clear from any vegetation that could introduce echoes. Each call represents a single vocalisation, multiple calls can be recorded from a single bat so counts cannot be used to estimate density, but provide a proxy for overall bat activity (Fenton, 1970; O'Farrell and Gannon, 1999).

Each week batteries were changed, and recordings were downloaded by local volunteers (Amherst and Kingston), a field assistant (Pelee Island) or provincial park staff (Pinery), who then transferred data to me for analysis. In 2013 recorders were programmed at regular intervals to account for changes in day length, thus assuring activity was recorded from before sunset until after sunrise. In 2014 recorders were programmed to monitor continuously from 19:30-07:00 all season to ensure continuity across all sites.

The recording parameters, which were optimised to detect bat echolocation vocalisations, were: batcorder – quality: 40, threshold: -36 dB, postrigger: 800 ms and critical frequency: 16 kHz (Jantzen and Fenton, 2013); SM2 – sampling rate: 192 kHz; compression: WAC0 / WAV, gain: 36 dB, dig hpf: fs/16, digLPF: off, trigger level: 15 SNR, Trigger Win: 1 s, div ratio: 16 (Adams et al., 2012). Any signals meeting the detection parameters were recorded as a .wav file onto a secure digital high capacity memory card. Both recorders have programmable trigger characteristics to avoid recording non-target sounds.

2.4 Species identification

I analysed recorded files using the 'Auto Detection' function of callViewer 18 (Skowronski and Fenton, 2008) to identify bat calls using the following detection parameters: minimum link length, 10; minimum energy, 14 dB; echo filter threshold, 10 dB and lower frequency cut-off, 14 kHz (Amanda Adams, personal communication). I then identified calls to species using a discriminant function analysis (DFA) written for the bats of Ontario (Adams, 2013) that was based on the following parameters, measured in callViewer 18: minimum frequency, maximum frequency, duration, frequency of most energy, 10th percentile of energy, 60th percentile of energy, 90th percentile of energy, median frequency slope, median energy slope, median frequency smoothness and median energy smoothness.

Bat calls are highly variable and identification to species using a single call is prone to error (Amanda Adams, personal communication) so I excluded cases where there were $<$ 5 calls of a species identified in a file.

I confirmed the DFA species identifications by manually verifying 5% of files where 5 or more calls of a species were recorded. I used SASlab Pro (Version 5.2.08, Avisoft Bioacoustics, 2014, Glienicke, Germany) to view and measure calls in every 20th file from a list sorted by date and the percentage of identifications confirmed for each species is listed in Table 2. I discarded identifications of *L. cinereus* at sub-site A7 on Amherst Island in 2014 because manual verification indicated a high number of false positives due to non-bat signals.

I also attempted to identify calls by species of *Myotis* combined in a single category because the low maximum frequency of the SM2 recorders hinders identification to species (Amanda Adams, personal communication). However, as a result of low identification accuracy (Table 2), resulting primarily from low signal to noise ratios, I did not include them in any further analysis.

Table 2: The percentage and number of files of each bat species for which calls were manually identified, and the percentage of files where the discriminant function analysis species identification was confirmed. *Myotis* species were excluded from further analysis due to low identification accuracy.

Species	**Percentage of total files verified**	**Percentage of identifications confirmed**
L. borealis	5% (n = 134)	81.36%
L. cinereus	5% (n = 722)	81.30%*
Myotis species	5% (n = 80)	57.50%
P. subflavus	5% (n = 34)	88.24 %

*74.14% with A7 included

2.5 Seasonal activity and migration

I evaluated nightly bat activity across the season to identify patterns suggestive of migratory activity. However, because of the large distances travelled by migrating bats (Fleming and Eby, 2003) I could not consider recorders within a site as independent samples, because an individual bat migrating across the island could be detected by several recorders. Thus, to avoid pseudoreplication I calculated the mean of the total calls of each species detected by each recorder within a location. However, due to technical issues (primarily exhausted batteries and equipment faults) some recorders did not work reliably, so I excluded nights when < 4 (2013) or < 2 (2014) recorders functioned. In 2014, recorders LM at Kingston, SR on Pelee and SH and VC at Pinery Provincial Park failed for extended periods so I removed those data from further analysis, to avoid having the intermittent functioning of the recorders being erroneously interpreted as changes in bat activity. One recorder failed due to accidental damage and all other failures resulted from faults that required manufacturer repair.

To visually assess seasonal trends, I plotted the seasonal activity for each location. The number of calls does not reflect a number of individuals, but rather a relative measure of activity, so I used a ln(x+1) transformation to compress the range of counts and allow easier visual comparison of seasonal change.

I used call counts to determine peaks of activity that could indicate migration at Amherst Island in 2013 and 2014, and at Kingston and Pelee Island in 2014. I could not identify migration at Pinery Provincial Park because I did not collect data after 31 July. I defined a migratory peak as a night in August or September where call numbers were three standard deviations higher than the average June and July activity (Hamilton, 2012). To avoid erroneous interpretation of a single event I only considered a site to have migratory activity if more than three peaks occurred during August and September.

2.6 Summer activity comparison

I used an ANOVA to determine whether activity of each bat species in July 2014 differed among the four study locations, using average nightly total calls of each species after transforming data by √(x) to meet ANOVA assumptions. I assumed that, in July, bats forage close to roosts and were unlikely to be detected at multiple recorders. When the ANOVA indicated a significant effect of site on activity I conducted additional contrasts to test for a difference between pooled data for mainland sites and island sites. I did not test for differences among individual sites.

Chapter 3

3 Results

3.1 Seasonal activity

My processed dataset included a total 1079447 calls by *L. borealis*, *L. cinereus* and *P. subflavus* recorded over 1002 recorder nights (Table 4). Raw nightly activity data are included in Appendices III - VII. Migratory activity is summarised in Table 3, and occurred as follows:

Lasiurus borealis activity on Amherst Island in 2013 was consistent during June and July, followed by a sustained activity peak in mid August that I interpreted as possible migratory activity (Figure 2a). In 2014, *L. borealis* activity on Amherst was more varied and I did not observe peaks during August and September (Figure 3a). At Kingston in 2014 *L. borealis* was absent for much of the year; most activity occurred during August and I interpreted this as possible migratory activity (Figure 4a). *Lasiurus borealis* was present on Pelee Island throughout the year and activity did not appear to increase in August and September, thus I recorded no activity peaks (Figure 5a).

Activity of *L. cinereus* was high throughout the year at Amherst Island in 2013, I observed no distinct migratory peaks in August, before a steady decline during September and October (Figure 2b). *L. cinereus* activity was consistent throughout the season at all sites in 2014 and I did not observe any increase in activity in August and September that could indicate migration by this species (Figures 3b, 4b and 5b).

Perimyotis subflavus activity on Amherst Island in 2013 was consistent throughout June and July, but it greatly increased in mid August, with a large peak in activity; most nights during August and September had more calls than the average calls per night in June and July, which I interpreted as possible migratory activity (Figure 2c). Activity of *P. subflavus* recorded on Amherst and Kingston in 2014 was lower, with no pattern indicating migration (Figures 3c and 4c). I recorded several activity peaks of *P. subflavus* activity on Pelee Island in 2014, which I interpreted as possible migratory behaviour (Figure 5c).

Table 3: The summer (June and July) activity level of each bat species at each study location and the number of migration peaks, nights with activity > 3 standard deviations higher than mean summer activity during the late season migration period (August and September). Possible migration was identified at locations with > 3 activity peaks.

Site	**Species**	**Summer activity (mean calls night^{-1} in June and July)**	**Activity Peaks**	**Possible Migration**
Amherst 2013	*L. borealis*	69	8	Yes
	L. cinereus	2158	0	No
	P. subflavus	10	26	Yes
Amherst 2014	*L. borealis*	22	0	No
	L. cinereus	515	3	No
	P. subflavus	1	0	No
Kingston 2014	*L. borealis*	< 1	4	Yes
	L. cinereus	107	1	No
	P. subflavus	< 1	3	No
Pelee 2014	*L. borealis*	29	0	No
	L. cinereus	28	2	No
	P. subflavus	4	6	Yes

Table 4: The total number of recorder nights, calls of *L. borealis*, *L. cinereus* and *P. subflavus*, and calls per recorder night at locations in southwestern Ontario in 2013 and 2014.

Site	Recorder nights	Species	Total calls	Calls recorder night^{-1}
Amherst Island 2013	476	*L. borealis*	37694	79
		L. cinereus	862096	1811
		P. subflavus	10523	22
Amherst Island 2014	175	*L. borealis*	1911	11
		L. cinereus	81010	463
		P. subflavus	3940	23
Kingston 2014	197	*L. borealis*	76	<1
		L. cinereus	17351	88
		P. subflavus	111	<1
Pelee Island 2014	81	*L. borealis*	3514	43
		L. cinereus	3980	50
		P. subflavus	504	6
Pinery Provincial Park 2014	73	*L. borealis*	7817	107
		L. cinereus	48503	664
		P. subflavus	417	6

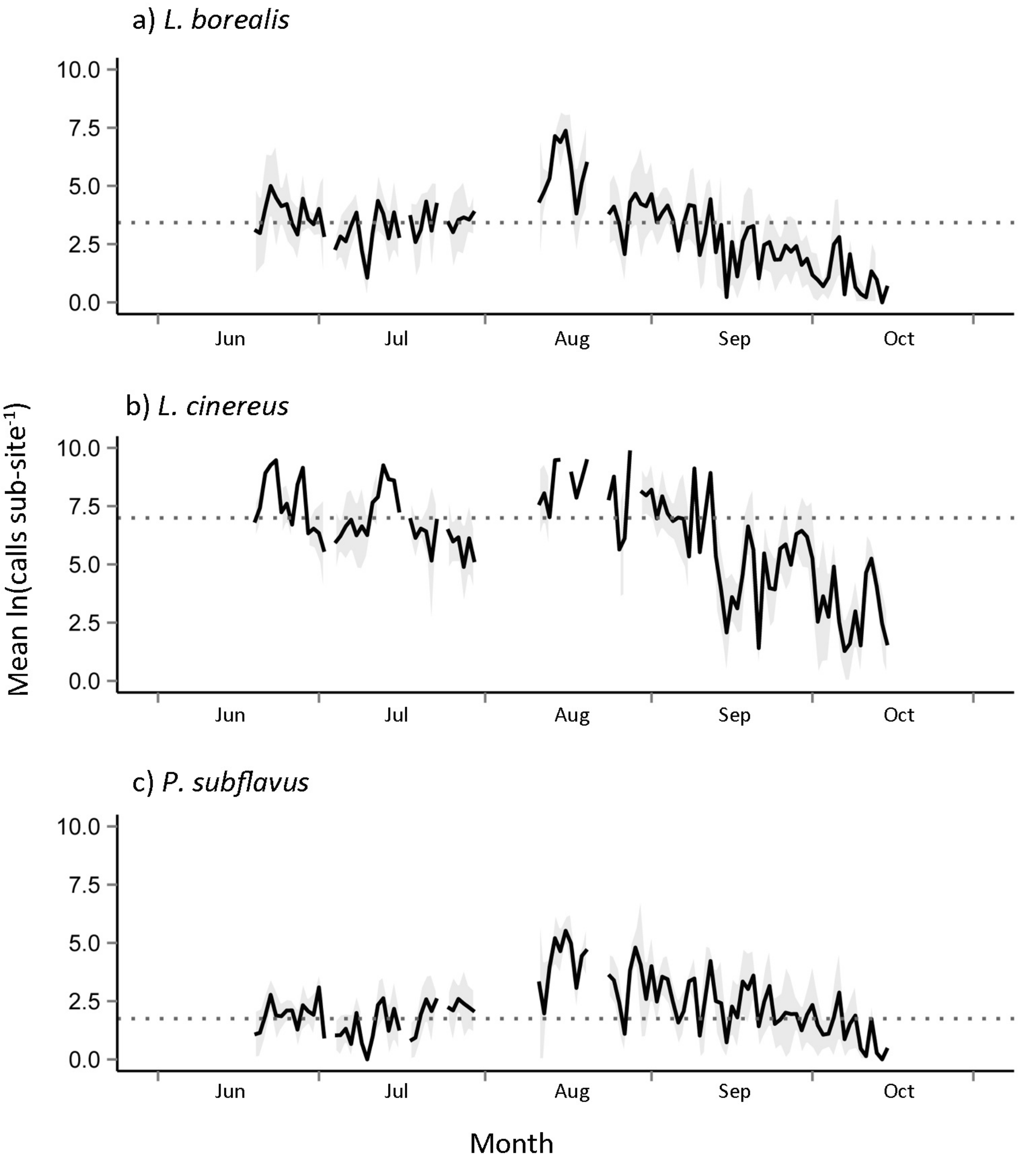


Figure 2: Activity levels of bat species on Amherst Island from 22 June to 31 October 2013. The graph shows mean ln calls recorder^{-1} night^{-1} (black line) ± 95% confidence interval (grey area) and average calls recorder^{-1} night^{-1} for nights in June and July (dotted line). Gaps indicate nights when fewer than half the recorders functioned.

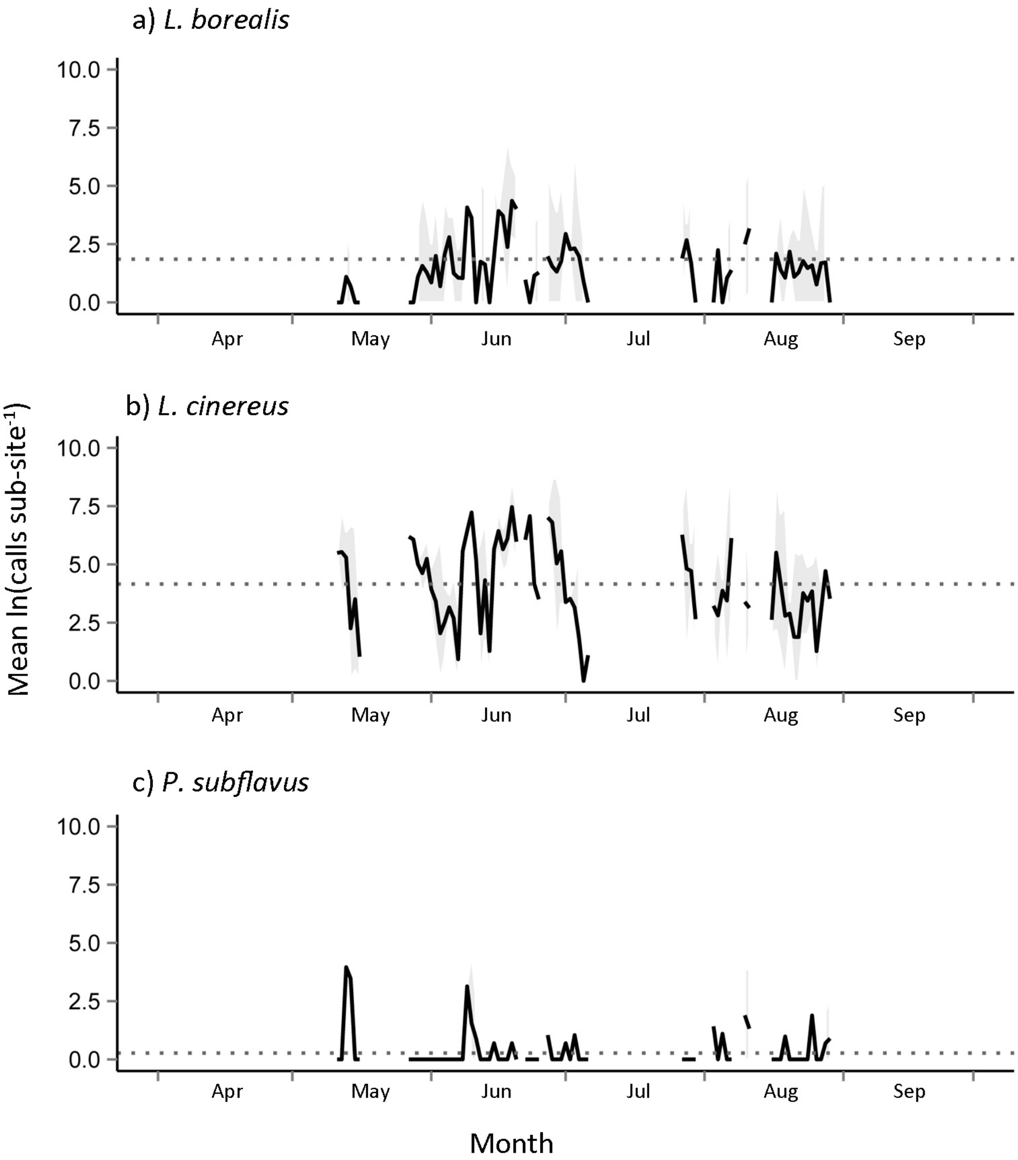


Figure 3: Activity levels for bat species on Amherst Island from 15 April to 15 September 2014. The graph shows mean ln calls recorder^{-1} night $^{-1}$ (black line) ± 95% confidence interval (grey area) and average calls recorder^{-1} night^{-1} for nights in June and July (dotted line). Gaps indicate nights when fewer than half the recorders functioned.

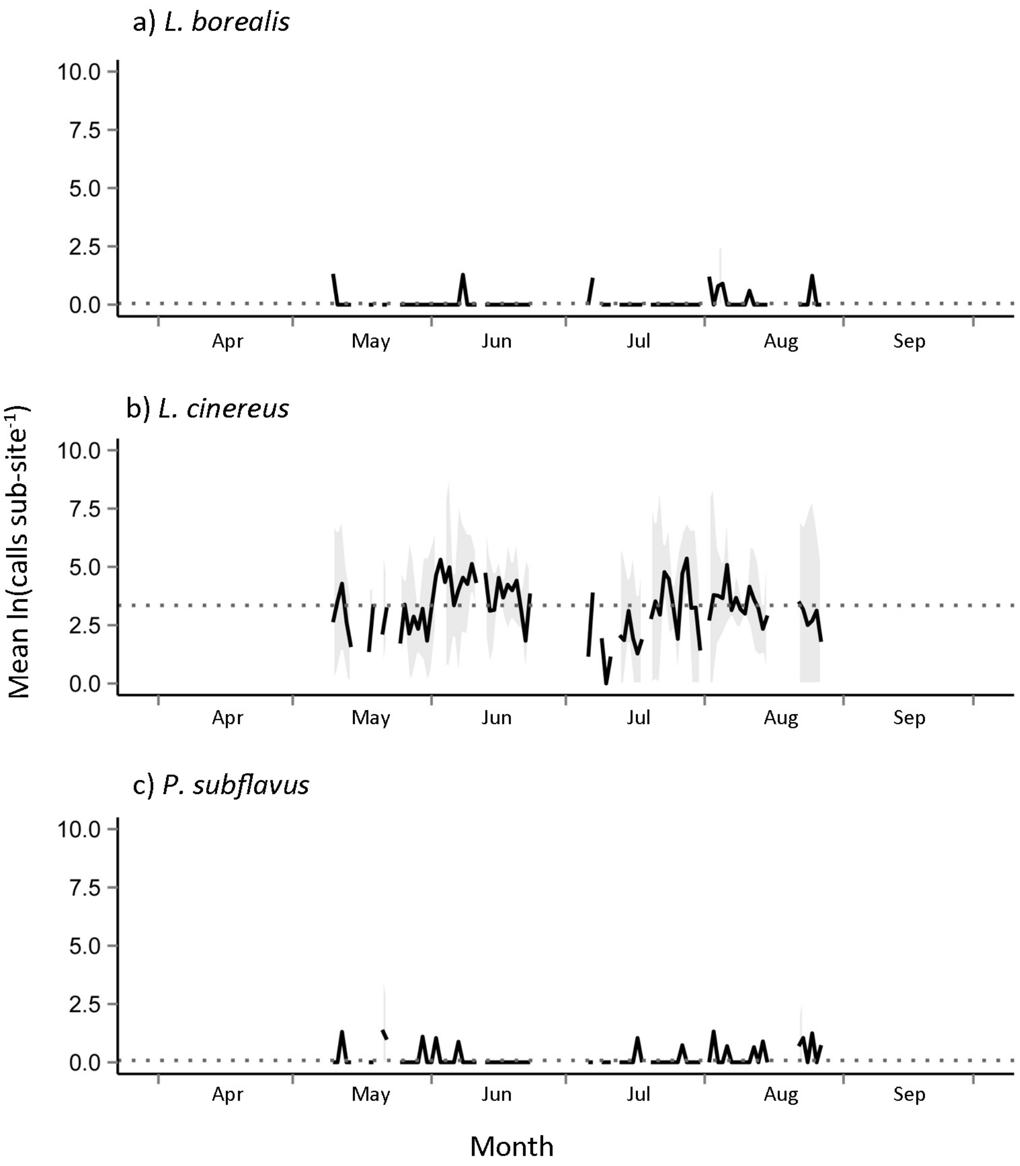


Figure 4: Activity levels for bat species at Kingston from 15 April to 13 September 2014. The graph shows mean ln calls recorder^{-1} night $^{-1}$ (black line) ± 95% confidence interval (grey area) and average calls recorder^{-1} night^{-1} for nights in June and July (dotted line). Gaps indicate nights when fewer than half the recorders functioned.

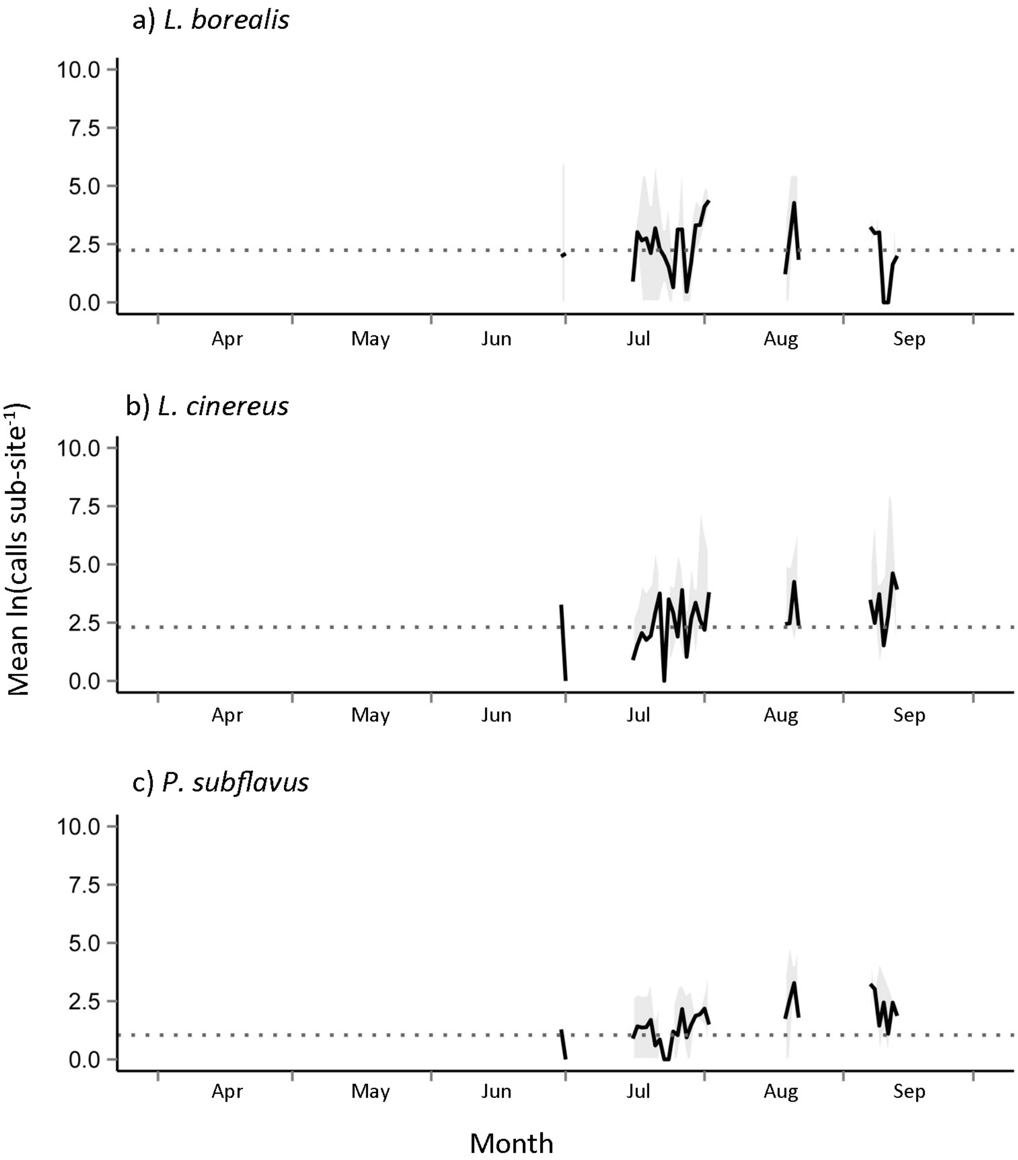


Figure 5: Activity levels for bat species on Pelee Island from 28 June to 30 September 2014. The graph shows mean ln calls recorder^{-1} night^{-1} (black line) ± 95% confidence interval (grey area) and average calls recorder^{-1} night^{-1} for nights in June and July (dotted line). Gaps indicate nights when fewer than half the recorders functioned.

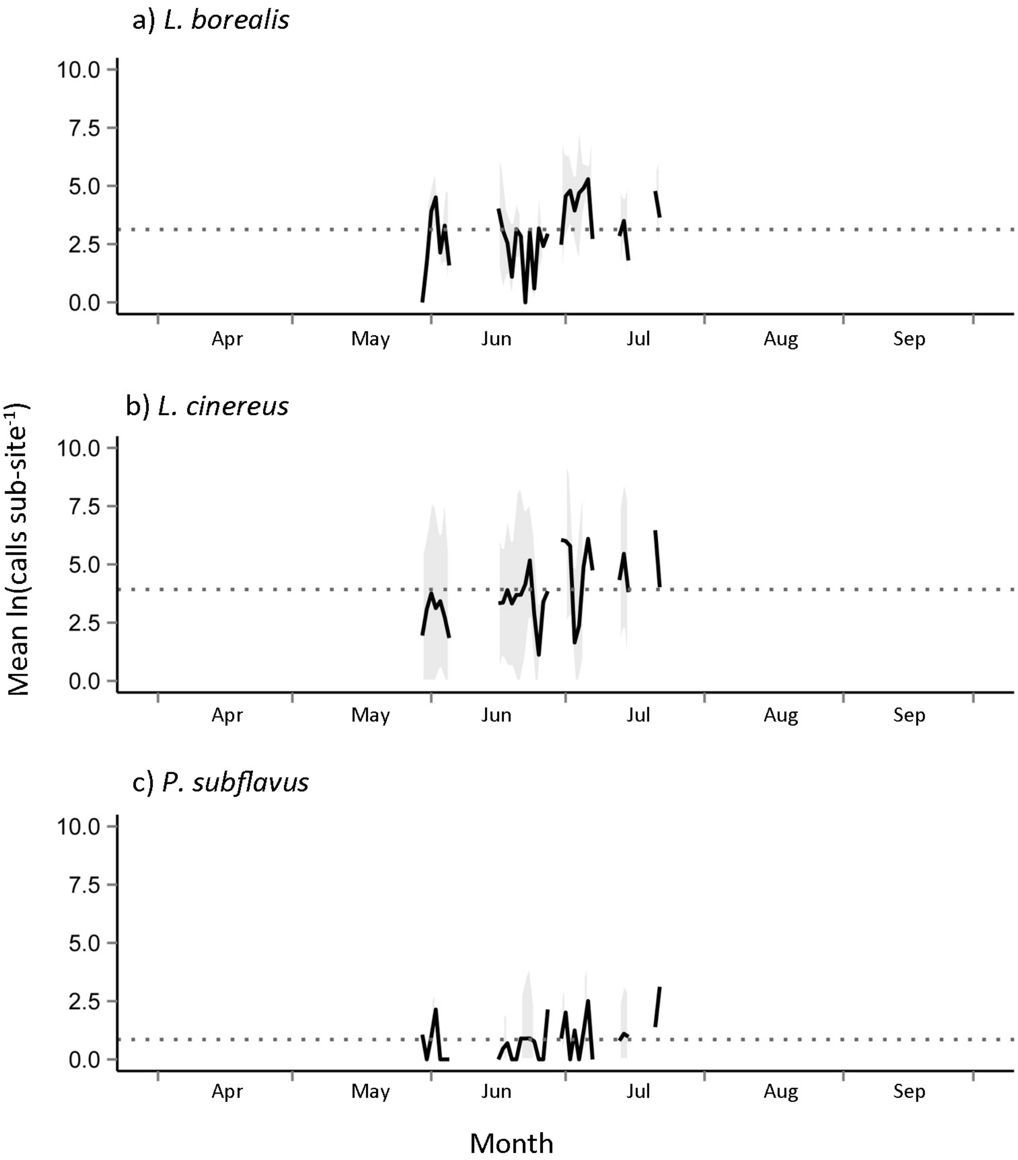
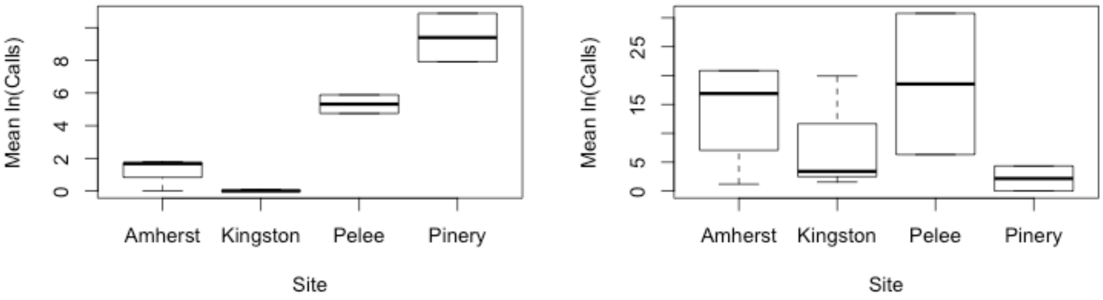


Figure 6: Activity levels for bat species on Pinery Provincial Park from 2 June to 31 July 2014. The graph shows mean ln calls recorder^{-1} night $^{-1}$ (black line) ± 95% confidence interval (grey area) and average calls recorder^{-1} night^{-1} for nights in June and July (dotted line). Gaps indicate nights when fewer than half the recorders functioned.

3.2 Summer activity comparison

I found no significant difference in July 2014 activity of *L. cinereus* ($F_3 = 0.99$, $p = 0.45$) at different locations. The activity of *L. borealis* ($F_3 = 41.83$, $p < 0.0001$) and *P. subflavus* ($F_3 = 9.19$, $p < 0.001$) varied significantly among sites in July 2014, but there was not a significant difference between island and mainland sites ($t = 12.51$, $p = 0.15$ and: $t = -0.07$, $p = 0.95$, respectively).



a) *L. borealis*

b) *L. cinereus*

c) *P. subflavus*

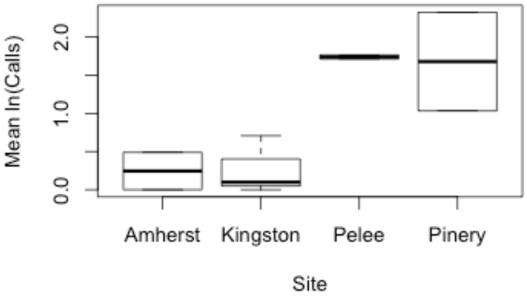


Figure 7: Mean calls night^{-1} recorder^{-1} for bat species in July 2014, grouped by site. Boxplots represent median values, interquartile range and minimum / maximum values. Site had a significant effect on activity for *L. borealis* (a) and *P. subflavus* (c). There was not a significant difference between island and mainland sites.

Chapter 4

4 Discussion

I tested the hypothesis that bats migrating south across the Great Lakes would use islands to reduce open water crossing distance and stopover, and thus predicted increased activity of *L. borealis*, *L. cinereus* and *P. subflavus* late in the season, particularly on the islands. The late season activity peaks that I observed of *L. borealis* and *P. subflavus* on Amherst Island in 2013 supported this hypothesis. However, in 2014 I did not observe activity peaks on Amherst Island, but did observe activity peaks of *L. borealis* at Kingston and *P. subflavus* on Pelee Island. I considered migration to be the most likely explanation these activity patterns. An alternative explanation of increased activity resulting from a population increase when the young of the year become volant is unlikely because such an increase would occur earlier in the season than observed (mid July). Further, increased acoustic activity resulting from a population increase might be expected to occur as a sustained effect, rather than the infrequent peaks I observed in most species.

4.1 Bat migration at islands

Due to the position of Amherst Island at the eastern extreme of Lake Ontario (Figure 1), migratory activity of *L. borealis* and *P. subflavus* in 2013 probably resulted from individuals travelling around the eastern end of the lake. Migrating bats follow linear landscape features such as shorelines (Hamilton, 2012) and may travel around the eastern extent of the lake rather than crossing open water (Barclay, 1984; Timm, 1989). These species are considered obligate migrants (Van Zyll de Jong, 1985) and it is likely they did so in 2014 even though I observed no significant activity peaks. The disparity in observed activity could result from different sampling effort in the two years (Table 4). I monitored bats on fewer nights in 2014 and migration may have occurred at other times. I also monitored activity at fewer sites on Amherst in 2014. However, in 2013 peaks of activity occurred at sites resampled in 2014 (Appendix VIII). The different observations could also result from inter-year variation in bat activity. Bat migration activity correlates with low wind speeds (< 6 m/s: Reynolds, 2006; < 5.4 m/s: Arnett et al., 2008) and at Amherst in 2013, 21 nights in August had wind gusts > 8.6 m/s, compared to 14 such nights in 2014 (Environment Canada, 2014).

Both of the recorders I used have ranges of approximately 10 m (Adams et al., 2012), and when positioned at a height of 2 m would detect bats flying at a maximum height of 12 m. Because migrating bats sometimes fly higher above the ground (e.g. 50 m; Reynolds, 2006) it is possible activity occurred beyond the detection range of the recorders. Bats stay longer at stopover sites during conditions unfavourable for migration (McGuire et al., 2012) and the migration activity on Amherst Island in 2013 may result from a higher proportion of windy nights forcing bats to stop more frequently and for longer periods during migration. If the bats were using the islands as stopover sites they would likely fly lower and be detectable at lower levels. However, bats using stopover sites should be detectable at lower heights (Dzal et al., 2009). My data cannot distinguish between the absence of migrating bats and the presence of migrating bats flying higher than the range of my recorders, but in either scenario bats would not use the site to stopover.

Amherst Island is close to the lakeshore and may be used for stopover during unfavourable conditions by bats migrating along the lakeshore. Pelee Island is more isolated, being ~14 km from the next largest landmass. The absence of migratory activity by *L. borealis* and *L. cinereus* suggests that Pelee Island is not an important stopover site for these species while late season activity of *P. subflavus* suggests that some individuals stop while crossing Lake Erie. *Perimyotis subflavus* overwinter in caves and are unlikely to overwinter on Pelee Island, where no caves are known (Kim Gardener, Personal Communication). *Perimyotis subflavus* has a slow, fluttering flight (Van Zyll de Jong, 1985) relative to *L. borealis* and *L. cinereus* and thus could be more likely to use stopover sites. A bat traveling at flight speeds proposed by McGuire et al. (2012), e.g. 7 m/s for a 10 g bat, would cross Lake Erie at its widest point in approximately 3.5 hours. Physiological studies indicate this is an achievable flight time for a migrating bat (McGuire, 2012), meaning that islands have little advantage as stopover sites for bats crossing relatively short distances (< 100 km).

Some studies (e.g. Reynolds, 2006; Hooton, 2010) suggested that bats migrate on a broad front. If bats do not use islands as stopover sites but rather travel in a broad front they may be less detectable through acoustic monitoring. In addition, the three species in this study all roost in foliage (Van Zyll de Jong, 1985), a widely available habitat. This may mean that there is a reduced likelihood of encountering aggregations of these species, which might be expected if roosts were a limiting resource.

High concentrations of acoustic activity could still occur if bats used islands as navigational landmarks. However, the value of islands distant from the shore as landmarks is debatable because the absence of features on a large body of water makes it challenging to accurately locate such a small target. Bats navigate using post sunset glows (Buchler and Childs, 1982), magnetic fields (Holland et al., 2006) and landscape features (Baerwald and Barclay, 2011; Hamilton, 2012). It is not impossible that known navigational mechanisms of bats would allow them to locate an island distant from the shore, but there are no data to support it.

That I did not find evidence of migration by *L. cinereus* is of particular note, given the strong evidence from other studies that this species is migratory (e.g. Cryan and Brown, 2007; Fleming and Eby, 2003). It seems unlikely that *L. cinereus* in Ontario do not migrate; a plausible alternative is that the species does migrate but is not detected by my methodology. *Lasiurus cinereus* is the largest of the three species in my study, and is adapted to relatively fast flight in open space (Van Zyll de Jong, 1985). This may reduce the difficulty of crossing the lakes, thereby decreasing the need for individuals to make use of stopover sites before crossing. Additionally, *L. cinereus* may fly at higher altitudes (Reynolds, 2006), reducing the detectability of migrating individuals due to the limited range of my microphones, as described above.

Monitoring acoustic activity is an effective for monitoring bat activity simultaneously across a number of locations, however a number of limitations must be considered. The limited detection range of available bat recorders is problematic, particularly in the case of bats flying outside the sampled altitudinal range. This appears to be the case for migrating bats, although few data are available (Fleming and Eby, 2003; Reynolds, 2006). Vertical microphone arrays can be used to address the altitudinal differentiation among species (Reynolds, 2006), although comes at the cost of increased methodological complexity.

Although I was able to sample more nights than many previous studies, sampling was further affected by low reliability of recorders. Multiple recorders within a site are recommended to increase accuracy of activity estimates and the detection of 'acoustically rare species', where there is a disparity between the likelihood of detection and actual abundance (Adams, 2013; Hayes, 1997). The low uptime of recorders in 2014 could have limited the assessment of activity in my study. Although uptime on Amherst Island in 2013 was a similar percentage to 2014, the overall greater number of recorders resulted in more active recorders per night, possibly leading to a more reliable measure of activity in that year.

Future studies could address this problem in part by improving the uptime and reliability of recorders. Autonomous full-spectrum recorders for bats are new technology, and those used in my study were first generation devices. Future studies could benefit from addressing reliability issues with recorders and power supplies. Additional data such as radar observations could be used to further elucidate the movements of bats crossing the lakes, and test whether they deliberately orient toward islands (Bonter et al., 2009; Fiedler and Henry, 2007; Kunz et al., 2007). Radio-telemetry of bats on islands would allow more detailed investigation of the behaviour of individuals encountered. In particular radio-telemetry could be used to identify the characteristics of any use of the islands as stopover sites, such as stopover duration and whether foraging occurs (McGuire et al., 2012). Monitoring acoustic activity at additional heights could be used to examine the presence of migrating bats beyond the range of detection in my study (Reynolds, 2006).

4.2 Bat conservation

The Great Lakes region has been identified to have high potential for wind-power development (Archer, 2005). Wind turbines are associated with mortality of migrating bats, although the mechanisms are not fully understood (Baerwald and Barclay, 2011;

Cryan and Barclay, 2009; Fiedler and Henry, 2007; Kunz et al., 2007). My results suggest the potential importance of Amherst Island to migrating bats, which could be of relevance to proposed wind-power development. I found limited evidence of stopover activity at Pelee Island, although logistical difficulties due to the greater distance to shore could make wind-power development on Pelee less likely.

4.3 Conclusions

1. I found evidence for migration and stopover use of Amherst Island by *L. borealis* and *P. subflavus*, suggesting that these species travel around the eastern end of Lake Ontario.

2. I found evidence of migration by *P. subflavus* at Pelee Island. This suggests migration across Lake Erie and supports the possibility of *P. subflavus* migrating longer distances than previously believed.

3. I found that summer activity of *L. borealis* and *P. subflavus* varied at different locations but did not result from a difference between island and mainland locations, suggesting other factors may affect the summer activity of these species.

4. Acoustic monitoring can be an effective means for investigating seasonal patterns in bat activity, but may not be appropriate for all species. Methods would benefit from the development of more reliable equipment and power sources.

5. Evidence of bat migration at islands and across the Great Lakes should be investigated further at an individual level. This is particularly important in the Great Lakes region where further wind-power development is likely.

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Google Earth, 2014a. Lakes Erie and Ontario. version 7.1.2.2041 42°54’42.50“ N 80°20’22.58” W.

Google Earth, 2014b. Amherst Island. version 7.1.2.2041 44°08’17.49“ N 76°42’38.44” W.

Google Earth, 2014c. Kingston area. version 7.1.2.2041 44°16’11.26“ N 76°54’14.29” W.

Google Earth, 2014d. Pelee Island. version 7.1.2.2041 41°46’37.37“ N 82°36’53.68” W.

Google Earth, 2014e. Pinery Provincial Park. version 7.1.2.2041 43°19’26.53“ N 81°57’09.77” W.

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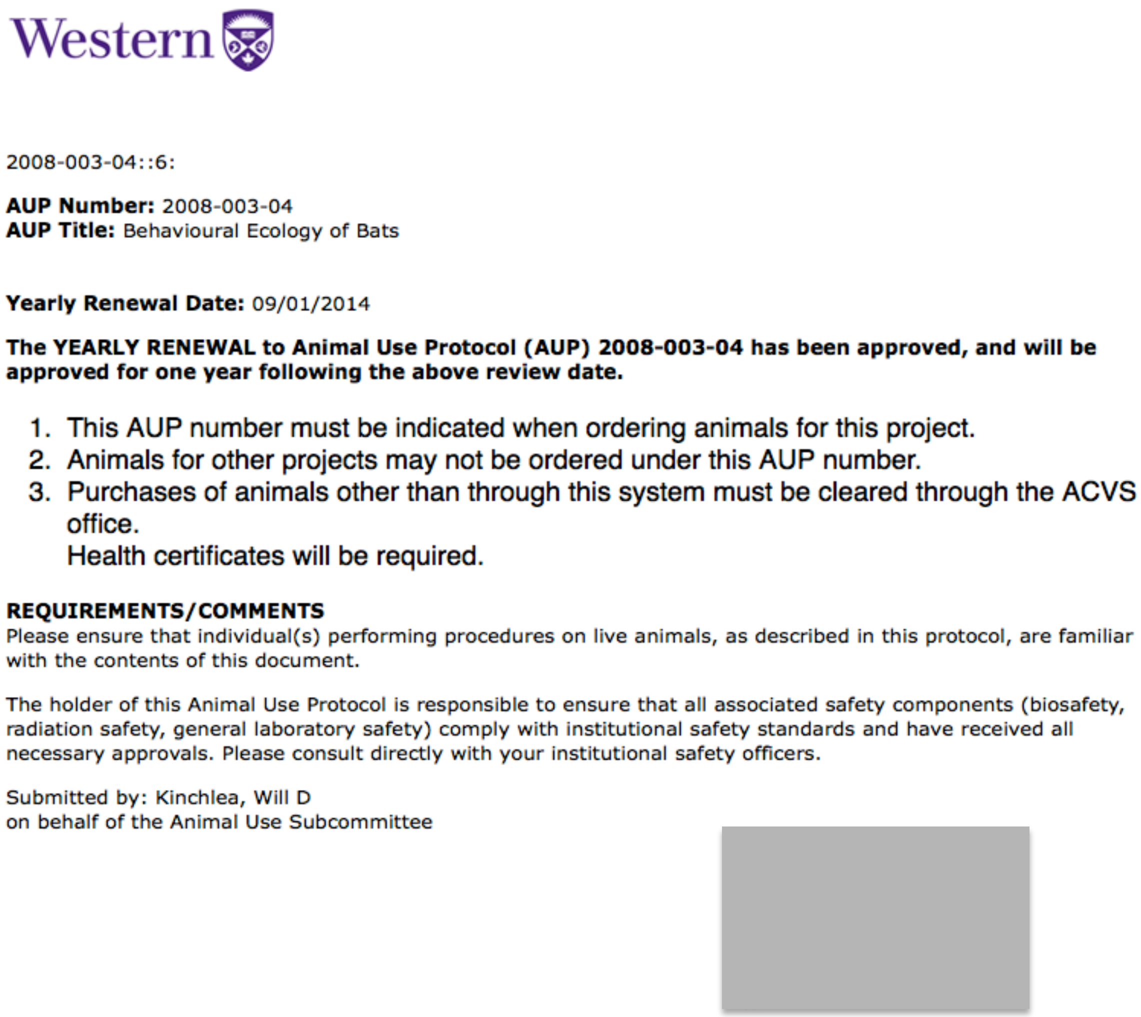
Appendices

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



Western

2008-003-04::6:

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

Yearly Renewal Date: 09/01/2014

The YEARLY RENEWAL to Animal Use Protocol (AUP) 2008-003-04 has been approved, and will be approved for one year following the above review date.

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: Kinchlea, Will D
on behalf of the Animal Use Subcommittee

[redacted]

Appendix II: Recorder sites

Figure A1: Map showing the locations of recorders in 2013 (all) and 2014 (A2, A3, A4 and A7) (Google Earth, 2014b).

Figure A2: Map showing the locations of recorders at Kingston in 2014 (Google Earth, 2014c).

Figure A3: Map showing the locations of recorders on Pelee Island in 2014 (Google Earth, 2014d).

Figure A4: Map showing the locations of recorders at Pinery Provincial Park in 2014 (Google Earth, 2014e).

Appendix III: Raw data from Amherst Island 2013

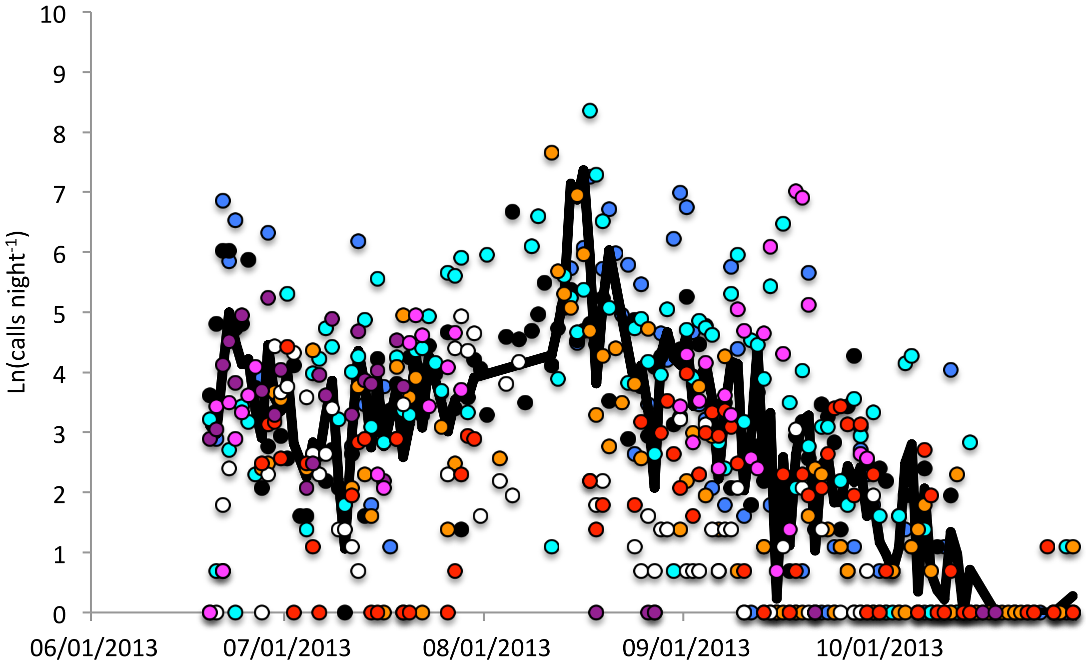


Figure A5: Ln calls night^{-1} of *L. borealis* recorded at individual recorders on Amherst Island in 2013. Colours represent recorders as follows: blue: 1, black: 2, teal: 3, orange: 4, white: 5, red: 6, purple: 7, magenta: 8. The black line represents a nightly mean activity of all active recorders.

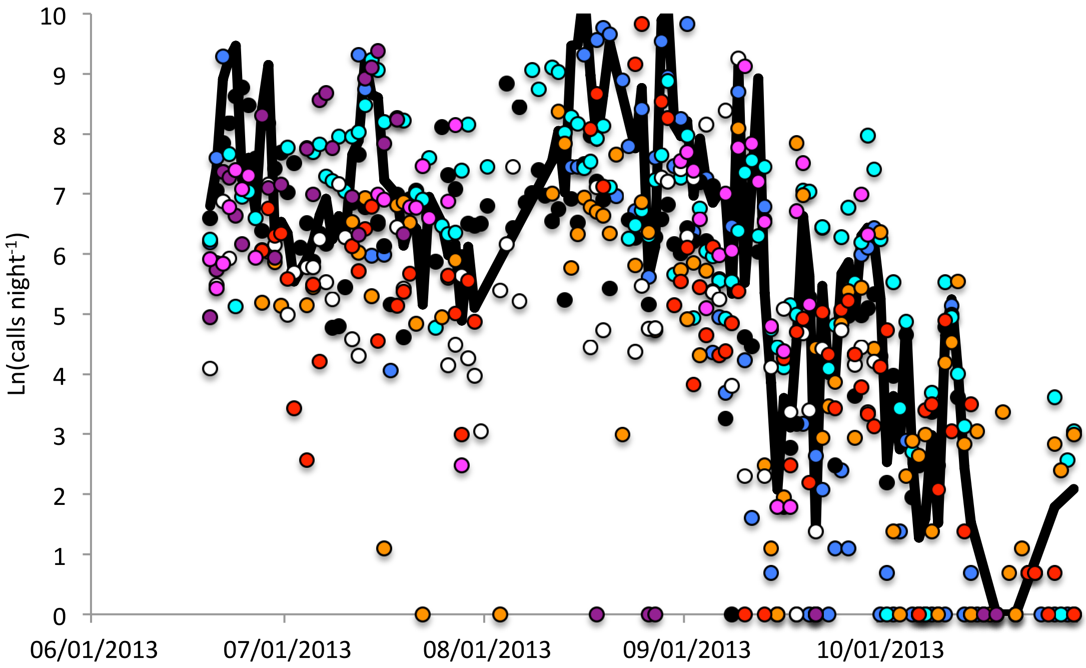


Figure A6: Ln calls night^{-1} of *L. cinereus* recorded at individual recorders on Amherst Island in 2013. Colours represent recorders as follows: blue: 1, black: 2, teal: 3, orange: 4, white: 5, red: 6, purple: 7, magenta: 8. The black line represents a nightly mean activity of all active recorders.

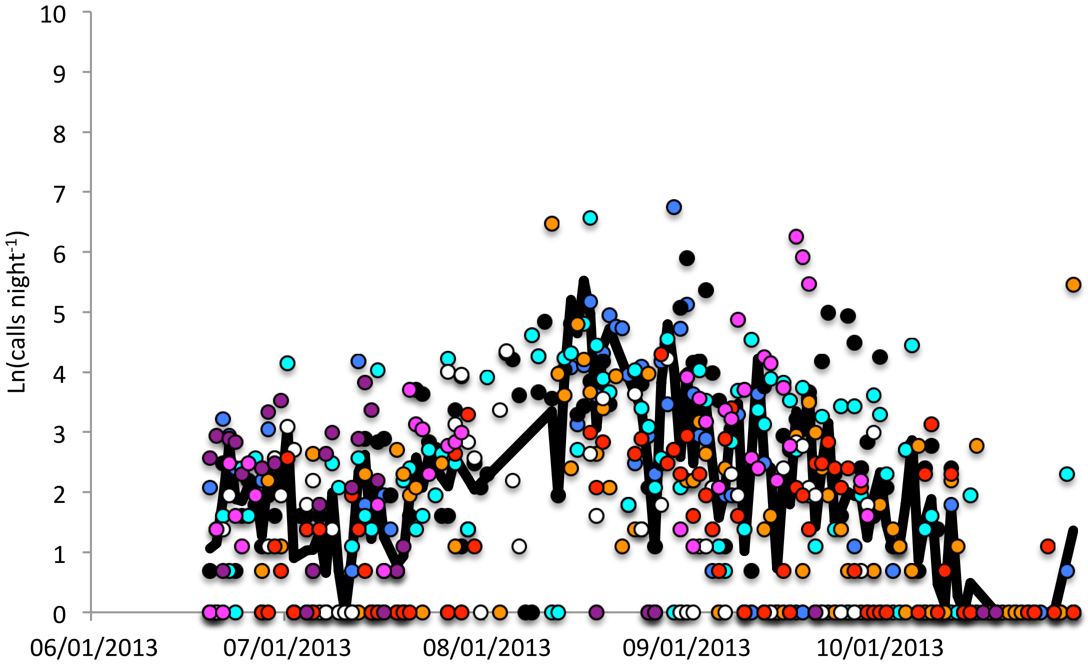


Figure A7: Ln calls night^{-1} of *P. subflavus* recorded at individual recorders on Amherst Island in 2013. Colours represent recorders as follows: blue: 1, black: 2, teal: 3, orange: 4, white: 5, red: 6, purple: 7, magenta: 8. The black line represents a nightly mean activity of all active recorders.

Appendix IV: Raw data from Amherst Island 2014

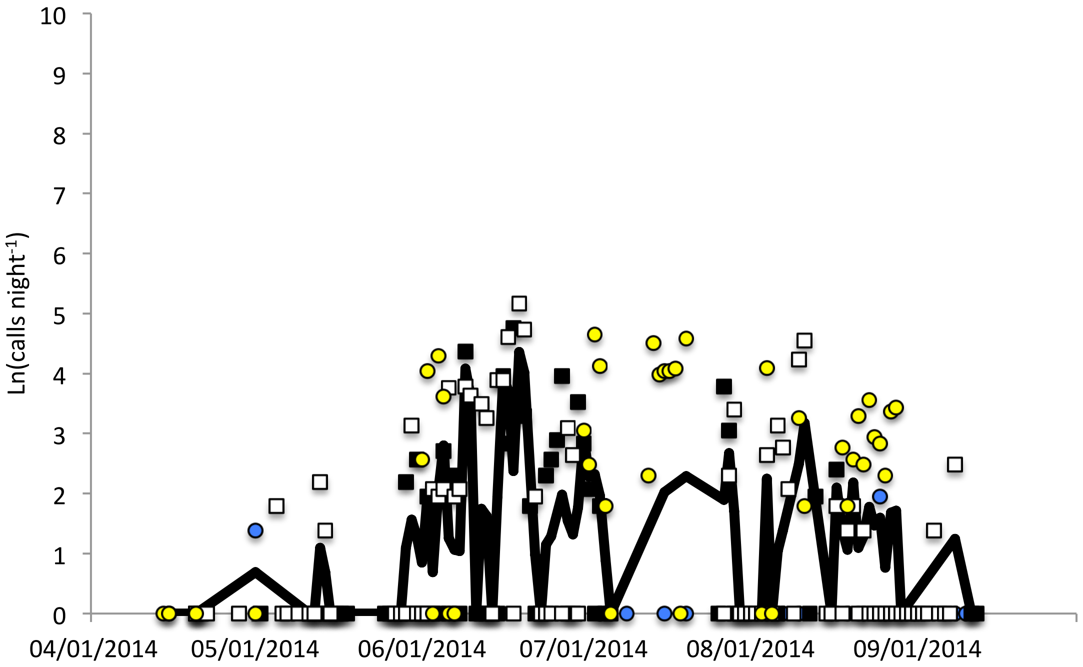


Figure A8: Ln calls night^{-1} of *L. borealis* recorded at individual recorders on Amherst Island in 2014. Colours represent recorders as follows: blue: A2, black: A3, white: A4, yellow: A7. The black line represents a nightly mean activity of all active recorders. Squares represent SM2 recorders and circles represent batcorders.

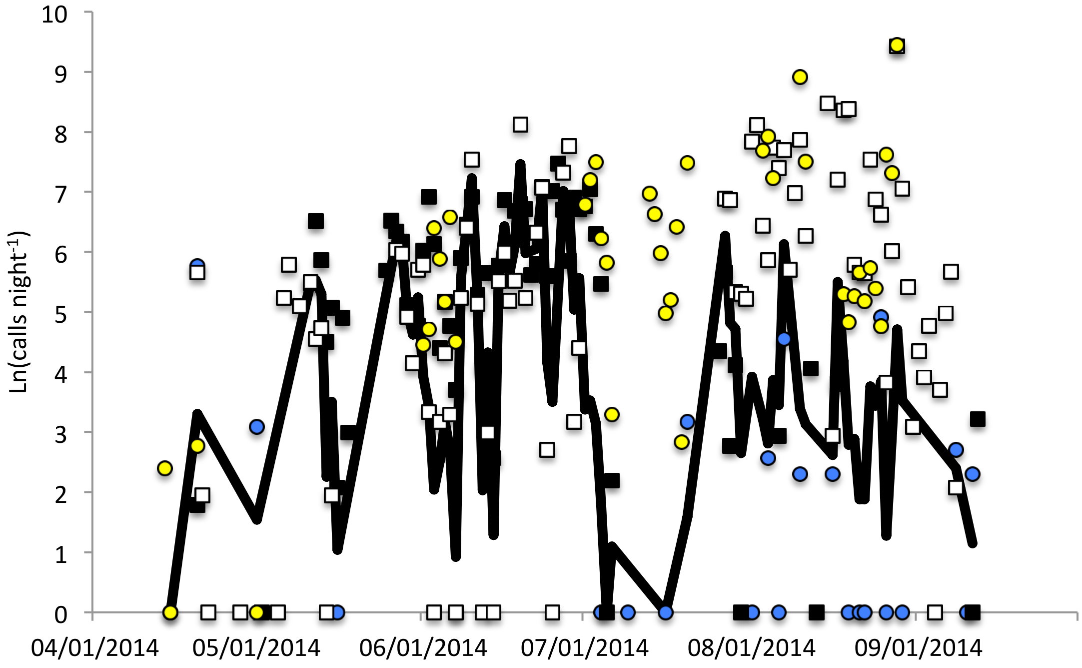


Figure A9: Ln calls night^{-1} of *L. cinereus* recorded at individual recorders on Amherst Island in 2014. Colours represent recorders as follows: blue: A2, black: A3, white: A4, yellow: A7. The black line represents a nightly mean activity of all active recorders. Squares represent SM2 recorders and circles represent batcorders.

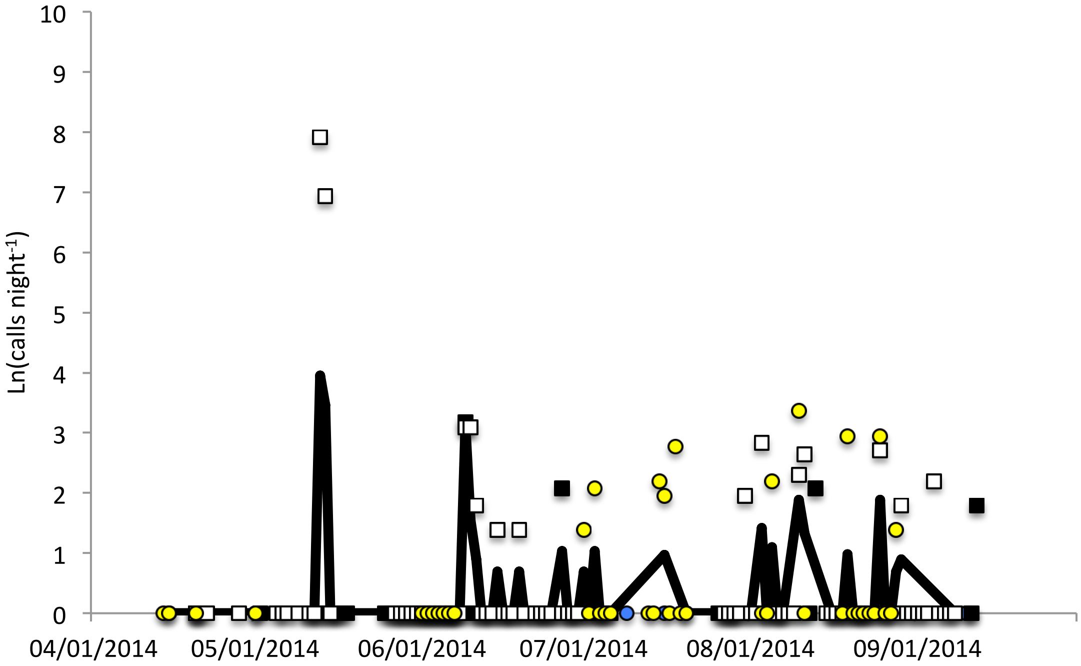


Figure A10: Ln calls night^{-1} of *P. subflavus* recorded at individual recorders on Amherst Island in 2014. Colours represent recorders as follows: blue: A2, black: A3, white: A4, yellow: A7. The black line represents a nightly mean activity of all active recorders. Squares represent SM2 recorders and circles represent batcorders.

Appendix V: Raw data from Kingston 2014

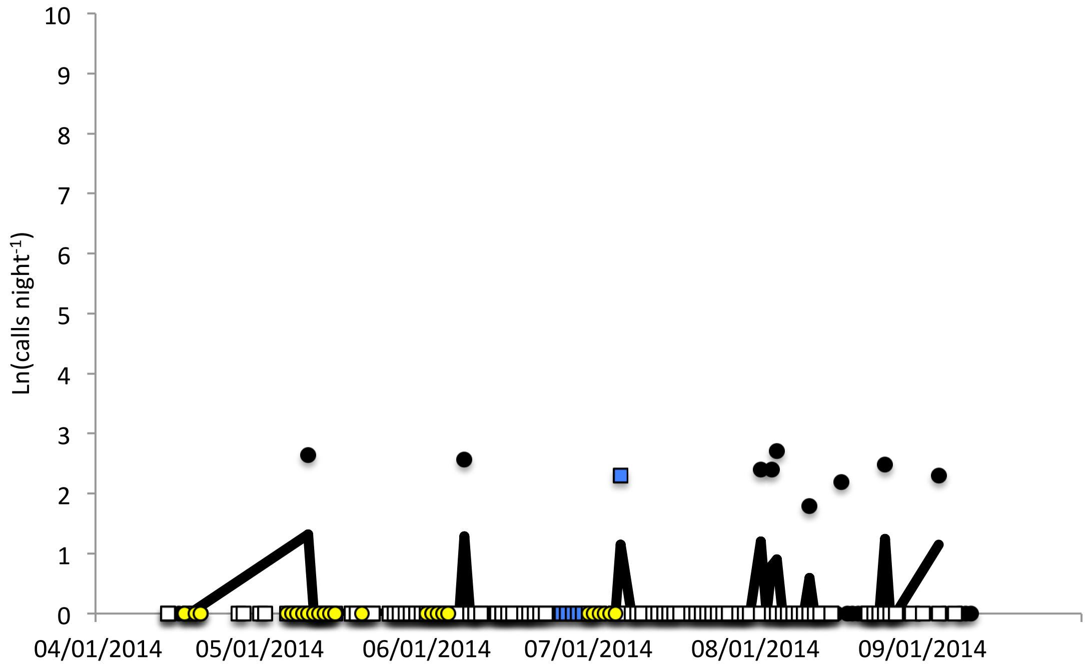


Figure A11: Ln calls night^{-1} of *L. borealis* recorded at individual recorders at Kingston in 2014. Colours represent recorders as follows: blue: BB, black: CG, white: PG, yellow: LM. The black line represents a nightly mean activity of all active recorders. Squares represent SM2 recorders and circles represent batcorders.

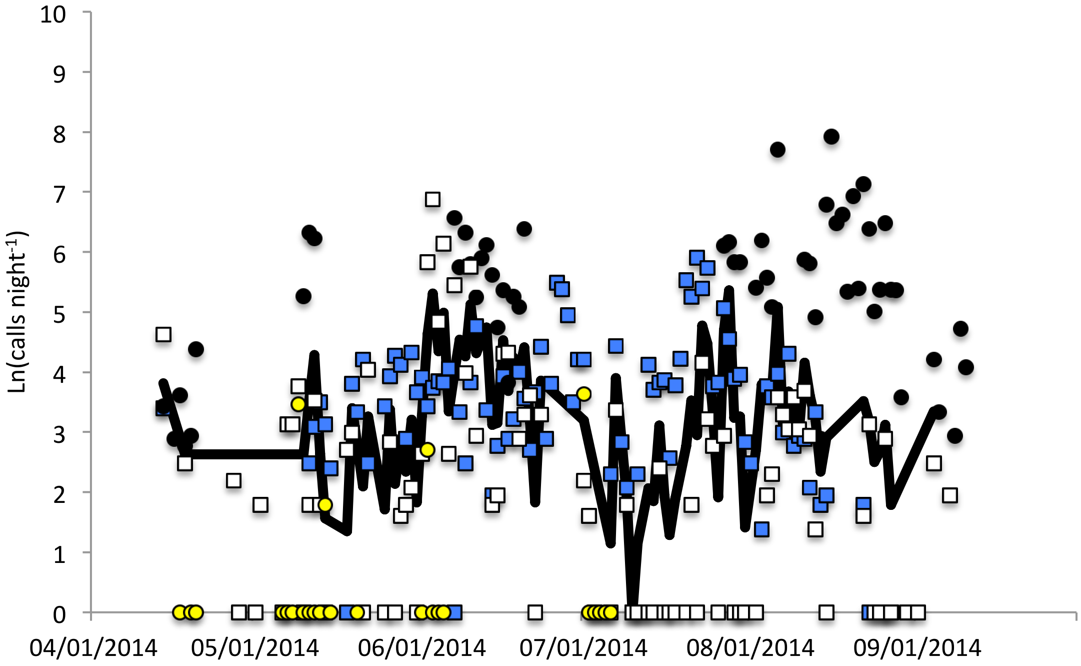


Figure A12: Ln calls night^{-1} of *L. cinereus* recorded at individual recorders at Kingston in 2014. Colours represent recorders as follows: blue: BB, black: CG, white: PG, yellow: LM. The black line represents a nightly mean activity of all active recorders. Squares represent SM2 recorders and circles represent batcorders.

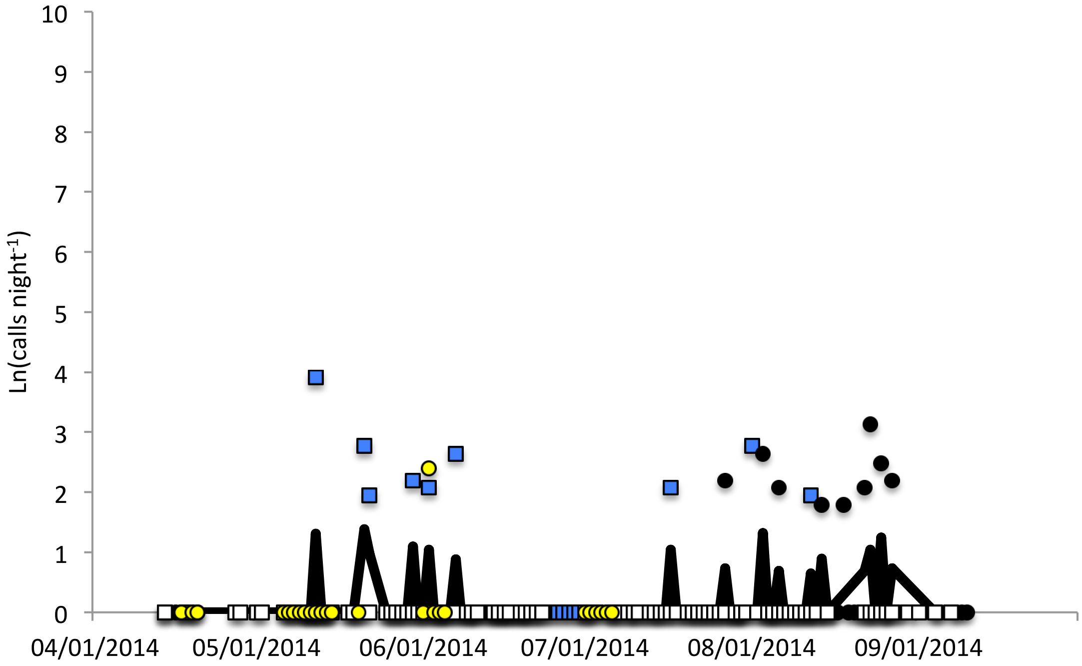


Figure A13: Ln calls night^{-1} of *P. subflavus* recorded at individual recorders at Kingston in 2014. Colours represent recorders as follows: blue: BB, black: CG, white: PG, yellow: LM. The black line represents a nightly mean activity of all active recorders. Squares represent SM2 recorders and circles represent batcorders.

Appendix VI: Raw data from Pelee Island 2014

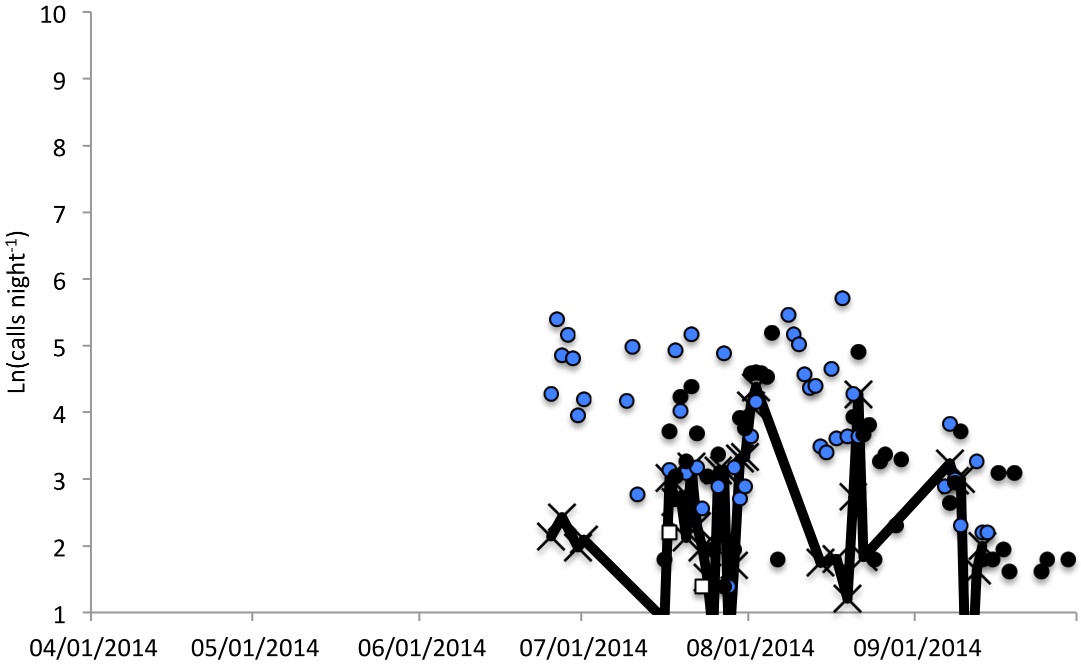


Figure A14: Ln calls night^{-1} of *L. borealis* recorded at individual recorders on Pelee Island in 2014. Colours represent recorders as follows: blue: JN, black: KG, white: NC. The black line represents a nightly mean activity of all active recorders. Squares represent SM2 recorders and circles represent batcorders.

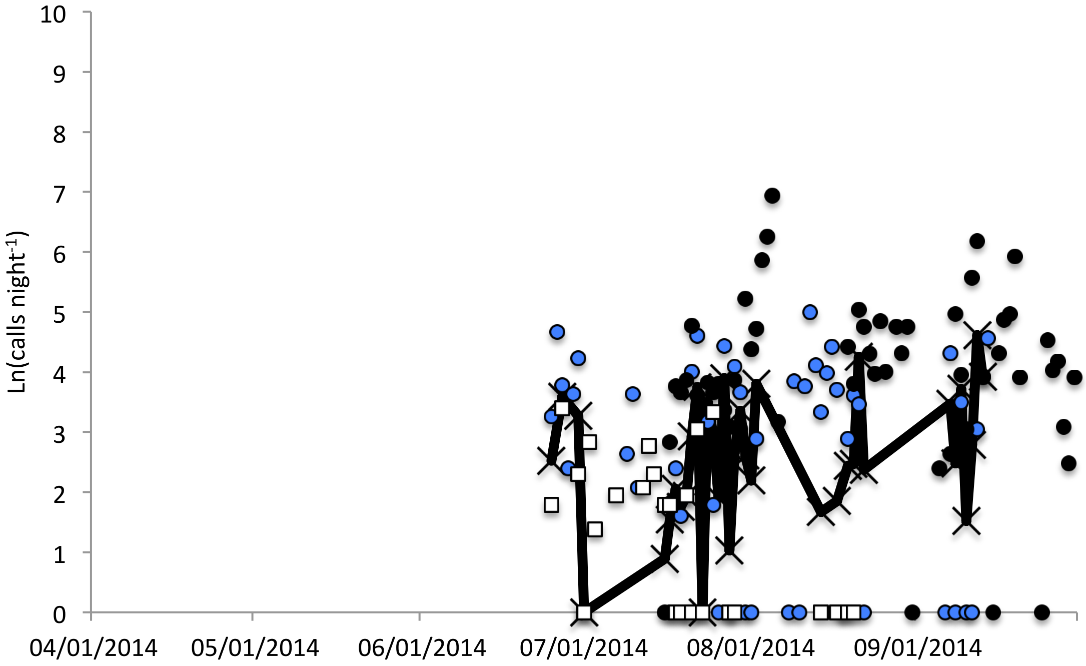


Figure A15: Ln calls night^{-1} of *L. cinereus* recorded at individual recorders on Pelee Island in 2014. Colours represent recorders as follows: blue: JN, black: KG, white: NC. The black line represents a nightly mean activity of all active recorders. Squares represent SM2 recorders and circles represent batcorders.

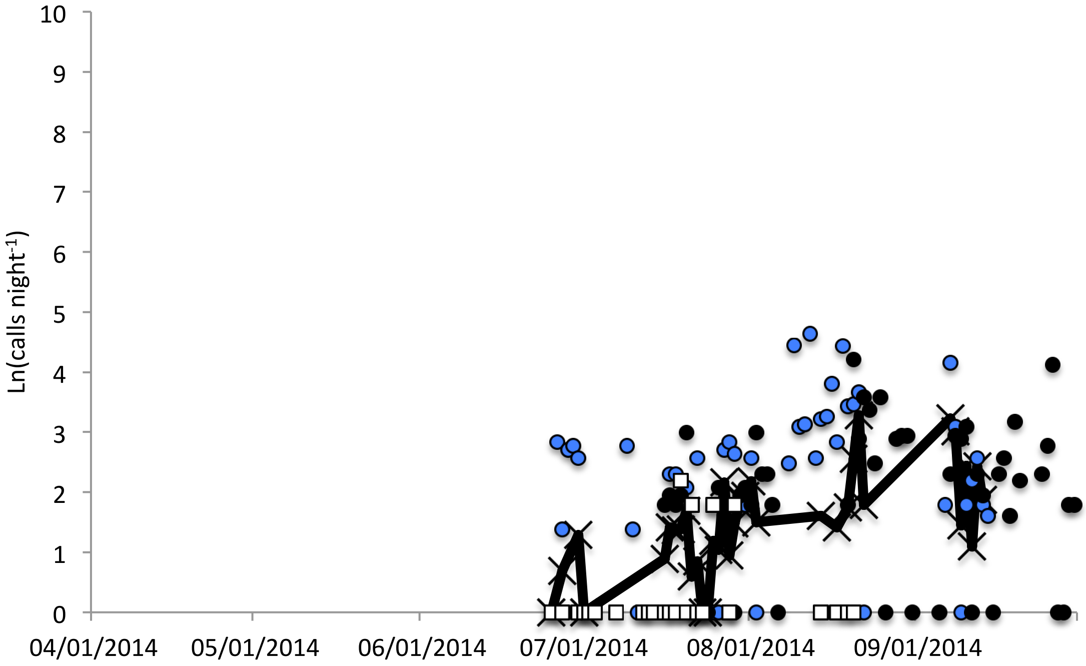


Figure A16: Ln calls night^{-1} of *P. subflavus* recorded at individual recorders on Pelee Island in 2014. Colours represent recorders as follows: blue: JN, black: KG, white: NC. The black line represents a nightly mean activity of all active recorders. Squares represent SM2 recorders and circles represent batcorders.

Appendix VII: Raw data from Pinery Provincial Park 2014

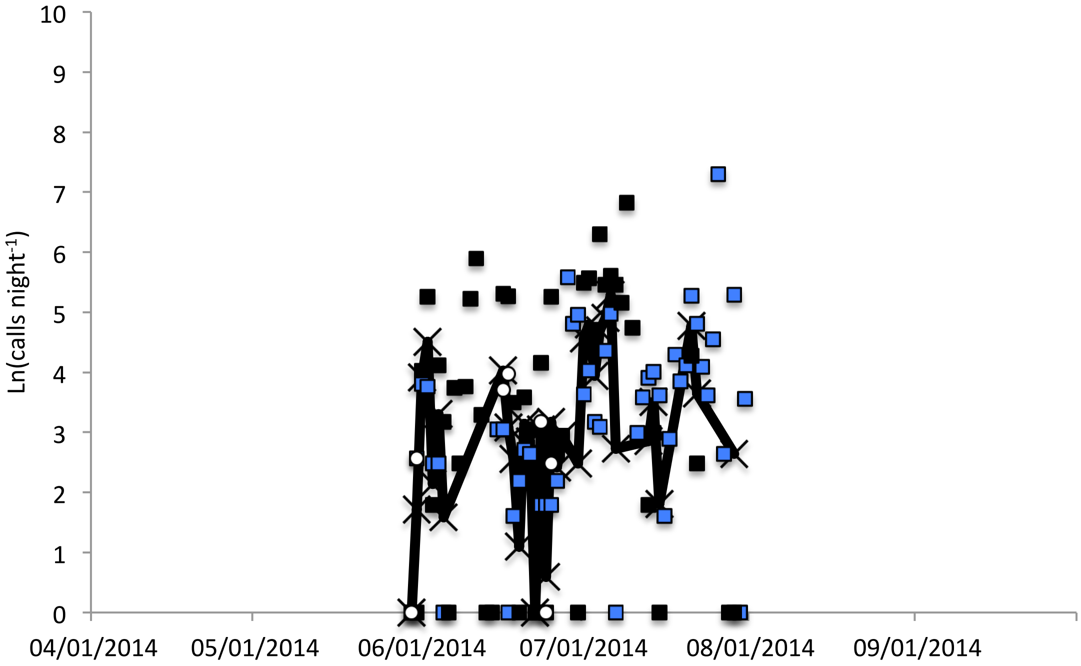


Figure A17: Ln calls night^{-1} of *L. borealis* recorded at individual recorders at Pinery Provincial Park in 2014. Colours represent recorders as follows: blue: BB, black: NB, white: SH. The black line represents a nightly mean activity of all active recorders. Squares represent SM2 recorders and circles represent batcorders.

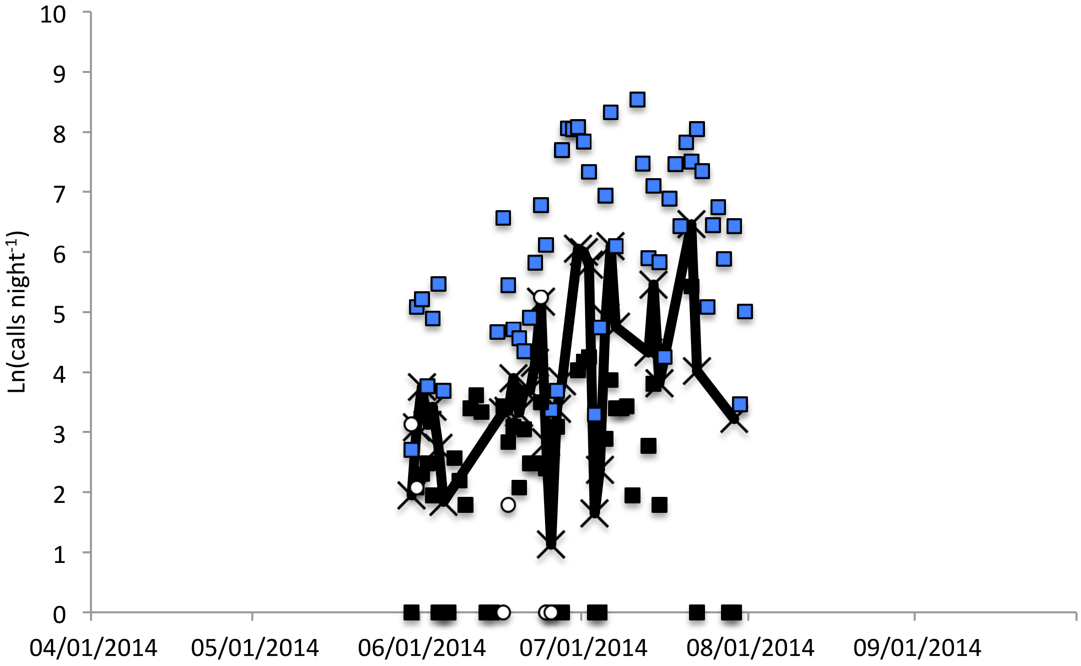


Figure A18: Ln calls night^{-1} of *L. cinereus* recorded at individual recorders at Pinery Provincial Park in 2014. Colours represent recorders as follows: blue: BB, black: NB, white: SH. The black line represents a nightly mean activity of all active recorders. Squares represent SM2 recorders and circles represent batcorders.

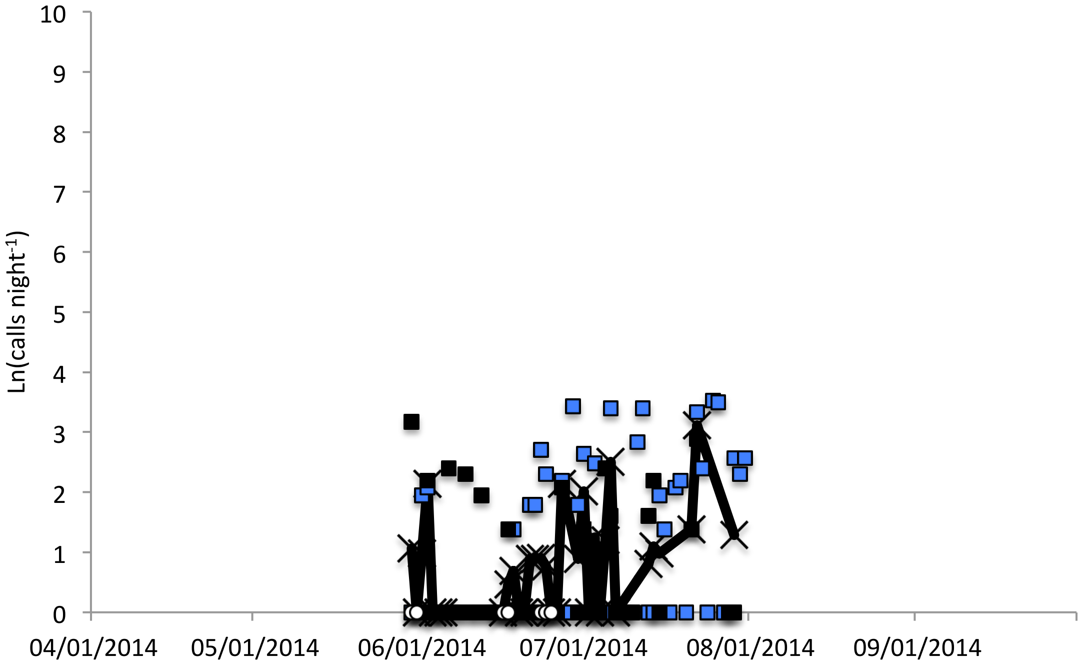


Figure A19: Ln calls night^{-1} of *P. subflavus* recorded at individual recorders at Pinery Provincial Park in 2014. Colours represent recorders as follows: blue: BB, black: NB, white: SH. The black line represents a nightly mean activity of all active recorders. Squares represent SM2 recorders and circles represent batcorders.

Appendix VIII: 2013 recorder comparison

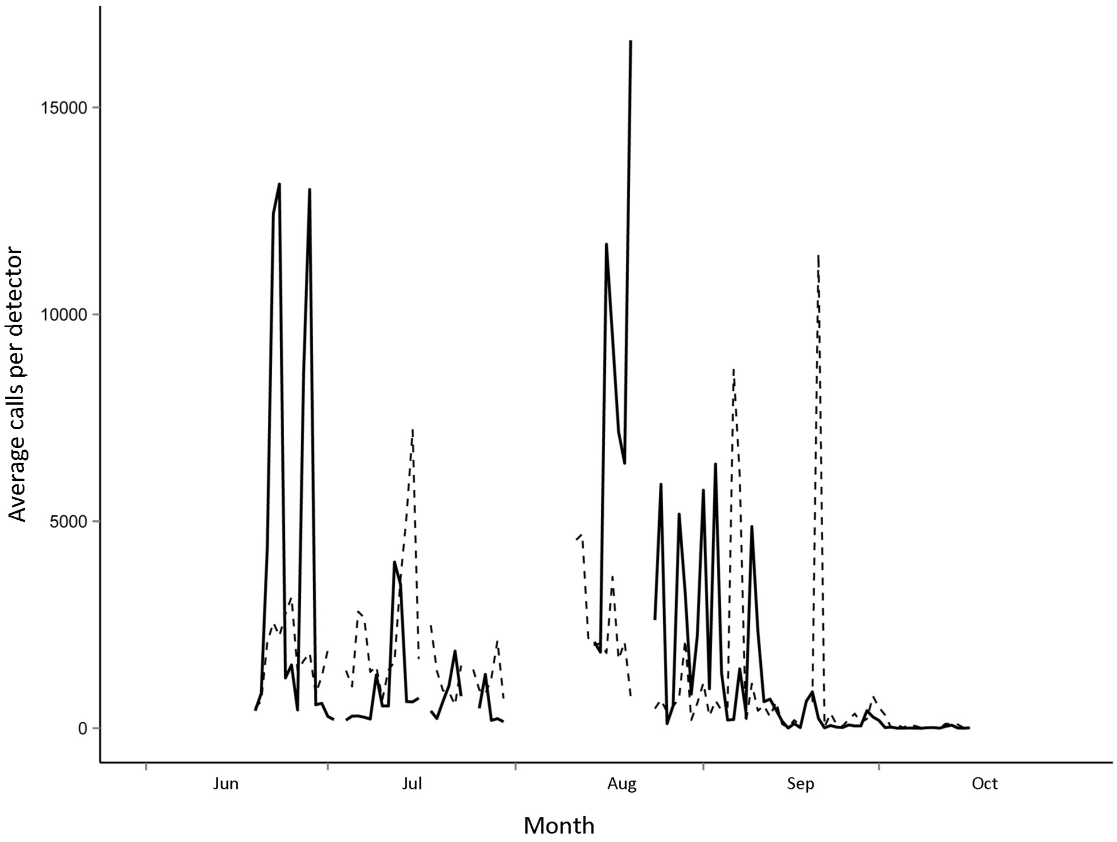


Figure A20: Total calls night^{-1} on Amherst Island in 2013 for recorders A1, A5, A6 and A8 (solid line) which were sampled only in 2013 and A2, A3, A4 and A7 (dashed line) which were sampled again in 2014.

Curriculum Vitae

Name:	Toby J. Thorne
Post-secondary Education and Degrees:	The University of Western Ontario London, Ontario, Canada 2013-2014 M.Sc
	University of Oxford Oxford, Oxfordshire, United Kingdom 2009-2012 B.A.
Honours and Awards:	Society of Graduate Students: Out of Province Bursary 2014 $500
	Department of Biology: Departmental Travel Award 2014 $250
Related Work Experience	Teaching Assistant The University of Western Ontario 2013-2014

Presentations:

Thorne T., Fenton B. 2014. Bat migration: the role islands in the Great Lakes. 44th Annual Symposion of the North American Society for Bat Research, Albany, New York, U.S.A.

Thorne T., Fenton B. 2014. The Use of Great Lakes Islands by Migrating Bats. 44th Ontario Ecology, Ethology, and Evolution Colloquium, University of Guelph, Guelph, Canada.

Thorne T. 2014. Bats and Wind Power, An Issue on the Great Lakes. Earth Day Colloquim 2014, University of Western Ontario, London, Canada.

Thorne T., Fenton B. 2013. The Use of Great Lakes Islands by Migrating Bats. Biology Graduate Research Forum, University of Western Ontario, London, Canada. (Poster Presentation).

Thorne T. 2013. Social Networks in Bats. Bambi Research Seminar, Smithsonian Tropical Research Institute, Barro Colorado Island, Panama.

Thorne T. 2012. Social Networks in Bats. Bat Conservation Trust National Conference, York, UK.