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Bioacoustic Monitoring of Nocturnal Songbird Migration in a Southern Great Lakes Ecosystem

Claire Elizabaeth Sanders
University of Windsor

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**BIOACOUSTIC MONITORING OF NOCTURNAL SONGBIRD MIGRATION
IN A SOUTHERN GREAT LAKES ECOSYSTEM**

By

CLAIRE ELIZABETH SANDERS

A Thesis

Submitted to the Faculty of Graduate Studies
through Biological Sciences
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the Degree of Master of Science at the
University of Windsor

Windsor, Ontario, Canada

2013

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Bioacoustic monitoring of nocturnal songbird migration in a southern Great Lakes ecosystem

By

Claire E. Sanders

APPROVED BY:

Dr. Aaron Fisk, External Reader
Department of Earth & Environmental Sciences, GLIER

Dr. Oliver Love, Internal Reader
Department of Biological Sciences

Dr. Daniel Mennill, Advisor
Department of Biological Sciences

Dr. Lisa Porter, Chair of Defence
Department of Biological Sciences

July 23, 2013

DECLARATION OF CO-AUTHORSHIP

I hereby declare that this thesis incorporates material that is the result of joint research. I am the sole author of chapters 1 and 4, and the principal author of data chapters 2 and 3. The research described in both chapters 2 and 3 was conducted under the supervision of Dr. Dan Mennill, who contributed input on the design of the research, the analysis of data, and the writing of the manuscripts, as well as financial and logistical support; he shares authorship on both chapters 2 and 3.

I am aware of the University of Windsor Senate Policy on Authorship and I certify that I have properly acknowledged the contribution of other researchers to my thesis, and have obtained written permission from my co-author to include the above material in my thesis. I certify that, with the above qualification, this thesis, and the research to which it refers, is the product of my own work.

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I declare that this is a true copy of my thesis, including any final revisions, as approved by my thesis committee and the Graduate Studies office, and that this thesis has not been submitted for a higher degree to any other University or Institution.

ABSTRACT

Many species of birds produce short vocalizations during nocturnal migration. My thesis uses bioacoustic monitoring of these night flight calls to study bird migration through a southern Great Lakes ecosystem. I deployed recording devices around western Lake Erie during spring and fall migrations. Analysis of thousands of hours of recordings revealed that night flight calls accurately predicted both the magnitude of migration, as well as the timing of migrant passage, as assessed by banding. The first arrival dates for 48 species of migratory birds were significantly earlier on Pelee Island than on mainland Ontario in the spring. More flight calls were detected over Pelee Island than over mainland comparison sites. These results suggest that many birds cross Lake Erie in spring and fall, and that islands are important for migratory birds. This research provides insight into the use of acoustics for monitoring birds in active migration.

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TABLE OF CONTENTS

DECLARATION OF CO-AUTHORSHIP	III
ABSTRACT.....	IV
ACKNOWLEDGEMENTS	V
LIST OF TABLES	IX
LIST OF FIGURES.....	X
LIST OF APPENDICES	XI
CHAPTER 1 - GENERAL INTRODUCTION	1
BIRD MIGRATION	2
MIGRATION MONITORING TECHNIQUES.....	3
NIGHT FLIGHT CALLS	5
Identification of species based on night flight calls	6
Function of night flight calls.....	7
MIGRATION MONITORING AND ECOLOGICAL BARRIERS	8
Bird migration in a western Lake Erie ecosystem	9
THESIS OBJECTIVES	10
LITERATURE CITED	12
CHAPTER 2 - ACOUSTIC MONITORING OF NOCTURNALLY MIGRATING BIRDS ACCURATELY PREDICTS THE TIMING AND MAGNITUDE OF MIGRATION THROUGH THE GREAT LAKES	18
CHAPTER SUMMARY	19
INTRODUCTION.....	21
METHODS.....	24
General field methods and study location	24
Acoustic recordings.....	25
Analysis of acoustic recordings	26
Diurnal migration monitoring data	28
Statistical analysis and sample size	29

RESULTS	30
Magnitude of migration	31
Timing of migration	31
Correlations within number of detections by week per species	32
DISCUSSION	33
LITERATURE CITED	40
CHAPTER 3 - ACOUSTIC MONITORING OF MIGRANT BIRDS REVEALS THE IMPORTANCE OF ISLAND GEOGRAPHY IN THE WESTERN BASIN OF LAKE ERIE	56
CHAPTER SUMMARY	57
INTRODUCTION	58
METHODS.....	62
General field methods and study location	62
Acoustic recordings.....	62
Analysis of acoustic recordings	63
Banding data	64
Statistical analysis and sample size	65
RESULTS	65
Number of migrants detected on mainland versus island	66
Species detected on mainland versus island	67
Date of arrival	68
DISCUSSION	69
LITERATURE CITED	74
CHAPTER 4 - THESIS SUMMARY	82
LITERATURE CITED	88
VITA AUCTORIS.....	90

LIST OF TABLES

Table 1.1. Strengths and limitations of five techniques used in migration monitoring.....16

Table 2.1. Comparison of the timing of migration as assessed through mist net data and night flight call acoustic data44

Table 3.1. Number of acoustic and mist net detections in spring and fall at mainland and island stations.....78

LIST OF FIGURES

Figure 1.1. Examples of night flight calls from recordings collected in spring and fall migrations of 2012.17

Figure 2.1. Map of Essex County, Ontario, Canada shows the seven acoustic recording locations and the two banding stations.45

Figure 2.2. Acoustic detections of nocturnal migrants can predict the number of birds of the same species or species-group mist-netted over the migration season.....46

Figure 2.3. Acoustic monitoring of nocturnal flight calls and banding show similar timing of migrant passage in spring and fall.47

Figure 2.4. Numbers of detections using acoustics and banding by week of spring and fall migration.....48

Figure 3.1. Map of Essex County, Ontario, Canada shows the seven acoustic recording locations and the three banding stations.....80

Figure 3.2. Average first acoustic detection dates for migrants crossing the western basin of Lake Erie81

LIST OF APPENDICES

Appendix 2.1. Species classification chart.....	49
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CHAPTER 1

GENERAL INTRODUCTION

BIRD MIGRATION

North America's migratory songbirds undergo one of the most spectacular animal migrations in the world. In the spring and fall, billions of individuals representing hundreds of species make the biannual journey between wintering areas in the United States, Mexico, Central America, and South America to breeding areas in Canada and the United States (Newton 2007). Each individual journey can be in excess of 4000 kilometers, with birds using numerous stopover locations along the way (Elphick 2007, Stutchbury et al. 2009). In many taxa—including warblers, thrushes, and sparrows—most of this movement takes place at night (Able 1973).

With a seasonal change in photoperiod, most songbirds undergo a significant shift in behaviour and physiology each spring and fall; instead of sleeping, they migrate for up to seven hours per night (Rattenborg et al. 2004). Species that are typically diurnal throughout the rest of the year may benefit by migrating at night for many reasons. Nocturnal migration may be associated with reduced predation pressure, cooler and calmer weather conditions, maximized day time foraging opportunities at stopover locations, and the use of stellar cues for orientation (Kerlinger 1995, Allerstam 2009, Muhkin et al. 2009). There is consensus that monitoring the migration *en route* can provide a wealth of critical information for studying population trends in birds. The shift to nocturnal behaviour, however, presents the obvious problem that migrants cannot be observed directly during active migration. Therefore, researchers have endeavoured to develop techniques to accurately count and monitor the behaviour of migrants at stopover locations (Dunn 2005, Milliken 2005). My thesis focuses on acoustic monitoring as a new approach for studying the nocturnal migration of birds through Essex County, Ontario.

MIGRATION MONITORING TECHNIQUES

The merits of monitoring migratory birds *en route* are twofold. First, monitoring birds *en route* allows researchers to collect data on populations of neotropical migrants that are difficult to assess on their northern breeding grounds through programs such as the Breeding Bird Survey, due to both cost and inaccessibility (Dunn 2005). Second, monitoring birds *en route* helps us to understand the seasonal concentrations and movements during migration, providing insight on what habitat and geographic features may be particularly important for migratory birds (Hussell and Ralph 2005, Francis et al. 2009). There are at least five different techniques used to monitor avian migration *en route*: (1) diurnal visual counts of migrants; (2) diurnal mist netting of migrants; (3) radar monitoring of migratory flocks; (4) geolocators and satellite transmitters that track the routes of individual migrants; (5) nocturnal moon watching to detect passing birds; and (6) nocturnal acoustic recordings. Each of these techniques has advantages and limitations, which I have summarized in Table 1.1.

For many years, moon watching was a valuable technique for studying the directionality and intensity of a migration event, facilitating counts of the number of birds that pass between the observer and the moon. This simple technique is useful on nights when the moon is bright and birds are traveling under 1km in altitude (Liechti et al. 1995). More recently, radar technologies have been recognized as an important tool for collecting data on the movement patterns of flocks of nocturnal animals in flight (Chilson et al. 2012). While general trends about temporal and geographic patterns and bird concentrations can be shown through moon watching and radar studies, the major limitation of these techniques is that species cannot be identified in either approach.

To date, diurnal migration monitoring stations remain the most widespread and most effective technique for observing patterns of migration at small geographic scales as well as to track long-term population trends of migratory birds (Dunn 2005). Most monitoring stations use mist nets to capture birds, and then apply numbered aluminum leg bands, to tally migrants while they are feeding during the day at stopover locations. In Canada, the development of migration monitoring using mist netting and bird banding programs occurred in the Lake Erie region over 60 years ago (Francis et al. 2009). Bird banding contributes counts of individual animals and produces tremendous information when banded birds are re-captured in other locations. Additionally, when banding is conducted with consistent effort from year-to-year, data can provide long-term population trends (Hussell and Ralph 2005). Limitations of bird banding include a habitat bias, since only birds in a particular habitat will be sampled with mist nets (Francis et al. 2009); a risk to birds that are occasionally injured by handling or suffer handling stress (Spotswood et al. 2012); and the fact that banding requires significant investment of time from skilled mist net operators and bird banders.

My thesis focuses on acoustic monitoring of night flight calls as a migration monitoring strategy. In contrast to the aforementioned techniques, acoustic monitoring has received little empirical attention. The primary advantage of monitoring the calls produced by birds on migration is that it provides species-specific information about the birds that are aloft in active migration. Acoustic monitoring of diurnal animal movements is an established technique (e.g. Mennill et al. 2006; Mennill et al. 2012) and the development of improved recording technology and sound analysis software provides researchers with tremendous application opportunities for monitoring animal communities (Blumstein et al. 2011). Acoustic monitoring has been used to study many animal taxa to understand animal behaviour, and also to determine

presence/absence and gain insight into communities of animals that are otherwise difficult to monitor such as marine animals, cryptic animals, species at risk, and nocturnal animals (e.g. Celis-Murillo 2009, Marques et al. 2013). Development of modern recording devices with high storage capacity and sensitive microphones has allowed tremendous growth in this field in the last decade (Mennill 2011). My thesis explores the idea that acoustic monitoring of nocturnal migrant birds can provide significant insight into the magnitude, timing, distribution, and migration strategy through an important region where birds concentrate seasonally.

NIGHT FLIGHT CALLS

Many migrating birds routinely produce short flight calls as they fly at night and preliminary research suggests that acoustic monitoring of nocturnal migrants could play an important role in monitoring bird migration (Evans and Rosenberg 2000, Farnsworth 2005). Although the form and function of these vocalizations are poorly understood, night flight calls offer a tool for tracking migratory birds. These vocalizations are characteristically short, typically between 50-200ms, ranging in frequency from 1-11 kHz (Farnsworth 2007; Evans and O'Brien 2002, see Figure 1.1). Many songbirds produce night flight calls including warblers (family Parulidae), thrushes (family Turdidae), sparrows (family Passeridae), cuckoos (family Cuculidae), and some buntings (family Emberizidae) as well as some non-passerines including herons (family Pelecaniformes), waterfowl (family Anatidae), and some shorebirds (order Charadriiformes; Evans and O'Brien 2002, Farnsworth and Russell 2005, Lanzone et al. 2009). Farnsworth and Lovette (2005) examined the nocturnal flight calls across the warblers (family Parulidae), with reference to differences in duration, frequency, and modulation of calls between species. They concluded that neither body mass nor bill length explained this variation and that atmospheric

and ecological conditions may have ultimately played a role in selection of call characteristics through acoustic adaptation (Farnsworth and Lovette 2005).

Observational studies of night flight calls of nocturnal migrants began as early as the 1900's, with the earliest recordings dating to the 1950's (Evans 2005). Owing to recent advances in recording technology, there has been a resurgence in interest in this subject both by the scientific community and by the birdwatching community. While we still have much to learn about the function of night flight calls, there is agreement that further study of this phenomenon could lead to a shift in approaches for monitoring nocturnally migrating songbirds (Evans 2005, Farnsworth 2005). Additionally, studying these nocturnal vocalizations may provide important clues about social information sharing and acoustic cues related to the migratory journey.

Identification of species based on night flight calls

In several bird species, night flight calls are the same as their diurnal "call" notes, though this is not typically the case; in many species, the night flight call has different bioacoustic properties than any daytime call (Farnsworth 2005). Traditionally, most night flight calling species have been identified from recordings made near dawn, when visual identity of the species can be confirmed (Evans and O'Brien 2002). Recent research has identified a new technique to elicit calls from captive birds by holding migratory birds in temporary captivity in a specialized cage, and playing back calls to them (Lanzone et al. 2009). This technique has played an important role in providing a "Rosetta Stone" for distinguishing different species night flight calls (Lanzone et al. 2009), although more research on individual variation and geographic variation in night flight calls is badly needed. Currently, up to 70 individual species can be

identified by their night flight call or divided into 8 “species-groups” that each includes between 2 to 8 species (Evans and Rosenberg 2000). In Chapter 2, I present a classification chart with spectrographic examples from my own recordings (see Chapter 2, Appendix 1).

Function of night flight calls

It is commonly believed that nocturnal flight calls are associated with *Zugunruhe*—migratory restlessness behaviour that is characterized by increased nocturnal fluttering in caged migrant birds (Hamilton 1962, Farnsworth 2005). Whether *Zugunruhe* serves a communication function, perhaps to motivate nearby conspecific animals to fly (Tyler 1916), or whether it is an epiphenomenon of increasing hormone levels, remains controversial. Hamilton (1962) recorded *Zugunruhe* of caged Bobolinks (*Dolichonyx oryzivorus*) during the migratory season and noted that the night flight calls began at the same time the fluttering behaviour began. He suggested the nocturnal calls indicated an increasingly intense excitement associated with a sustained fluttering behaviour in caged migrants, and he realized that this activity stimulated the same behaviour in conspecifics. Using playbacks of flight calls, Hamilton (1962) was able to induce fluttering responses from birds if they had previously shown some kind of migratory readiness. This result suggested that flight calls might motivate grounded birds to join a flock of migrants aloft (Hamilton 1962). Whatever the case, the established interest in *Zugunruhe* indicates that ornithologists have long known that migratory birds produce short vocalizations, although the function of these vocalizations remains an open question.

A combination of moon watching and radar studies have shown that songbirds engage in grouping behaviours during nocturnal migration (Newton 2007), as do observations of diurnal mixed-species flocks foraging at stopover sites (Hobson and van Wilgenburg 2006). Larkin and Szafoni (2008) characterized the behaviour of daytime mixed-species flocks and the more loosely

associated flocks seen during migration at night. Through radar studies, they showed that birds could be up to 200 metres apart and still be actively traveling together—in the same direction, at the same altitude, and at the same speed. The major benefit to migrating in flocks may be the collective effort in navigation (Newton 2007) and night flight calls may play a considerable role in maintaining flock cohesion and communicating directional information when visual signals are absent (Farnsworth 2005). Moore (1990) also suggested that nocturnal flight calls help to aid flock formation as dawn approaches, a behaviour that is suggested to assist in predator avoidance and facilitate foraging as the nocturnal migration ends each night (Hobson and van Wilgenburg 2006).

MIGRATION STRATEGIES AND ECOLOGICAL BARRIERS

Optimal migration strategies and behavioural decisions made by birds in migration are a well-studied area of ornithology (Moore and Kerlinger 1987, Alerstam 2001, Spina 2011). Using geolocators, Stutchbury et al. (2009) revealed that spring migration occurs two to six times faster than fall migration in Purple Martins (*Progne subis*) and Wood Thrushes (*Hylocichla mustelina*). The phenomenon of a rapid spring migration and a protracted fall migration, with longer periods of time spent at stopover locations, has been described in many songbird species including American Redstarts (*Setophaga ruticilla*; Morris and Glasgow 2001) and Wilson's Warblers (*Cardellina pusilla*; Yong et al. 1998). It is commonly believed that this is because birds benefit from arriving quickly on the breeding grounds in a timely manner as soon as the spring weather permits, or else they risk not being able to acquire a high quality territory (Kokko 1999).

Monitoring migrants *en route* can provide us with population indices for hundreds of neotropical bird species, and can also help us to understand migrant movements at a smaller

geographical scale. Identifying preferred routes and seasonal timing of migrants has been identified as a priority for further research (Faaborg et al. 2010). For example, migratory birds are able to make non-stop flights consisting of hundreds of kilometres, yet there are numerous factors that might cause them to select longer routes comprised of multiple short flights, rather than crossing an ecological barrier, such as a lake, desert, or mountain range (Allerstam 2001). Recent studies have shown carryover effects of the cost of migration, where the physical condition of a migrant arriving on its breeding ground will impact its ability to obtain a territory in high quality habitat (e.g. Garamzegi et al. 2008). A successful spring migratory journey reflects a balance between speed of migration and maintaining body condition, so that a migratory bird arrives on its breeding ground in sufficiently good physical condition to sing at a sufficiently high rate to maintain a high quality territory and attract a mate (Nystrom 1997). Therefore, the routes and the behaviour of migratory birds is influenced by many factors, and increased monitoring of migrants *en route* can facilitate a better understanding of migration ecology.

Bird migration in a western Lake Erie ecosystem

Essex County stands at the confluence of two major migratory flyways: the Mississippi flyway and the Atlantic flyway. Several sites within Essex County, including Point Pelee, Pelee Island, and other locations within the western basin of Lake Erie, have long been heralded by bird watchers for their seasonal concentrations of migratory birds. Yet, much of what is known about migrant movement through the area is anecdotal and based on daytime observations collected largely during spring migration. The spring migration occurs from approximately April 1 until June 10 of each year and the fall migration from approximately August 1 until November 15. During this time, millions of individuals representing hundreds of different species pass through the region (Lincoln et al. 1998). The green spaces within a few kilometers of the

shoreline on either side of the lake provide critical stopover habitat for refuelling (Bonter et al. 2009) and are home to several longstanding migration monitoring stations.

Given their size, the Great Lakes may represent an ecological migration barrier that can affect the migratory routes of songbirds (Diehl et al. 2003, Deutschlander and Muheim 2009) and possibly even survival during migration. Studies using Doppler radar technology to monitor migration over the Great Lakes explored ecological barrier avoidance (Diehl et al. 2003), as well as habitat use by migrant birds and stopover ecology in the region (Bonter et al. 2009). Radar data demonstrate that there are likely seasonal and geographical differences in the distribution of migrants in the western basin (Diehl et al. 2003), yet little is known about the species-specific nature of these differences. Acoustic monitoring has the potential to expand our understanding of bird movements through this important migratory flyway by distinguishing individual species.

THESIS OBJECTIVES

The central goal of my Master's thesis is to use nocturnal acoustic recordings to expand our understanding of avian migration along a major flyway in southwestern Ontario. My research evaluates nocturnal acoustic analysis as a technique for studying avian migration and examines, for the first time, how well this technology complements existing methods of studying migration. In my first data chapter (Chapter 2), I evaluate night flight call recordings as a tool for migration monitoring in a southern Great Lakes ecosystem by comparing thousands of hours of acoustic night flight call data to banding data from two migration monitoring stations in southwestern Ontario, Canada. I compare the nocturnal bioacoustic technique to the diurnal mist netting technique during both the spring and fall migration, focusing on both the timing of

migration and the number of animals migrating through the Great Lakes migratory flyway. This chapter is written for submission to the journal *Avian Conservation and Ecology*.

In my second data chapter (Chapter 3), I explore the spatial distribution of passerine migration patterns in the western basin of Lake Erie. I use nocturnal acoustic data from an array of seven microphones deployed across the north shore of Lake Erie and Pelee Island to investigate the temporal and geographic distribution of nocturnal migrants. Based on our understanding of how birds interact with ecological barriers, and the timing of migration in passerines, I investigate how birds detected over mainland compare to birds detected over Pelee Island. I also explore whether there are seasonal differences in first acoustic detection dates on the mainland and the island for each species or species-group. This chapter is written for submission to the *Canadian Field Naturalist*.

With increasing urban and industrial development and greater interest in wind turbine development in and around Lake Erie, improved monitoring techniques could lead to a better understanding of how migrants use the region. Locally, my research will contribute to our knowledge of seasonal and temporal patterns of bird movement at a globally important site for migrant songbirds and may have significant implications for conservation initiatives within the western basin of Lake Erie. Broadly, my research will help clarify the role acoustics can play in monitoring migrants and transient bird populations and could have significant implications for global biodiversity surveys.

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TABLES

Table 1.1. Strengths and limitations of five techniques used in migration monitoring

Monitoring Technique	Advantages	Limitations
Diurnal Visual Counts	<ul style="list-style-type: none"> - Can take place in multiple habitat types 	<ul style="list-style-type: none"> - There can be an observer bias effect, according to observer skill - Birds may not always “stop over” if migration weather is ideal
Mist Netting and Bird Banding	<ul style="list-style-type: none"> - Identification of species is definitive - Can collect additional morphological data and apply bands that could lead to potential band recoveries 	<ul style="list-style-type: none"> - Mist netting requires significant time commitment from highly trained bird banders - Restricted to sampling birds in a specific habitat and specific location - Birds may not always “stopover” if migration weather is ideal
Radar	<ul style="list-style-type: none"> - Useful for understanding large scale movements of many migrants - NEXRAD/Doppler radar is useful for monitoring at 100s to 1000s of kilometres; tracking radar is useful under 5-10km 	<ul style="list-style-type: none"> - Expensive - Species identification is impossible - Bats and insects confound interpretation - Can only track birds above a certain height
Geolocators and Satellite Telemetry	<ul style="list-style-type: none"> - Can collect exact location information about precise migration routes that individual birds take 	<ul style="list-style-type: none"> - Expensive - Tracks only one individual at a time - Must be able to retrieve geocator satellite transmitter from bird to access information - Equipment may encumber small birds, and influence their migration behaviour
Moon Watching	<ul style="list-style-type: none"> - Affordable and accessible 	<ul style="list-style-type: none"> - Dependent on weather and moon phase - Species identification difficult or impossible - Can only track birds flying below ~1km in altitude
Acoustic Monitoring	<ul style="list-style-type: none"> - Provides species-specific information on birds in flight - Affordable and accessible 	<ul style="list-style-type: none"> - Not all migrants make night flight calls - Inability to distinguish flight calls of several groups - Variability of call rates is unknown - Can only detect birds below a certain (unknown) height - Species identification can be challenging

FIGURES

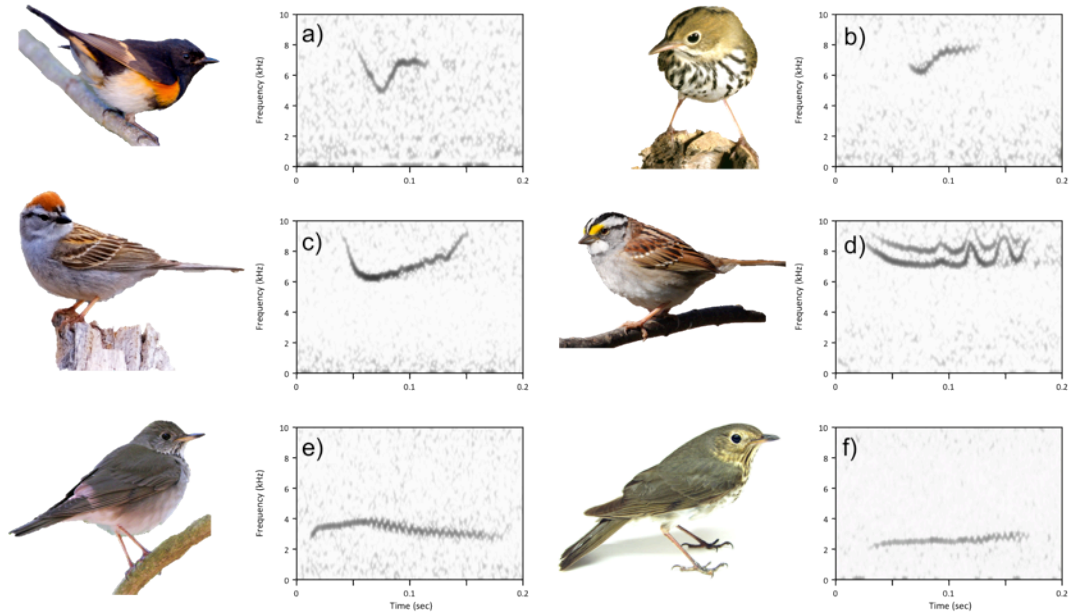


Figure 1.1. Examples of night flight calls from recordings I collected during spring and fall migrations of 2012: (a) American Redstart, (b) Ovenbird, (c) Chipping Sparrow, (d) White-throated Sparrow, (e) Gray-cheeked Thrush, and (f) Swainson's Thrush. Photographs are in the public domain from Wikimedia Commons.

CHAPTER 2

**ACOUSTIC MONITORING OF NOCTURNALLY MIGRATING BIRDS ACCURATELY PREDICTS
THE TIMING AND MAGNITUDE OF MIGRATION THROUGH THE GREAT LAKES**

CHAPTER SUMMARY

Tracking the movements of migratory birds poses many challenges because much of their lengthy journey takes place at night. One promising method for studying migration relies on microphones to record the nocturnal flight calls produced by migrating birds. Yet little is known about how recordings of nocturnal flight calls relate to the current monitoring techniques used to study migration at stopover sites during the day, such as mist netting. During the 2012 spring and fall migrations, we deployed seven autonomous recording units in a southern Great Lakes ecosystem. Concurrent with the recordings, banding data were collected at two banding stations, one on the north shore of Lake Erie and one on an island in the middle of Lake Erie. We analyzed over 6,200 hours of nocturnal recordings and detected over 60,000 flight calls from migratory birds, 46,800 of which we classified to the species level or to a bioacoustic category including several species. We compared these acoustic data to records of 5,624 birds captured at the two migration monitoring stations. We found that acoustic monitoring accurately predicted the magnitude of migration; comparison with mist net data revealed significant positive relationships between the number of acoustic detections and the number of mist net detections. We also found that acoustic monitoring accurately predicted the timing of migration; we found significant positive relationships between the date of passage of the 10th, 50th, and 90th percentile of the populations of up to 25 groups of passage migrant species, as detected through acoustics and mist netting. A careful examination of six species that produced distinctive flight calls highlights seasonal differences between peak detections via acoustic monitoring and mist netting. We discuss strengths of acoustic migration monitoring and compare its viability to other monitoring techniques. This research enhances our understanding of the role acoustics can play

in monitoring the bird migration and suggests that acoustic monitoring is an appropriate tool for assessing the seasonal timing of migratory birds.

INTRODUCTION

Obtaining accurate and long-term population trend data on North America's migratory birds is critical for guiding future conservation actions. The inaccessibility of remote northern habitats in Canada makes it difficult to monitor many populations of migratory songbirds on their breeding grounds using standard monitoring techniques, such as the Breeding Bird Survey (Dunn et al. 1997). Monitoring the biannual bird migration *en route* is an efficient means of collecting population data on numerous species from multiple breeding habitats (Millikin 2005).

Current migration monitoring programs, including conservation initiatives like the Canadian Migration Monitoring Network, are invaluable for collecting population data on neotropical migrant species at stopover locations along their migration routes. Population estimates generated through Breeding Bird Surveys and through migration monitoring are positively correlated, demonstrating that migration monitoring *en route* represents an accurate tool for tracking populations of particular neotropical songbirds (Dunn 2005, Osenkowski et al. 2012). Not only can monitoring migrants provide us with population indices for hundreds of bird species, it can also help us to understand migrant movement patterns (Hussell and Ralph 2005). Identifying preferred routes and timing of migratory movements has been recognized as a priority for further research (Faaborg et al. 2010). Furthermore, gaining an understanding of appropriate monitoring techniques for movements of migratory birds on a local landscape level can inform potential human developments such as wind-turbines (Evans and Mellinger 1999).

There is a long history of migration monitoring in North America (see Dunn 2005, Hussell and Ralph 2005). Migration monitoring stations often use a combination of different kinds of counting techniques, including mist netting, daily walking censuses, and incidental observations in a specified area to produce daily count totals. Combining multiple count methods can increase

the number of species monitored and the quality of the data (Hussell and Ralph 2005). A significant shortcoming of most current migration monitoring techniques is that they are diurnal; birds that migrate at night will be missed by daytime migration monitoring efforts unless they stop to spend the day foraging and resting at the stopover site (Dunn 2005). Furthermore, migration monitoring stations are limited to sampling birds in the immediate vicinity of the mist nets or census routes, and population estimates may be influenced due to local habitat features, or changes in migratory routes (Francis et al. 2009). Moreover, mist netting is a labour intensive strategy for migration monitoring, often depending on groups of dedicated volunteers, and requires significant training to ensure safe bird handling.

In many bird species, including most songbirds and shorebirds, much of the migratory journey takes place at night, when cool, calm weather conditions and fewer predators contribute to favourable migratory conditions (Able 1973, Kerlinger 1995). Monitoring the nocturnal activities of migrants presents tremendous challenges to researchers because the migrating birds cannot be observed directly, so it is impossible to visually estimate species abundance and identity. Radar has been shown to be a useful tool for estimating the magnitude and directionality of migration events (Gauthreaux 1996) and there is a consistent relationship between radar analysis of nightly migration events and ground census data the following day (Zehnder and Karlsson 2001). Radar aeroecology continues to provide significant information on avian nocturnal migration (Chilson et al. 2012), such as the responses of migratory animals to different weather conditions and major landscape influences, such as the Great Lakes (see Diehl et al. 2003). However, a major limitation of radar is that species identity and flock composition is impossible to ascertain using this method, which restricts its usefulness in population studies (Larkin et al. 2002).

One under-studied method of migration monitoring is through the recording of nocturnal flight calls. Some species of migratory birds routinely produce short flight calls on the wing. Night flight calls are characteristically short, high frequency, narrow bandwidth vocalizations that range from 1-11 kHz (Farnsworth 2007; Evans and O'Brien 2002). Many migratory taxa produce night flight calls—including warblers, thrushes, and sparrows—and in many cases their vocalizations are species-distinctive (Evans and O'Brien 2002, Lanzone et al. 2009). Not all birds produce night flight calls. While most woodpeckers, corvids, larks, swallows, and finches give flight calls regularly, they are diurnal migrants and rarely call at night (Farnsworth 2005). It has been suggested that several species of nocturnal migrants do not make flight calls at all, including New World flycatchers, vireos, and mimids (Farnsworth 2005). While the functions of night flight calls are not well understood, they have been suggested to stimulate migratory restlessness (*Zugunruhe*), maintain flock contact during migration, and assist in orientation (Hamilton 1962, Farnsworth 2005). Recent radar research supports earlier anecdotal reports that birds move in much looser flocks during migration at night than their day-time feeding flock behaviour at stopover locations (Larkin and Szafoni 2008); flight calls might therefore help to orient individuals in these loose flocks.

Interest in night flight call analysis has grown over the last decade and technological developments have resulted in better recording techniques. However, the identification of migrants based on their flight calls alone, as well as gaining an understanding of call structure variation among different ages and sexes of the same species, continues to be a major challenge in this field (Graber and Cochran 1960; Lanzone et al. 2009). Spectrograms of some species' night flight calls often show very high similarity, or exhibit extensive variability, making them difficult to distinguish from other species (Evans and Rosenburg 2000). Careful quantitative analyses of night flight call recordings, such as those of Evans and Mellinger (1999) and Lanzone

et al. (2009), are required before we can confidently use this technique alongside existing migration monitoring strategies.

In this study, we evaluate night flight call recordings as a tool for migration monitoring in a southern Great Lakes ecosystem. We compare thousands of hours of acoustic night flight call recordings to mist net data from two migration monitoring stations in southwestern Ontario, Canada. We evaluate acoustic nocturnal monitoring data during both the spring and fall migration, assessing both the timing of migration and the number of animals migrating through the Great Lakes migratory flyway. If night flight call recordings represent a compelling migration monitoring tool, we predicted that we would find a strong correspondence between acoustic data and mist net data for the magnitude and timing of migration. This is the first peer-reviewed study we are aware of examining night flight call monitoring of migratory birds at a species-level. This technique could vastly expand migration monitoring around the world, particularly in remote or inaccessible areas where automated recording devices could be deployed with little required maintenance.

METHODS

General field methods and study location

Millions of spring and fall migrants are funnelled through the western basin of Lake Erie each year (Diehl et al. 2003) and the island geography of the basin presents us with a unique opportunity to study migration and nocturnal flight calling behaviour. We deployed seven digital recorders during the 2012 spring migration from April 15 to June 10, and the fall migration from August 15 to November 10. Three recording units were deployed on Pelee Island: two recording

units were placed 100 metres apart from each other at the banding station on Pelee Island, located in Fish Point Provincial Nature Reserve (41°44'N, 82°40'W); a third unit was deployed 15km north at Lighthouse Point Provincial Nature Reserve (41°47'N, 82°38'W) at the northern end of Pelee Island. Four recording units were deployed on mainland, on the north shore of Lake Erie: one recording unit was placed at Holiday Beach Migration Observatory in the Holiday Beach Conservation Area (42°02'N, 83°02'W); a second within Point Pelee National Park (41°56'N, 82°30'W), a third at Cedar Creek Conservation Area (41°00'N, 82°47'W), and a fourth at a private woodlot near the town of McGregor, Ontario (42°06'N, 82°59'W; Figure 2.1). These locations were selected not only because of their association with two longstanding migration monitoring stations (see detailed description below), but also because they were in regional conservation areas within minimal ambient noise and artificial light. The lack of artificial light at the study locations ensured that we were counting true fly-over migrants with our acoustic monitoring and not birds that were attracted to a light source or had increased their calling rate due to disorientation (Evans 2007, Poot et al. 2008).

Acoustic recordings

We used Wildlife Acoustics SM-2 Song Meter recorders with SMX-NFC Night Flight Call Microphones at all seven recording stations. Recordings were collected with 44100 Hz sampling frequency with 16 bit accuracy in WAVE format in files that were 1 h 59 min in length; we left a one minute gap between each file to allow recorders to write the recordings to flash memory. To reduce interference from noise originating below the microphones, each microphone was mounted on a 30cm² piece of Plexiglas baffle, which was then mounted on top of a 5.8 metre pole. Our objective at each site was to get the microphone above the tree canopy to reduce any interference noise from leaves, insects, and amphibians. In most locations, this was achieved by

lashing the microphone pole to the side of a tree or a post. At both migration monitoring stations, we set up the recorders in the immediate vicinity of the mist nets (at the Pelee Island banding station we set up two recorders 100 m apart at either end of the netting area). All units were visited every three to five days to collect recordings and change batteries.

Following the Nocturnal Flight Call Count Protocol developed by eBird (<http://ebird.org/content/ebird/about/nfc-count-protocol>), we programmed the Song Meters to record between the period of astronomical dusk and astronomical dawn, when the sun was lower than 18 degrees below the horizon. We used data from the United States Naval Observatory website (<http://aa.usno.navy.mil>) to determine these times for each of our recording locations. Given this recording window, we assumed that we avoided recording individuals that were calling from the ground shortly after dusk (a behaviour that has been argued to stimulate *Zugunruhe*; Farnsworth 2005), or near dawn (a behaviour that may assist with habitat selection during descent or landscape relocation flights; Graber and Cochran 1960, Farnsworth 2005), a behaviour that may be common in the *Catharus* thrushes.

Analysis of acoustic recordings

We visualized recordings as sound spectrograms with Syrinx-PC sound analysis software (J. Burt, Seattle, Washington). A team of 12 volunteer sound analysts visually scanned 30 seconds of recording at a time, limiting the frequency range to 0Hz to 11,000Hz (spectral settings: 1024 FFT size, Blackman window) and used the time and frequency cursors in Syrinx-PC to annotate each night flight call. Recordings were then analyzed in two stages. During the first level of analysis, we broadly separated sounds as “high” calls (i.e. any night flight calls above 5kHz, matching the calls produced by sparrows, warblers, and kinglets for example) and “low”

calls (i.e. any night flight calls below 5kHz, matching the calls produced by thrushes and shorebirds). We attempted to use automated detection software approaches to speed up this process, however, due to the number of false detections from background noise such as insects, wind, and rain, we chose to scan through recordings manually to ensure the highest possible accuracy in detecting all sounds of interest (as recommended by Swiston and Mennill 2009). The first stage of analysis was completed when all hours of nocturnal recordings had been scanned, and each night flight call had been annotated in Syrinx-PC.

In the second stage of our analysis, I examined all annotations and assigned annotated sound to a particular species or group of species. I visualized each sound that was annotated in the first stage of analysis in Syrinx-PC (spectral settings: 0.5ms/line, 256 FFT size, Blackman window). Using an existing library of reference recordings, *Flight calls of Migratory Birds: Eastern North American Landbirds* CD-ROM (Evans and O'Brien 2002), as well as other reference guides including recordings and spectrograms from OldBird.org, XenoCanto, and Cornell Lab of Ornithology, I constructed a classification chart modified from Evans and Rosenburg (2000; Appendix 1). After comparing our own recorded flight calls to the reference libraries, I determined that 67 species of night migrants could be classified to the species level (i.e. their night flight calls were distinct at the species level) or into eight distinct bioacoustic categories (see Appendix 1). Some of these bioacoustic categories contained only two species (for example, the "loose u" category included Song Sparrows and Fox Sparrows), while other bioacoustic categories contained up to nine species (such as the "zeep" category, which included many species of warbler as listed in Appendix 1). Several species with variable night flight calls spanned multiple bioacoustic categories or were classified as distinct at the species level as well as a member of a broader category (see Appendix 1); for example, Ovenbirds produce a distinctive checkmark-shaped flight call that is species-specific, but also produces calls that

consist only of a frequency modulated upsweep (i.e. the “up” complex). Hereafter, we refer to these bioacoustic categories as “species-groups,” each comprising multiple bird species that produce flight calls that cannot be distinguished from one another. Any night flight calls that were quiet, distorted, or that did not match the reference library were classified as “unidentified high” (i.e. above 5 kHz) or “unidentified low” (i.e. below 5 kHz).

Diurnal migration monitoring data

We compared our bioacoustic data to banding data that were collected by two migration monitoring stations concurrent with the recordings. At both stations, the 9-metre long, 38mm mesh, songbird mist nets were checked at least every 30 minutes and captured birds were extracted, taken to a nearby banding laboratory, and fitted with uniquely numbered Canadian Wildlife Service leg bands. Morphological measurements including weight, wing chord, and amount of subcutaneous fat were taken. Age and sex were determined using standard methods (see Pyle 1997). During high-volume bird days, individuals were occasionally released without being banded and these birds were recorded as “captures” and included in our analyses.

The banding station on Pelee Island operates 10 mist nets and, as a member of the Canadian Migration Monitoring Network, follows the monitoring protocol recommendations of Hunsell and Ralph (2005). During the spring of 2012, they banded birds from April 15 to June 10; during the fall of 2012 they banded birds from August 15 to November 10. The nets at this station were open one half-hour before sunrise and operated for six hours, excluding down time when nets were closed either due to inclement weather (rain or wind) or high bird volume (when too many birds were captured to process safely). The banding station on the mainland (the Holiday Beach Migration Observatory) operated only during the fall migration (August 13 to

November 11) and used up to 16 nets. As a volunteer banding station, this observatory varies its netting hours with the availability of volunteers. In order to standardize the capture effort between the two banding stations, the number of net-hours was calculated using a standard method (Ralph et al. 1993).

In the second stage of our mist net data analysis, we assigned each captured bird to a corresponding acoustic category to facilitate direct comparison to our acoustic data. We pooled together mist net data for bird species whose night flight calls are indistinguishable (see Appendix 1 for details). For example, all Song Sparrows and Fox Sparrows captured in mist nets were assigned to the “loose u” species-group. This enabled us to make direct comparisons between the species and species-groups detected through acoustics and mist netting.

Statistical analysis and sample size

Using banding data as independent variables and acoustic data as dependent variables, we used linear regression to assess the similarity in the number of migrants detected by the two techniques. Banding data were normally distributed, and acoustic data were log-transformed to achieve normality. We plotted the log number of total acoustic detections for each species or species-group against the log number of total mist net detections for the same species or species-groups.

Using banding data as independent variables and acoustic data as dependent variables, we used linear regression to determine whether diurnal migration counts and nocturnal acoustic recordings yielded similar results in timing of passage through the season. We ranked both the mist net data and night flight call data by Julian Date, with each species or species-group detected with both techniques representing a data point, and calculated the date at which the first 10% of detections occurred for each species-group identifiable by its characteristic night

flight call each season and investigated if it correlated with the first 10% of banding capture records of the same species-group. Similarly, we used the median 50% and last 10% of acoustic detections of a particular species-group during a season and investigated the degree of correlation with the median 50% and last 10% of banding data of the same species-group. All statistical tests are two-tailed and all descriptive statistics are presented as mean \pm standard error.

RESULTS

We collected 2,157 hours of nocturnal recordings over 58 nights at the seven recording stations during the spring migration, and 4,080 hours over 63 nights at the recording stations during the fall migration, for a total of 6,237 hours of recordings over the year. Within these recordings, we annotated 60,013 nocturnal flight calls: 22,554 during the spring migration (10.5 calls per hour) and 37,459 during the fall migration (9.2 calls per hour). We were able to classify with confidence 46,846 (78%) of the calls into species or species-groups: 16,646 (74%) into 60 categories in the spring and 30,200 (81%) of the calls into 48 categories in the fall.

On Pelee Island, 834 birds of 62 species were banded during the spring migration and 2,079 birds of 75 species were banded during the fall migration. At Holiday Beach Migration Observatory, a total of 2,711 migrants of 63 species were banded during the fall migration.

Some birds such as flycatchers and vireos were only detected in the banding data; other birds such as cuckoos, White-crowned Sparrows, and Chipping Sparrows were only detected in the acoustic data. In total, we were able to match up 33 species-groups, comprised of 40 species, which were detected in both the banding data and the acoustic category.

Magnitude of migration

To evaluate whether acoustic monitoring provides reliable estimates of the number of migrants, we compared the number of detections in our acoustic data against the mist net data. We found that the number of migratory birds detected by night flight call monitoring showed a positive relationship with the number detected in mist nets. This pattern was statistically significant for spring data from one of the Pelee Island recorders (net data versus acoustic data from island recorder one: $r^2=0.19$, $p=0.01$, $n=33$ species or species-groups), for fall data from both Pelee Island recorders (net data versus acoustic data from island recorder one: $r^2=0.36$, $p=0.002$, $n=25$ species or species-groups; net data versus acoustic data from recorder two: $r^2=0.35$, $p=0.002$, $n=26$ species or species-groups); this pattern was not statistically significant for spring data from the second Pelee Island recorder (net data versus acoustic data from island recorder two: $r^2=0.17$, $p=0.10$, $n=17$ species or species-groups) or fall data from mainland (net data versus acoustic data from mainland recorder one: $r^2=0.10$, $p=0.17$, $n=21$ species or species-groups), although these patterns were in the same direction. This same pattern also held true when we pooled together the night flight call data from all seven recorders (spring Pelee Island net data versus acoustic data from all recorders: $r^2=0.25$, $p=0.003$, $n=33$ species or species-groups; fall Pelee Island net data versus acoustic data from all recorders: $r^2=0.36$, $p=0.001$, $n=27$ species or species-groups; fall mainland net data versus all recorders: $r^2=0.19$, $p=0.02$, $n=29$ species or species-groups; Figure 2.2).

Timing of migration

To evaluate whether acoustic monitoring provides reliable information on the timing of migration, we compared the time-of-year when each species or species-group was detected.

For all birds that were detected in both our acoustic data and the mist net data, we compared the median arrival date. We found strong positive correlations between all acoustic stations and the banding data from Pelee Island in the spring and fall, as well as the banding data from the mainland in the fall (Figure 2.3; Table 2.1). The positive relationship held true whether we compared banding data to the acoustic data from only the local microphone at the banding station, or the pooled acoustic data from all of our recorders. We found very similar relationships amongst the passage dates for the 10th percentile and 90th percentile of the total detected population (Table 2.1).

Correlations within number of detections by week per species

To further evaluate whether acoustic monitoring provides reliable information on the peak of migration, we compared bioacoustic and mist-netting data for six focal species that produce species-distinctive night flight calls, and were present in both datasets in ample numbers (American Redstart, Chestnut-sided Warbler, White-throated Sparrow, Black-throated Blue Warbler, Swainson's Thrush, Gray-cheeked Thrush). For all six species the timing of migration was similar in the banding and acoustic datasets (Figure 2.4), sometimes with the peak in migration coincide in the acoustic and banding datasets. For four of these six species, however, there was a difference between peak detections in the acoustics versus banding in the fall. The peak in acoustic detections lagged behind the peak in banding detections by approximately two weeks.

DISCUSSION

Acoustic detections of night flight calls accurately predict both the number of spring and fall migrants, as well as the timing of their migration, in a southern Great Lakes ecosystem. The thousands of hours of nocturnal recordings we collected during the spring and fall migration matched our reference dataset, comprised of diurnal banding records from two long-term migration monitoring stations. We conclude that night flight call monitoring generates reliable data on the magnitude and timing of migration, comparable to the patterns revealed by bird banding data. This is the first investigation to substantiate night flight call monitoring in comparison to bird banding data from migration monitoring stations.

We found a close correspondence between the numbers of animals detected with night flight call monitoring and banding efforts, confirming that acoustic recordings are a compelling migration monitoring strategy. Few studies have examined call rates in relation to birds detected by banding over an entire migratory season. Rather, flight call rates have been assessed on an hourly or night-to-night basis. Prior studies designed to evaluate the effectiveness of acoustic monitoring in assessing the numbers of migrants in a given night, most often in comparison to radar data, have also supported the conclusion that night flight call recordings are a compelling migration monitoring technology. Both Farnsworth et al. (2004) and Gagnon et al. (2010) found positive associations between Doppler radar reflectivity density and acoustic detections on a nightly basis, although both studies stressed the variability of this relationship. Unpublished investigations by Murray (2004) and Holberton et al. (2012) also support the reliability of night flight call data; these studies have shown that night flight call analysis can reflect diurnal counts of migrant birds.

Acoustic detections of night flight calls yielded similar insight into the timing of migration in comparison to banding data; there were strong correlations between the 10th, 50th, and 90th percentile of birds to pass by our recorders and to be captured in the mist nets. Therefore, these methods produce comparable insight on the timing of the migration events in both spring and fall. As far as we are aware, this is the first investigation of night flight call recording accuracy in monitoring the seasonal timing of the migration. Understanding the seasonal plasticity of passage schedules for migrants has become an important topic in migration studies, particularly in response to possible emerging environmental influences such as climate change (Francis et al. 2009). Acoustic monitoring could enable us to recognize patterns in changes to migratory route or timing changes at a scale that is beyond the scope of a traditional migration station. Acoustic monitoring stations deployed repeatedly at the same sites will facilitate inexpensive assessments of whether nocturnally calling species are responding to climate change.

In addition to our comparison across all species, we examined the timing of migration in six focal species with distinctive night flight calls. Previous radar-based studies of Dickcissels (*Spiza americana*) by Larkin et al. (2002) found a high correlation between radar and acoustic detections on a nightly basis. We compared detections on a weekly basis, rather than a nightly basis, because early studies like Graber and Cochran's (1960) showed little correlation between acoustics and ground counts the following day, and because the relatively small number of banded birds (several thousands of individuals) compared to the relatively large number of recorded birds (many tens of thousands of individuals) meant that weekly totals provided a better comparison dataset. For all six species, we found general similarity in the timing of migration based on acoustic and mist net data. In the fall, we discovered a lag of approximately

two weeks in the peak of acoustic detections behind the peak in mist net detections for almost all species. This difference may reflect seasonal variation in young and old birds; hatch year birds of some species migrate later than adult birds, or vice versa, due to moult patterns (Woodrey and Chandler 1997, Carlisle et al. 2005). Young birds may also produce more night flight calls in migration (Farnsworth 2005) since they are more easily disoriented by external influences (Gauthreaux 1982), which could have led to the delayed peak in acoustic detections. Another possibility is that the delay in peak migratory activity by acoustic detection was due to the masking influence of background noise in our early-fall recordings; analysis of the first two weeks of fall recordings (August 15 – 30, 2012) was very difficult owing to the excessive insect noise that often obscured flight calls, particularly those with vocalizations in the 3-7kHz range. This methodological difference may have resulted in many warbler species being detected sooner, and in greater numbers, in the banding dataset. Continued heavy insect noise between 2-3kHz range likely contributed to the same delay in detecting thrushes during the first week of September as well.

We were surprised to find substantially different numbers of night flight calls at the two recording stations on Pelee Island that were separated by only 100 metres. In the spring migration, the more northerly of the two recorders detected over eight times as many calls as the recorder that was just 100 metres to the south. In the fall, this pattern was reversed, with the more southerly microphone detecting almost twice as many calls. We examined both the recordings, and the recording equipment, to ensure that these differences were not the result of any technical differences between the two sets of recordings. In spite of the differences in numbers detected by the two nearby recorders, both acoustic datasets still showed a positive correlation with the date of passage banding data, and in the fall both datasets showed a positive correlation with the number of migrants data. Further investigation into the

transmission properties of flight calls and the detection range of night flight call microphones will provide insight into how much airspace is sampled by each night flight call microphone. The differences we detected between the two nearby recorders suggest that detection rates and sampling efforts are highly localized. Furthermore, we found significant positive relationships using the pooled acoustic data from all seven microphones in our study area and compared them to the banding data from each station, but the relationships became even stronger when we only used the data from the microphones placed adjacent to the nets. This may indicate that the temporal migration patterns are localized on a relatively small geographic scale. However, the combined data from all seven microphones across the landscape revealed additional species that were not detected locally through acoustic monitoring, but that were detected through banding. Therefore, not all of our microphones sampled all possible flight-calling species, and suggests that future efforts will benefit from using multiple microphones at nearby locations, rather than a single microphone at a single location.

Historically, techniques for monitoring bird populations and understanding the movements of migratory birds have included daily counts and mist netting at stopover locations, and radar (reviewed by Milliken 2005, Dunn 2005). More recently, radio tracking has been useful for tracking stopover and departure times of individual birds (e.g. Schmaljohann and Naef-Daenzer 2011, Mitchell et al. 2012), and geolocators have been instrumental in understanding individual migratory routes of larger passerines (e.g. Bairlein 2012, Stutchbury 2012). One limitation of banding as a migration monitoring strategy is that the number of migrants captured during one morning at a migration station is relatively small, and may not necessarily represent of the magnitude of the nocturnal migration from the previous night; opportune weather conditions might result in many birds passing over the netting area and therefore not be

sampled by the banders. Additionally, differences in vegetation at banding stations, or habitat succession at banding stations can also bias annual count trends or mask possible changes in migratory routes (Francis et al. 2009). Acoustic monitoring does not suffer these shortcomings. For example, Chipping Sparrows, an open habitat specialist, were often detected in the recorders above the island mist nets, but were never captured in the mist nets owing to the placement of nets in a young forest. Therefore, the use of acoustics can play a role in monitoring the timing of migration across a much wider geographic area than banding migration stations alone and eliminate the bias effect from habitat succession.

Across many different taxa, passive acoustic monitoring has been used to determine presence/absence and estimate group sizes, particularly in marine or nocturnal animals, which are challenging to monitor using visual surveys alone (see Vaughn et al. 1997, Wang et al. 2005, Mellinger et al. 2007). Night flight call monitoring has numerous advantages for studying migratory birds: (1) It is the only method in which we can identify species composition during active flight; (2) It can be conducted in remote locations or inaccessible areas when banding or visual surveys are not feasible; (3) It samples birds in active migration, eliminating any effects of habitat; (4) It samples a much larger number of birds than mist netting or individual tracking can; (5) It is more accessible to birdwatchers and the public, requiring less training than mist netting and no permits. For these reasons, acoustic monitoring can play an important role in characterizing spring and fall global flyways.

One drawback of a solely acoustic approach to migration monitoring is that we may never be able to further separate species from the larger species-groups. For example, the spectrogram of the flight call of the Lincoln's Sparrow cannot be reliably differentiated from that of the Swamp Sparrow. While this may restrict this technique's usefulness in certain studies of some *Setophaga* species in the "zeep" category and the *Oreothlypis* species in the "up" category,

it should not diminish the usefulness of this technology as a tool for monitoring the seasonal movements of other species of migratory birds. There are also species detected through each technique that is not detected through the other. Specifically, acoustic monitoring cannot detect migrant flycatchers and vireos, which do not appear to produce flight calls but are detected regularly through banding. Similarly, using acoustics we detected thousands of Savannah Sparrows, which are not detected through banding, in part because the nets are not in habitat appropriate for catching this grassland species. The acoustic data we collected suggests that the two migration monitoring stations severely underestimate the number of Savannah Sparrows that pass through the region, which is likely also the case for other grassland species such as the Bobolink and White-crowned Sparrow that might not make use of the more mature habitat where both banding stations are located. This indicates that some species that are not adequately monitored with banding, or other approaches, could be accurately counted with acoustic monitoring. As with any multi-species, broad-scale study, a variety of approaches to migration monitoring would be optimal in gaining the greatest understanding of bird movement on a large and small landscape scale (Milliken 2005, Porzig et al. 2011).

Through this study, we have demonstrated that acoustic monitoring of nocturnal migrants provides an accurate tool for estimating species composition and timing during migratory events, as well as the magnitude of migration. On a broad geographic scale, recording the long-term trends in the timing of spring and fall migrations can give insight into impacts from overarching influences such as climate change, which can potentially have complex and varied effects on the annual life cycle of migratory birds (Jenni and Kery 2003, Van Buskirk et al. 2009). On a local scale, documenting the timing of migration with acoustic monitoring can assist with managing the timing of resource or wind turbine development during the migratory seasons.

These data are a confirmation of the importance of using multiple techniques to monitor migratory birds during these major life history events. Additional exploration of night flight call monitoring as a technique for monitoring passage migrations will continue to provide significant information on migration corridors, population trends, and the seasonality of bird behaviour.

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TABLES

Table 2.1. Comparison of the timing of migration as assessed through mist net data and night flight call acoustic data; detections of night flight calls can accurately predict the timing of the 10th percentile, 50th percentile, and 90th percentile of passage migrants in spring and fall as detected through banding.

Season	Net Data	Acoustic Data	10 th Percentile			50 th Percentile			90 th Percentile		
			r ²	P	n	r ²	P	n	r ²	P	n
Fall	Mainland	All recorders	0.20	0.04	21	0.50	0.0003	21	0.64	0.0001	21
Fall	Mainland	Mainland recorder 1	0.82	0.0001	16	0.58	0.0006	16	0.61	0.0003	16
Fall	Island	All recorders	0.37	0.006	19	0.74	0.0001	19	0.64	0.0001	19
Fall	Island	Island recorder 1	0.77	0.0001	17	0.70	0.0001	17	0.59	0.0003	17
Fall	Island	Island recorder 2	0.72	0.0001	18	0.74	0.0001	19	0.74	0.0001	18
Spring	Island	All recorders	0.23	0.01	25	0.45	0.002	25	0.29	0.006	25
Spring	Island	Island recorder 1	0.51	0.0003	21	0.65	0.0001	21	0.56	0.0001	21
Spring	Island	Island recorder 2	0.62	0.06	6	0.69	0.04	6	0.63	0.06	6

FIGURES

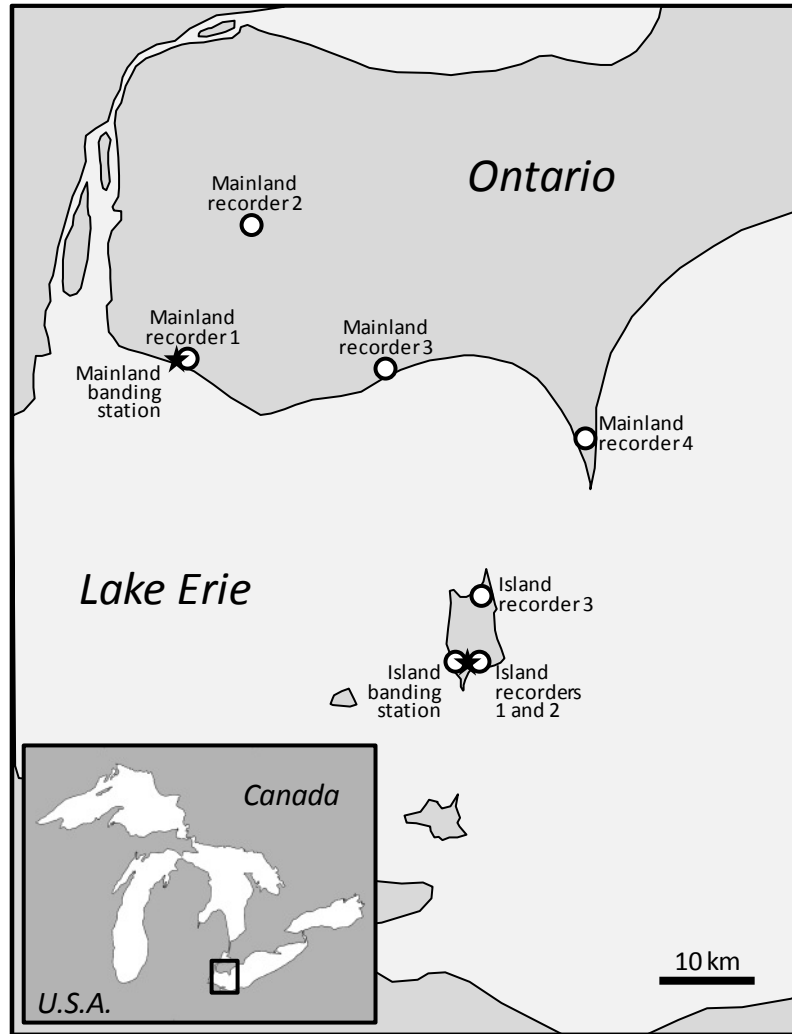


Figure 2.1. Map of Essex County, Ontario, Canada shows the seven acoustic recording locations and the two banding stations.

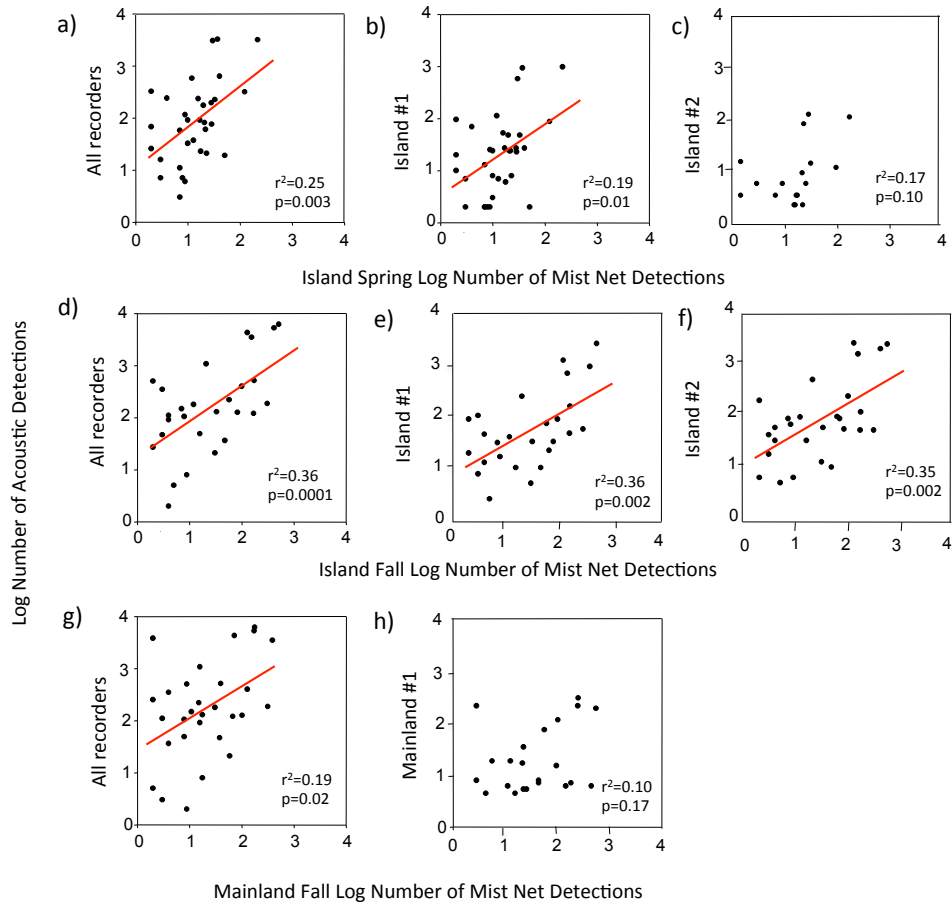


Figure 2.2. The number of migrants detected by acoustic monitoring showed a strong positive correlation with the number detected by bird banding. Each data point represents the log number of detections of a species or species-group. Several comparisons are shown: (a) All recorders combined versus Island nets, (b) Island recorder 1 versus Island nets (c) Island recorder 2 versus Island nets, (d) All recorders versus Island nets, (e) Island recorder 1 versus Island nets, (f) Island recorder 2 versus Island nets, (g) All recorders versus Mainland nets, (h) Mainland recorder 1 versus Mainland nets.

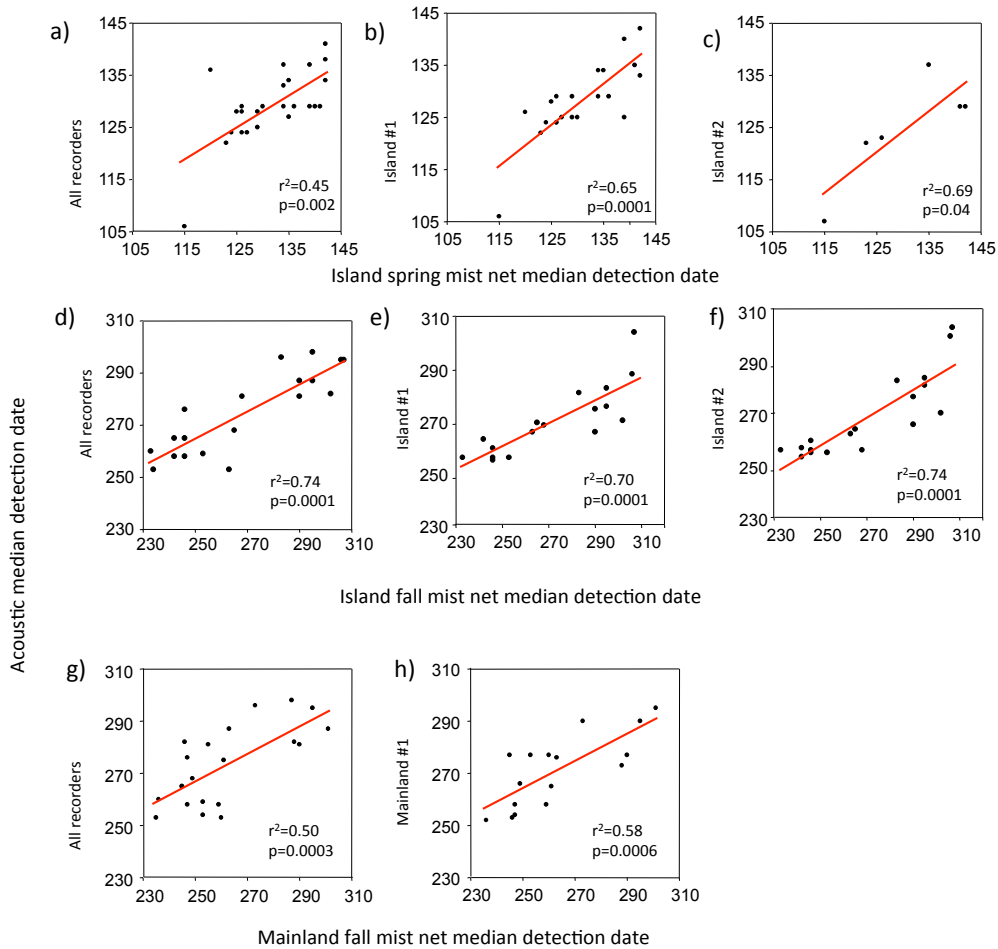


Figure 2.3. Acoustic monitoring of nocturnal flight calls and banding show similar timing of migrant passage in spring and fall. Each data point represents the median detection date across all detections for each species or species-group. Several comparisons are shown: (a) All recorders combined versus Island nets, (b) Island recorder 1 versus Island nets, (c) Island recorder 2 versus Island nets, (d) All recorders versus Island nets, (e) Island recorder 1 versus Island nets, (f) Island recorder 2 versus Island nets, (g) All recorders versus Mainland nets, (h) Mainland recorder 1 versus Mainland nets. Statistical details are given in Table 2.1.

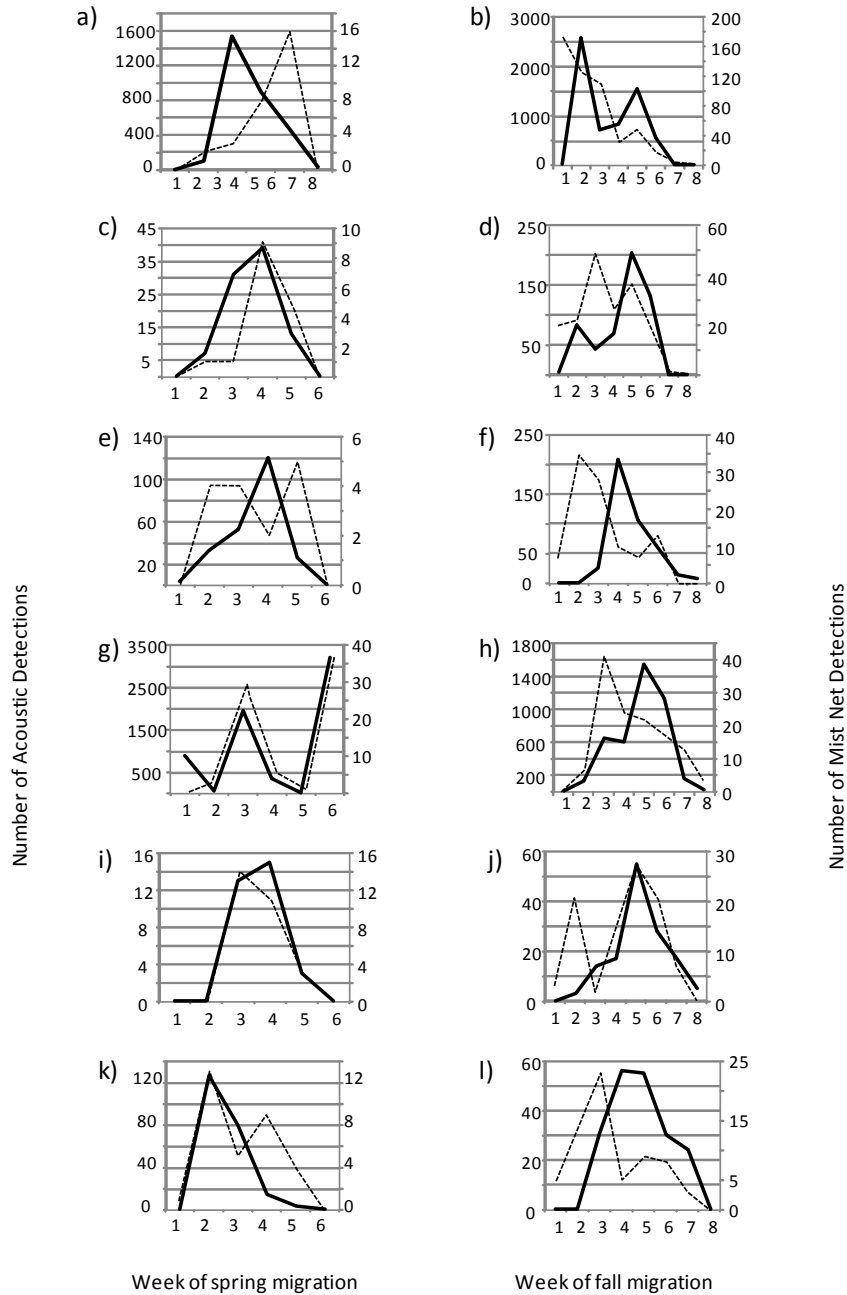
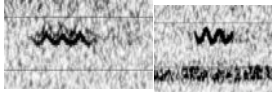
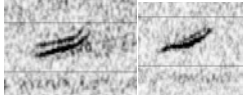
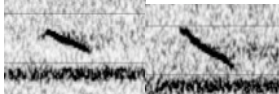
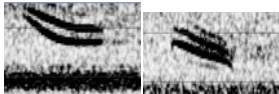

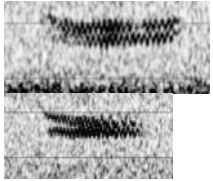
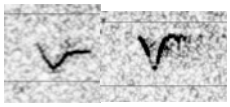

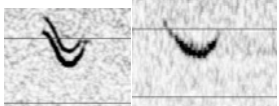
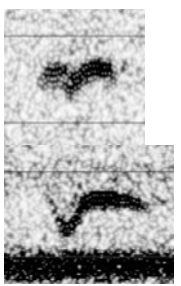




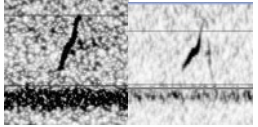
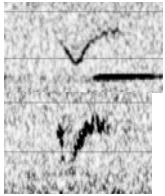

Figure 2.4. Numbers of detections using acoustics and banding by week of spring and fall migration show different patterns. Solid line represents acoustic detections, dashed line represents banding detections. Data are shown for: (a) Swainson's Thrush in spring, (b) Swainson's Thrush in fall, (c) Gray-cheeked Thrush in spring, (d) Gray-cheeked Thrush in fall, (e) American Redstart in spring, (f) American Redstart in fall, (g) White-throated Sparrow in spring, (h) White-throated Sparrow in fall, (i) Black-throated Blue warbler in spring, (j) Black-throated Blue Warbler in fall, (k) Ovenbird in spring, and (l) Ovenbird in fall.

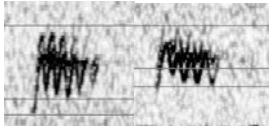
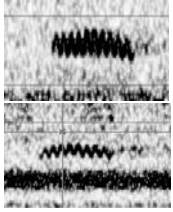
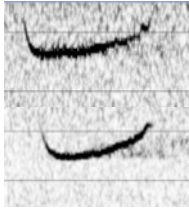
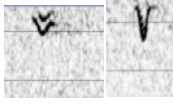
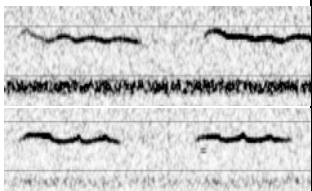

APPENDIX

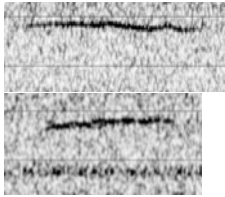
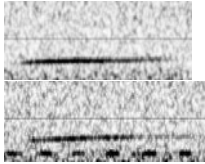
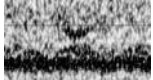
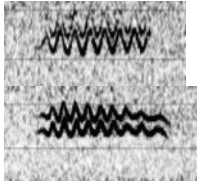
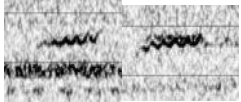
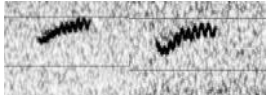
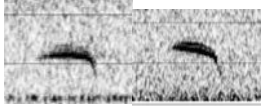
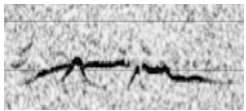
Appendix 2.1. Species Classification chart constructed using Flight calls of Migratory Birds: Eastern North American Landbirds CD-ROM (Evans and O'Brien 2002) and modified based on information in Evans and Rosenberg (2000). All spectrograms viewed at 256 FFT size, Blackman window, 1.5ms time resolution.



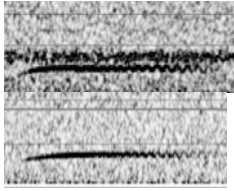
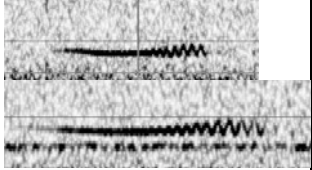
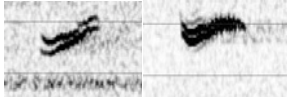
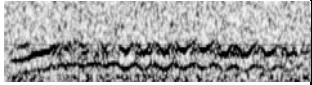
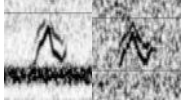
Sound type	Species	Description	High or Low (Above or Below 5kHz)?	Length (ms)	Number of acoustic detections	Examples from our recordings
ZEEP	Bay-breasted Warbler, Blackburnian Warbler, Blackpoll Warbler, Cerulean Warbler, Connecticut Warbler, Louisiana Warbler, Magnolia Warbler, Worm-eating Warbler, Yellow Warbler	Two to six peaks	High	60	4135	
UP SWEEP (Up)	Tennessee Warbler; Nashville Warbler; Black-throated Green Warbler; Orange-crowned Warbler; Mourning Warbler; Yellow-rumped Warbler; Vesper Sparrow; White-crowned Sparrow, Ovenbird	Short upsweep, sometimes with harmonic and modulation	High	30-50	8465	
SINGLE DOWN (SgDn)	Northern Parula, Pine Warbler	Short down sweep	High	50	833	
DOUBLE DOWN (DbDn)	Savannah Sparrow, Field Sparrow	Large down sweep with harmonic	High	100-160	4919	
LOOSE U	Fox Sparrow, Song Sparrow	Shallow, long 'U' with a longer upsweep and often with harmonic	High	120	1690	

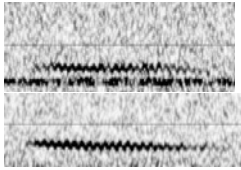
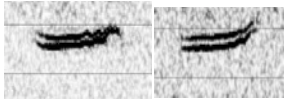
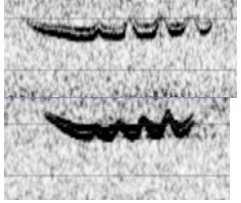
SWSP/ LISP	Swamp Sparrow, Lincoln's Sparrow	Long, flat tremolo with harmonic	High	125	163	
AMBI	American Bittern	Low block of noise	Low	160	0	None detected
AMPI	American Pipit	Lightening bolt shaped downward slur with a second low frequency down sweep	Mid	70	0	None detected
AMRE	American Redstart	V shape that rapidly descends then ascends and levels off with slight tremolo at end	High	75	663	
AMRO	American Robin	Two to four humped "M" made of tremolo, Low harmonic-rich hump	High	200	57	
ATSP	American Tree Sparrow	Tight Backwards 'J' with down sweep bolder than upsweep, sometimes with harmonic	High	50	360	
BAWW	Black and White Warbler	V shape that rapidly descends then ascends and levels off made of rapid and bold tremolo	High	75	42	

CUCK	Black-billed Cuckoo Yellow-billed Cuckoo	Flat 'Kow' with harmonic	Low	110	66	
BLGR	Blue Grosbeak	Long zeeep with six to eight peaks, with a harmonic	High	110	0	None detected
BITH	Bicknell's Thrush	Begins with significant up slur to slight, declining, rapid tremolo	Low	200	0	None detected
BOBO	Bobolink	Up slurred tone with many harmonics	Low	90	75	
BTBW	Black-throated Blue Warbler	Up slurred tone with an inflection in the middle and sometimes a hook at the top right	High	30	160	
CAWA	Canada Warbler	Distinctive wavy V with a very low initial dip, right hand side is longer with several bold inflections	High	40	27	
CMWA	Cape May Warbler	Down slurred shallow hump consisting of a 3-5 humped 'M'	High	50	146	

COYE	Common Yellowthroat	Distinctive longer, broader 'zeep' with prominent harmonic; three to seven mountain peaks (usually five or six)	High	60	249	
CSWA	Chestnut-sided warbler	Distinctive generally flat tremolo (can have slight up or down sweep)	High	75	263	
CHSP	Chipping Sparrow	Tight U with modulation on the upsweep	High	90	2353	
DEJU	Dark-eyed Junco	Tiny, high 'V', often repeated	High	20	157	
DICK	Dicksissel	Series seven to ten of upside-down 'Vs'	Mid	120	1	Poor example
GCKI	Golden-crowned Kinglet	Series of five to eight tiny mountain peaks	High	150	187	
GCTH	Gray-cheeked Thrush	Begins with significant upslur to slight, declining, rapid tremolo	Low	200	388	

GRSP	Grasshopper Sparrow	High, flat, long	High	150	40	
HETH	Hermit Thrush	Long, low, flat	Low	400	312	
HOWA	Hooded Warbler	Flat or slightly dipped tremolo with six to eight peaks	High	50	10	
INBU	Indigo Bunting	Long zeeep with eight to ten mountains, often with a harmonic	High	100	199	
NOWA	Northern Waterthrush	Slightly upswept tremolo with harmonic	High	75	85	
OVEN	Ovenbird	Checkmark made of rapid and bold tremolo	High	70	420	
PAWA	Palm warbler	Short, flat slightly modulated often with harmonic and a down sweep at the end of the note	High	50	428	
PISI	Pine Siskin	Distinctive low double peak			27	

RBGR	Rose-breasted Grosbeak	Low tremolo, Low harmonic stack	Low	90	83	
RCKI	Ruby-crowned Kinglet	Short harmonic stack with wide frequency range	Mid	25	0	None detected
RHWO	Red-headed Woodpecker	Long harmonic stack with some modulation	Low	250	0	None detected
SCTA	Scarlet Tanager	Flat note with very slight upsweep at end, Harmonic stack with a dip and rapid tremolo at end	Low	150	23	
SWTH	Swainson's Thrush	Rapid quiet upsweep levels off on flat section with tremolo growing increasingly modulated at end	Low	200	9286	
VEER	Veery	Very slight down sweep or flat note with tremolo growing increasingly modulated at end	Low	200	790	
VESP	Vesper Sparrow	Long shallow checkmark with moderate tremolo and harmonic	High	85	52	
VIRA	Virginia Rail	Low, long and modulated with harmonic	Low	200	20	
WIWA	Wilson's Warblers	N-shaped often with long initial upsweep and extra modulation at end	High	45	51	

WOTH	Wood Thrush	Long flat note with very rapid tremolo at 3.5kHz	Low	200	119	
WCSP	White-crowned Sparrow	Upsweep with harmonic	High	60	636	
WTSP	White-throated Sparrow	Very distinctive, long, slight down sweep with three to five mountain humps at the end, pronounced harmonic	High	140	7437	
unID high short	Unidentified species (likely a warbler)	Can be any shape; often of poor quality	High	Under 60ms		
unID high long	Unidentified species (likely a sparrow)	Can be any shape; often of poor quality	High	Over 60ms		
unID low thrush	Unidentified thrush species	Low long sometimes with tremolo	Low	200		
unID low	Unidentified low frequency call (that is not a thrush)	Can be any shape; often of poor quality	Low	100-200		

CHAPTER 3

ACOUSTIC MONITORING OF MIGRATING BIRDS REVEALS THE IMPORTANCE OF ISLAND GEOGRAPHY IN THE WESTERN BASIN OF LAKE ERIE

CHAPTER SUMMARY

Understanding seasonal distributions of migrating birds is critical for informing conservation actions and management decisions. In this study, we examined the temporal and geographic distribution of birds during active migration in the southern Great Lakes. During the spring and fall of 2012, we collected data on migrating birds using both acoustic nocturnal monitoring and banding records at sites on Pelee Island in the middle of Lake Erie, and from mainland sites on the north shore of Lake Erie. Given that Lake Erie may represent a substantial ecological barrier to migratory birds, we predicted that the mainland and island sites would show different patterns in both the number of passage migrants and the timing of their migration. Analysis of over 60,000 flight calls from 6,200 hours of recordings revealed many more flight calls were detected per hour of recording over the island as opposed to mainland. This pattern held true for almost all species or species-groups we examined in the spring and fall. Analysis of 6,500 banding records revealed no differences between island and mainland sites in the fall, but showed significantly more birds per thousand net hours on the island in the spring. These results suggest that Lake Erie is not a major barrier to migration and that birds may concentrate their flight over Pelee Island in the middle of the lake. Acoustic data revealed that birds were detected significantly earlier on Pelee Island than on the north shore of Lake Erie in the spring, but they were not detected earlier on the mainland in the fall. In contrast, analysis of banding data revealed no differences in the first detection date during spring or fall. These data highlight Pelee Island as an important part of the Mississippi flyway and provide valuable information on the migratory routes of birds through the Great Lakes.

INTRODUCTION

Migratory birds have the ability to make non-stop flights of thousands of kilometres (e.g. Egevang et al. 2010, Bairlein 2012, Battley et al. 2012). During migration, birds are likely to encounter ecological barriers, such as bodies of water, mountain ranges, or stretches of deserts in their path. There are numerous factors that might lead birds to select longer, land-based routes, rather than crossing such ecological barriers (Allerstam 2001). Recent research suggests that birds have an ability to adjust their route when they encounter ecological barriers, based on their own body condition and external information, such as weather conditions (Schmaljohann and Naef-Daenzer 2011). The increased risk of crossing an ecological barrier may be offset by the time or energy saved by using the shortest route across the barrier (Bruderer 2001). This may be particularly important in springtime migration, when urgency drives males to travel to their breeding grounds to compete for prime territories and attract mates (Francis and Cooke 1986).

Optimal migration strategies and behavioural decisions made by migrating birds are a well-studied area of ornithology (see Moore and Kerlinger 1987, Gauthreaux and Belser 1999). During a migratory journey from Africa to Europe, migratory birds encounter the Saharan Desert, the Mediterranean Sea, and the Alps, all of which could pose a threat to the safety of a long-distance migrant. Radar studies in the Mediterranean show that some birds cross directly over the sea, although concentrations of migrants over water was often two to three times lower than that over the Iberian Peninsula, demonstrating that most birds preferred to circumnavigate the sea (Bruderer and Liechti 1999). Historically, researchers believed that birds were distributed homogeneously across the landscape when navigating the Mediterranean (Bruderer 2001). Banding studies, however, have demonstrated that birds exhibit diverse

migration strategies when encountering ecological barriers (Spina and Pilastro 1999).

Furthermore, islands and peninsulas appear to play a very important role for migrants that choose to cross the Mediterranean Sea, although the use of island stopovers varies between species and even individuals based on age or sex (Barriocanal and Robson 2007).

The Gulf of Mexico is the most well-studied ecological barrier in North America. Recent tracking studies revealed that different species, and even different individuals, vary in their propensity to cross the Gulf (Stutchbury et al. 2009). For example, geolocator data from one migratory Wood Thrush (*Hylocichia mustelina*) suggested that it crossed over the Gulf of Mexico on its northward migration, but went around the Gulf of Mexico on its southward migration; another thrush chose a land-based route around the Gulf of Mexico on his northward spring migration but then chose to cross the Gulf of Mexico in the two subsequent spring migrations (Stanley et al. 2012). In the Gulf coast system, the barrier islands along the Mississippi coast also play an important role for some migrants and provide habitat for foraging before or after the substantial journey across the gulf (Moore et al. 1990).

North America's Great Lakes represent an ecological obstacle that influences the migration of songbirds (e.g. Diehl et al. 2003, Deutschlander and Muheim 2009). The geography of the lakes plays a significant role in funnelling millions of spring and fall migrants. The north and south shores of Lake Erie, as well as the Lake Erie Island Archipelago, serve as important stopover locations; many areas in this region have been identified as Important Bird Areas by Bird Studies Canada and Nature Canada for their seasonal concentration of migratory birds (see www.ibacanada.ca). Yet, due to the technical challenges involved in monitoring the nocturnal migration of many bird species, we lack significant information on the ecology and behaviour of migratory birds that pass through the Great Lakes. Recent radar studies in the Great Lakes region have explored ecological barrier avoidance (Diehl et al. 2003), as well as habitat use by

migrant birds and stopover ecology in the region (Bonter et al. 2009). Radar data confirm that many migrants cross the Great Lakes in spring and fall, though higher densities of birds were always detected over land than over water during migratory events (Diehl et al. 2003). Little is known about the role that the western Lake Erie islands play in funnelling migrant bird species in the spring or the fall.

While general trends about temporal and geographic patterns in barrier avoidance can be revealed through radar studies, one major limitation of this technique is that particular species cannot be identified. Additionally, if fall nocturnal migrants travel at lower altitudes than diurnal migrants over the Great Lakes, as has been reported over the Gulf of Mexico, they may not be detected by radar (Farnsworth and Russell 2005). Acoustic monitoring overcomes these limitations, and can provide detailed population and behavioural information for species that are hard to monitor, such as cryptic species, aquatic species, or nocturnal species, such as bats and many migratory birds (Marques et al. 2013). We recently showed that night flight call data accurately predicts the timing and magnitude of the spring and fall migration in this ecosystem (Chapter 2). Therefore, night flight call data can give insight and improve the resolution and our understanding into the spatial distribution of passerine migration patterns in the western basin of Lake Erie.

In this investigation, our objective was to describe the migration patterns of birds in and around western Lake Erie using night flight calls and banding station data. If Lake Erie serves as an ecological barrier to migratory birds, then we expected to find that the recorders and mist nets on the island in the middle of the lake would detect significantly fewer migrants in both spring and fall. Given that prior studies suggest that north temperate migrants have less of a tendency to cross Lake Erie in the spring *en route* to the breeding grounds than in fall *en route* to

wintering grounds, we predicted that any lake-crossing avoidance would be more pronounced in the spring than fall. If Lake Erie serves as a barrier to only some species of migratory birds, we expected to find that some species were detected only on mainland, but not at island sites. If Lake Erie does not serve as an ecological barrier, but instead islands within the lake serve to concentrate birds as they cross the lake, then we expected to detect more migratory birds over the island than mainland sites. Finally, if Lake Erie does not serve as a barrier, but an obstacle that temporarily delays the migration of birds, we expected to see a lag in detection between the southerly island and the northerly mainland sites in spring migration; we expected to see the reverse pattern in the fall.

Identifying preferred routes and timing of movements of migrants has been identified as a priority for further research (Faaborg et al. 2010), since this represents a vulnerable period in the annual life cycle of migratory animals (Silllett and Holmes 2002). Preliminary investigations using acoustic approaches to study nocturnal migrants have shown that nocturnal acoustic monitoring provides an opportunity to gain a better understanding of flock composition of active migrants around major installations such as oil platforms, Department of Defence aircraft sites, and wind turbine sites (Farnsworth and Russell 2005, Farnsworth et al. 2009, Gage et al. 2009). Acoustic monitoring of nocturnal migrants can provide some of the species-specific information about the seasonal movement of tens of thousands of birds in the Great Lakes region that radar and individual tracking studies cannot give us.

METHODS

General field methods and study location

We studied patterns of bird migration in Essex County, Ontario during the 2012 spring migration from April 15 to June 15, and the 2012 fall migration from August 15 to November 10. We recorded night flight calls at seven locations, three on Pelee Island and four on the north shore of Lake Erie. Three recording sites were located on Pelee Island in the middle of Lake Erie; two sites at the banding station on Pelee Island (41°44'N, 82°40'W) in Fish Point Provincial Nature Reserve at the southern end of the Island, and a third site 15km north at Lighthouse Point Provincial Nature Reserve (41°47'N, 82°38'W) at the northern end of the Island. Four recording sites were located on the mainland on the north shore of Lake Erie: Point Pelee National Park (41°56'N, 82°30'W), Cedar Creek Conservation Area (41°00'N, 82°47'W), Holiday Beach Migration Observatory in the Holiday Beach Conservation Area (42°02'N, 83°02'W), and a private woodlot near the town of McGregor, Ontario (42°06'N, 82°59'W) (see Figure 3.1).

Acoustic recordings

At each of the seven recording sites, we deployed an autonomous digital recorder (model: SM-2 Song Meter, Wildlife Acoustics, Concord, MA) equipped with a single night flight call microphone (model: SMX-NFC, Wildlife Acoustics). Microphones were mounted on a 30cm² piece of Plexiglas to minimize recording of sounds below the microphone. We attached the microphone plate to a 5.8 metre long pole that we lashed to trees or posts at the seven recording sites. To minimize interference noise from leaves, insects, and amphibians, we positioned the microphones just above tree height. As in the Nocturnal Flight Call Count Protocol

developed by eBird (<http://ebird.org/content/ebird/about/nfc-count-protocol>), we programmed recorders to begin sampling at astronomical dusk and conclude sampling at astronomical dawn (approximately 70 minutes after sunset until 70 minutes before sunrise), when the sun was lower than 18 degrees below the horizon. Recordings were collected with 44100Hz sampling frequency with 16 bit accuracy in WAVE format in one hour and 59 minute files. Each recorder was visited every three to five days to collect recordings and change batteries.

Analysis of acoustic recordings

We processed recordings in two stages (following the protocol we developed in Chapter 2). Recordings were processed manually to ensure the highest possible accuracy in detecting all flight calls, as recommended by Swiston and Mennill (2009). Briefly, recordings were first visualized as sound spectrograms using Syrinx-PC sound analysis software (J. Burt, Seattle, Washington) and scanned manually 30 seconds at a time by a team of 12 volunteer sound analysts for the presence of night flight calls (spectral settings: 1024 FFT size, Blackman window). We used the time and frequency cursors in Syrinx-PC to annotate each night flight call, broadly classifying the calls as ‘high’ calls (those above 5kHz) and ‘low’ calls (those below 5kHz.)

In the second stage of processing, I examined all annotated calls and classified the calls to the correct species or species-group. We used a library of reference recordings, *Flight Calls of Migratory Birds: Eastern North American Landbirds* CD-ROM (Evans and O’Brien 2002) and constructed a classification chart modified from Evans and Rosenberg (2000; see Chapter 2, Appendix 1). After comparing our own recorded flight calls to the reference libraries, I determined that 67 species of night migrants could be classified to the species level (i.e. their night flight calls were distinct at the species level) or into eight distinct bioacoustic categories (details in Chapter 2, Appendix 1). Hereafter, I refer to these categories as “species-groups,”

each comprising multiple bird species that produce flight calls that cannot be distinguished from one another. Any night flight calls that were distorted, too quiet to be visualized, or that did not match our reference library were left as 'unidentified high' or 'unidentified low'.

Banding data

Banding data were collected by two migration monitoring stations that operated mist nets concurrent with our recordings. During the spring of 2012, birds were banded on Pelee Island and at Hillman Marsh Conservation Area from April 15 to June 10. During the fall of 2012, birds were banded on Pelee Island and at Holiday Beach Conservation Area from August 15 to November 10. The banding station on Pelee Island operates 10 mist nets and, as a member of the Canadian Migration Monitoring Network, follows the monitoring protocol recommendations from Hussell and Ralph (2005). The nets at this station were open one half-hour before sunrise and run for six hours, excluding down time when nets were closed due to bad weather (rain or wind) or high bird volume when nets were closed to ensure safe and efficient bird handling. The Holiday Beach Migration Observatory runs both the banding stations on the mainland at Hillman Marsh and Holiday Beach. As a volunteer organization, this observatory's research efforts vary with the availability of volunteers, operating seven nets at Hillman Marsh in spring and sixteen nets at Holiday Beach in fall. In order to standardize the capture effort between the three banding stations, number of net-hours was calculated using a standard method (Ralph et al. 1993). To facilitate comparison to our acoustic data, we created "species-groups" for the banding data by pooling banding records for species that make up each of our acoustic species-groups. For example, Fox Sparrow and Song Sparrow produce very similar night flight calls,

therefore we pool the banding detections for these species into the “loose u” species-group category (see Chapter 2, Appendix 1).

Statistical analysis and sample size

To test whether there were more detections (per species or species-group) over the island or the mainland, we combined the detections for all of the mainland recorders and all of the island recorders, controlled for the number of hours per recorder, and averaged the number of calls per recording station; this produced a relative number of calls per recording station for each species (or species-group). We used Sign Tests to determine whether the number of acoustic detections over the island than was less than the number over the mainland for all of the species and species-groups. We repeated this analysis with our banding data from our island and mainland sites, controlling for the number of net hours at each station. To examine whether some species were detected over the mainland, but not the island, we examined each acoustic dataset for presence or absence of each species or species-group in both spring and fall.

To examine whether there were different dates of first detection on the island versus the mainland, we used Paired T-tests to compare average arrival dates for all species. We pooled the data for the four mainland recorders and the three island recorders, and calculated the average first detection date for all species or species-groups at the mainland and island sites. We performed a parallel analysis using banding data to compare first arrival dates for banding detections at the island banding station and mainland banding station in spring and fall.

RESULTS

We collected 2,157 hours of nocturnal recordings over 58 nights at the seven recording locations during the spring migration, and 4,080 hours of nocturnal recordings over 63 nights at

the same seven recording locations during the fall migration, for a total of 6,237 hours of recordings over the year. Within these recordings, we annotated 60,013 nocturnal flight calls: 22,554 during the spring migration and 37,459 during the fall migration. We were able to classify, with confidence, 46,846 (78% of recorded calls) of the calls into species or species-groups: 16,646 (74% of recorded calls) into 60 categories in the spring recordings and 30,200 (81% of recorded calls) into 48 categories in the fall recordings.

During the spring migration, 834 birds of 62 species were banded on Pelee Island and 910 birds of 69 species were banded at the mainland site. During the fall migration, 2,079 birds of 75 species were banded on Pelee Island and 2,711 birds of 63 species were banded at a nearby mainland site. To facilitate comparison to the night-flight call data, we pooled together banding data for bird species whose night flight calls are indistinguishable so that our acoustic data and banding data were categorized into the same species-groups.

Number of migrants detected on mainland versus island

In the spring, we detected more night flight calls per species (or species-group) on the island than on the mainland (37 species or species-groups were more abundant on the island, 8 were more abundant on mainland; Sign Test: $p < 0.0001$). Similarly, in the fall, we detected more calls on the island than on the mainland (41 species or species-groups were more abundant on the island, 4 were more abundant on mainland; Sign Test: $p < 0.0001$). After controlling for the number of nets and net hours at each of our banding stations, we did not find a significant difference in the number of individuals detected by species or species-group in the spring banding data (16 species or species-groups were more abundant on the island, 14 were more abundant on mainland; Sign Test: $p = 0.86$). However, in the fall, we detected significantly more

migrants per thousand net hours on the island than on the mainland (21 species or species-groups were more abundant on the island, 9 were more abundant on the mainland; Sign Test: $p=0.04$).

Species detected on mainland versus island

Acoustic monitoring revealed that the same composition of species passed over the mainland and the island (Table 3.1). We found no evidence in the acoustic recordings that any species avoided crossing Lake Erie. In spring migration, all species or species-groups were detected in both mainland and island recordings (Table 3.1); in fall migration, American Robins were recorded only on the island, and a single Virginia Rail was recorded on the mainland but none on the island. The banding data show a similar pattern, where the vast majority of species or species-groups were captured in both mainland and island mist nets (Table 3.1). In spring migration, the “double-down” species group was captured in mainland but not island mist nets, whereas Hooded Warbler, Mourning Warbler, and White-crowned Sparrow were captured on island but not mainland mist nets. In fall migration the “double down” species group, Mourning Warblers, Palm Warblers were captured on the mainland but not the island mist nets, whereas a Rose-breasted Grosbeak was captured on the island but not the mainland mist nets. Several species (American Robin, Wood Thrush, and the cuckoos) were detected in spring but not detected in the fall (Table 3.1).

We inspected the spring and fall data and found no substantial differences in the proportion of each species or species-group across the two seasons. Only the “zeep” species-group showed a difference between the spring versus fall; they comprised 1.68% (mainland) and 1.96% (island) of the total identified calls in the spring, but they comprised 15.2% (mainland) and 11.81% (island) of the total calls identified in the fall.

Date of arrival

In the spring, based on the date of first detection for each species or species-group at the mainland and island recorders, we found that birds were detected significantly earlier at the island recorders (island mean Julian date of first arrival: 114.2 ± 1.48 , i.e. April 23; mainland mean Julian date of first arrival: 117.1 ± 1.47 , i.e. April 26; Wilcoxon Sign-rank Test; $W = 154.5$; $p=0.0006$, $n=41$). This matched our prediction that birds would be detected earlier at the more southerly site during the northward migration. In the fall, there was no significant difference between the first Julian day of arrival on the mainland (mean Julian date 257.1 ± 2.58 , i.e. September 13) as compared to the island (mean Julian date 253.9 ± 1.84 , i.e. September 9; Wilcoxon Sign-rank test; $W=73.5$; $p=0.09$). We compared the first detection dates from the island banding station and the mainland banding station, and found no significant difference in first detection arrival dates for spring (island mean Julian date of first arrival: 120.1 ± 1.90 , i.e. April 29; mean mainland Julian date of first arrival 120.6 ± 1.89 , i.e. April 29; t-test; $t=0.51$; $p=0.61$; $n=22$) or fall (island mean Julian date of first arrival: 250.72 ± 5.15 , i.e. September 6; mainland mean Julian date of first arrival: 248.84 ± 4.34 , i.e. September 4; Wilcoxon Sign-rank test; $W=36.0$; $p=0.28$; $n=25$; Figure 3.2).

DISCUSSION

Acoustic monitoring of nocturnal migrants in western Lake Erie showed that migratory birds do not avoid crossing Lake Erie, and that birds likely concentrate over Pelee Island in the middle of Lake Erie on both their northward and southward migration. Island microphones detected significantly more calls in the spring and the fall than the mainland microphones located on the north shore of Lake Erie. Thousands of classified calls over the mainland and the island showed that the migrant communities were similar in composition, although minor seasonal differences were revealed through acoustic monitoring. Species were detected earlier in the spring on the island through acoustics in comparison to the mainland. Based on the differences in the number of birds and the timing of migration, we conclude that Lake Erie does not serve as an ecological barrier to migratory birds, and that crossing over Pelee Island is an especially important migratory route in this region.

Thousands of night flight call detections revealed a substantially greater number of calls over Pelee Island than over mainland Ontario during both the spring and fall migration. The many flight call detections over Pelee Island in the spring and fall implies that birds use the island archipelago in large numbers during migration. This pattern was not as evident in the banding data, which showed significantly more detections on the island in the fall only. The pattern of high rates of call detection may be particularly pronounced on the island since the island's geography could cause a funnelling effect, concentrating birds as they approach the north or south tip of the Island (Evans and Mellinger 1999). Additionally, it has been suggested that geographical features and coastlines can concentrate migrants, thereby increasing the number of flight call detections (Farnsworth 2005). Point Pelee National Park, a peninsula that juts into Lake Erie, may also serve to concentrate birds as they migrate south in the fall (Lincoln

et al. 1998), although our acoustic recorder in the centre of the park did not detect significantly more migrants per hour than the other mainland sites (Point Pelee spring 341.08 calls per 100 hours of recording; Point Pelee fall 452.79 calls per 100 hours of recording; Cedar Creek spring 1157.52 calls per 100 hours of recording; Cedar Creek fall 1035.05 calls per 100 hours of recording; Holiday Beach spring calls 182.88 per 100 hours of recording ; Holiday Beach fall 319.22 calls per 100 hours of recording; McGregor spring calls 524.26 per 100 hours of recording; McGregor fall 1013.16 calls per 100 hours of recording). This idea is supported by an interesting pattern we found where the microphone at the north end of Pelee Island showed higher number of calls in spring, whereas the microphones at the south end of Pelee Island detected far more calls in the fall (spring north end 2906.40 calls/ 100 hours of recording; spring south end 936.04 calls / 100 hours of recording; fall north end 616.93 calls/100 hours of recording; fall south end 1223.01 calls /100 hours of recording).

Although we interpret the higher number of acoustic detections over Pelee Island in both seasons as evidence of more migrants passing over the island, this pattern could also arise if birds increase their calling rate as they pass over islands. While the functions of night flight calls are still controversial, one idea is that they are important in maintaining flock cohesion and communicating directional information to flock mates (Hamilton 1962, Farnsworth 2005). As birds approach a shoreline and detect open water, this may be an especially opportune time to communicate, perhaps to aid orientation between flock mates, leading to higher numbers of flight calls (Farnsworth 2005). However, confirming this pattern requires further investigation at multiple positions, such as microphones mounted in the middle of the lake, away from islands, for direct comparison to island recordings. It is noteworthy that radar research also suggests that birds in active migration may drop in altitude by as much as 9% when crossing bodies of

water (Bruderer and Liechti 1998), which might make them more likely to be detected by our island microphones than mainland microphones. Therefore, a drop in altitude by migrants crossing the island, or an increased calling rate while crossing the island, may contribute to the increases we detected in our acoustic dataset. That we also found higher numbers of migrants in our mist net data, and that previous radar data indicate that the island is an important part of the migratory (Diehl et al. 2003), suggests that these alternative explanations alone cannot account for the higher number of migrants detected on the island.

All songbird species or species-groups were detected by the island recorders in both the spring and the fall, with only very subtle differences in the mist net data. This suggests that the lake itself is not an insurmountable barrier to any of the nocturnal migratory species or species-groups that we studied. This supports previous radar studies demonstrate that nocturnal migrants cross Lake Erie in significant numbers in both spring and fall (Diehl et al. 2003), although radar studies cannot reveal which species are crossing the lake. Our results confirm that all species and species-groups that we could distinguish do indeed cross over Lake Erie in both fall and spring migration. However, the acoustic data implies that members of the “zeep” family (a group including Bay-breasted Warbler, Blackburnian Warbler, Blackpoll Warbler, Magnolia Warbler, and Yellow Warbler) exhibit some kind of lake avoidance in the spring since the proportion of “zeeps” detected in the spring was significantly lower at both the mainland and island sites. The “up” acoustic group of warblers, mostly of the *Oreothlyps* genus (which includes the Tennessee Warbler, Orange-crowned Warbler, Yellow-rumped Warbler, and Nashville Warbler), appear to be more likely to cross the water in the spring and fall and be detected by both mainland and island recorders. These data suggest that some species may be more likely to cross the lake than other species at different times of years.

In the spring, the first individuals from each species or species-group were detected earlier in the Pelee Island recordings than in the mainland recordings. This result matched our expectation and is consistent with the seasonal direction of migration. However, contrary to our expectation, we did not find a similar pattern in the fall when the dates of first detection were not statistically different at the mainland and island sites. If the significant delay that we report between the first detection in the spring on the island versus mainland sites is due solely to the more southerly location of the island, rather than the ecological barrier of Lake Erie, then we might see a similar delay between southerly and northerly sites of the same distance on the mainland. This is unlikely since it is such a short distance (i.e. 15 km from the north shore of Pelee Island to the nearest point on mainland); however further investigation is required to gain a better understanding of whether the delay we detected is due to Lake Erie serving as a temporary barrier to spring migrants, but not fall migrants.

Further examination of the stopover times on the island might elucidate this pattern and demonstrate that birds may be spending a longer stopover on the island in the spring than in the fall, leading to a delay in detection on the mainland. This idea stands at odds with the general consensus that the spring migration window is shorter, with birds flying faster and spending shorter stopover times for many species (e.g. American Redstart; Morris and Glasgow 2001). Furthermore, our banding data showed no significant effect of first arrival date for the spring or the fall, with first detection of each species or species-group arriving at the same time to the island and mainland banding stations. Altogether, these results suggest that acoustics may be a more effective tool for monitoring the arrival dates of many migrants, particularly in the spring, in part because acoustic monitoring allows for sampling far more animals than does banding.

While Lake Erie may not be an insurmountable barrier to migrants, poor weather conditions may amplify the risk of crossing. There is consensus that wind strength and direction, visibility, cloud cover, and temperature all play a critical role in determining the intensity of migration events (Elphick 2007, Gagnon et al. 2011). Low cloud cover may concentrate migrants at lower altitudes, resulting in higher acoustic detection rates (Evans and Mellinger 1999). Furthermore, artificial light may cause disorientation and reorient birds in flight towards the island or cause individuals to increase their calling rate due to disorientation (Evans et al. 2007, Poot et al. 2008). This could be particularly frequent under poor or deteriorating weather conditions when stars are obscured by cloud cover (Farnsworth and Russell 2005, Huppopp and Hilgerloh 2012). An investigation into the composition of nocturnal migrants detected over Pelee Island on nights preceding and during strong winds or precipitation could lead to a better understanding of which species are most affected by poor weather while navigating the Great Lakes.

In the western basin of Lake Erie, acoustic and banding data reveal that Pelee Island is an important geographic feature for migratory birds. Many individuals of all species passed over the island in spring and fall, with little indication that they avoided crossing Lake Erie, suggesting that islands in the middle of potential geographic barriers are important for migratory animals. Given that many species of North American migrants are in decline, monitoring migratory bird behaviour at smaller geographic scopes are important for local management and development decisions in regions where birds are known to concentrate seasonally.

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TABLES

Table 3.1. Number of acoustic and mist net detections in spring and fall at mainland and island stations

Species	Number Acoustic Detections Mainland Spring	Number Acoustic Detections Island Spring	Mist net detections Mainland (per 1000 net hours) Spring	Mist net detections Island (per 1000 net hours) Spring	Number Acoustic Detections Mainland Fall	Number Acoustic Detections Island Fall	Mist nets detections Mainland (per 1000 net hours) Fall	Mist net detections Island (per 1000 net hours) Fall
American Redstart	70	163	10.23	10.09	144	13	21.16	35.50
American Robin	20	16	13.88	8.07	0	15	1.32	1.07
American Tree Sparrow	2	12	0	0	2	180	0.50	0.71
Black-and-white Warbler	7	15	7.31	11.44	166	13	9.59	10.65
Bobolink	14	30	0	0	16	15	0	0
Black-throated Blue Warbler	13	18	2.19	6.05	51	78	16.70	29.11
Canada Warbler	3	17	5.12	14.80	2	5	2.81	2.84
Chipping Sparrow	586	700	0	0	473	594	0	0
Cape May Warbler	10	15	0.73	0.67	41	65	2.48	1.07
Common Yellowthroat	25	50	54.80	18.84	50	99	1.65	2.13
Chestnut-sided Warbler	15	65	8.04	13.45	67	116	4.96	3.91
DOUBLE DOWN	365	711	2.92	0	1921	1922	0.17	0
Dark-eyed Junco	15	14	0	0	40	88	2.81	11.36
Golden-crowned Kinglet	0	0	0	0	76	111	52.57	109.35
Gray-cheeked Thrush	39	51	9.50	10.76	298	238	6.45	61.07
Grasshopper Sparrow	7	31	0	0	1	1	0	0
Hermit Thrush	72	121	18.27	18.16	41	78	10.91	60.36
Hooded Warbler	3	3	0	1.35	1	3	0	0
Indigo Bunting	30	61	7.31	6.05	35	73	0.33	1.07
Killdeer	58	40	0	0	34	12	0	0
LOOSE 'U'	124	505	8.77	0	404	657	2.48	7.10
Mourning Warbler	39	7	0	4.04	1	5	0.17	0

Northern Waterthrush	7	21	7.31	6.05	21	33	1.16	5.33
Ovenbird	72	159	10.23	21.53	93	103	4.96	24.14
Palm Warbler	3	133	5.12	12.78	77	179	0.17	0
Pine Siskin	0	0	0	0	17	10	0	0
Rose-breasted Grosbeak	27	30	0.73	4.04	7	19	0	0.36
Scarlet Tanager	8	10	0	0	4	1	0	0
Single Down	95	228	0.73	0.67	239	271	1.32	0.36
Sora	48	32	0	0	2	3	0	0
Swamp Sparrow/Lincoln's Sparrow	13	46	59.19	14.13	35	69	1.16	2.49
Swainson's Thrush	1175	1865	9.50	19.51	2066	4180	28.93	199.89
Swainson's Thrush/Veery	304	325	0	0	12	35	0	0
Unidentified	1668	4240	0	0	3310	3847	0	0
UP	962	2191	86.23	145.31	2496	2816	28.27	148.76
Veery	218	350	11.69	7.40	87	135	2.31	21.66
Vesper Sparrow	9	3	0	0	10	30	0	0
Virginia Rail	3	16	0	0	1	0	0	0
White-crowned Sparrow	96	143	0	2.02	189	208	0	0
Wilson's Warbler	3	2	4.38	5.38	21	25	6.11	0.71
Wood Thrush	42	73	2.92	5.38	0	4	0.17	1.42
White-throated Sparrow	578	2627	84.03	24.22	1147	3085	11.90	45.80
ZEEP	98	220	62.11	82.07	1871	2126	64.64	54.32

FIGURES

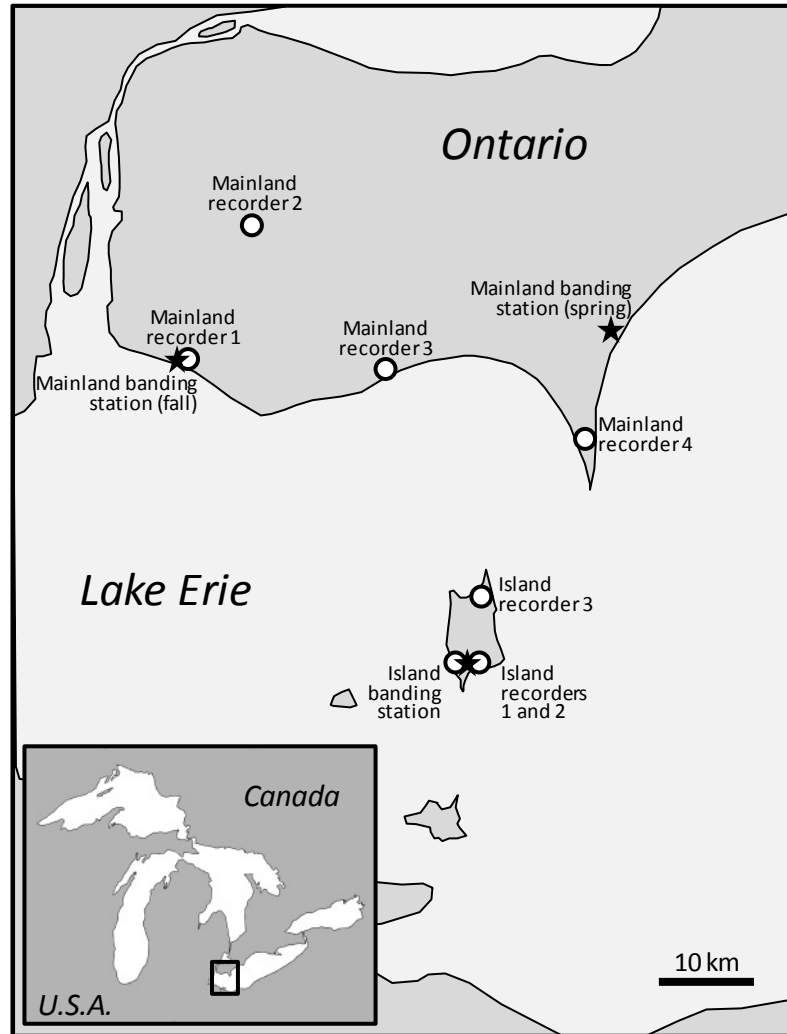


Figure 3.1. Map of Essex County, Ontario, Canada shows the seven acoustic recording locations and the three banding stations.

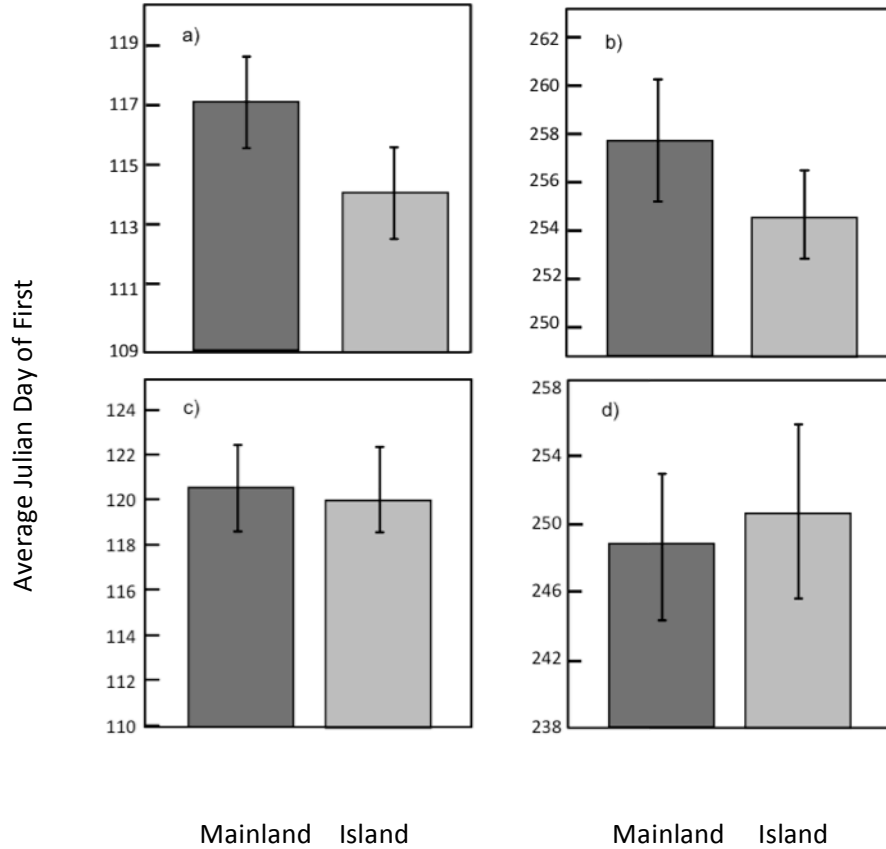


Figure 3.2. Average first acoustic detection dates for migrants crossing the western basin of Lake Erie show significantly earlier arrival of birds detected on Pelee Island, than on mainland Ontario, only in the spring. Dark gray bars represent mainland sites and light gray bars represent island sites. Means \pm SE are shown for: a) spring acoustic data, n=41 species, b) fall acoustic data, n=38 species, c) spring banding data, n=22 species, d) fall banding data, n=25 species (see text).

CHAPTER 4

THESIS SUMMARY

Acoustic monitoring is an established tool for monitoring bird behaviour and bird populations (Haselmayer and Quinn 2000; Celis-Murillo et al. 2003; Blumstein et al. 2011). However, acoustic monitoring has not been used widely to study birds in migration. During their nocturnal bi-annual migratory journeys, many passerines including thrushes, sparrows, and warblers, as well as some non-passerines birds, produce night flight calls (Evans and O'Brien 2000). These vocalizations may play an important role in stimulating migratory restlessness among conspecifics and in maintaining flock contact and orientation for birds on the wing (Farnsworth 2005). Acoustic monitoring of night flight calls is the only method of migration monitoring that can provide us with species-specific identification of birds in active migration (Farnsworth 2009), although little work has been done to ground-truth the efficacy of night flight call monitoring. In this thesis, I analyzed two migratory seasons of acoustic data, and demonstrated that monitoring the vocalizations of nocturnal migrants can play an important role in providing information about the seasonal movement of migrant birds around western Lake Erie.

Using thousands of hours of acoustic data collected at seven recording stations across Essex County, Ontario, and banding data collected at two banding stations, in my first data chapter (Chapter 2) I revealed significant positive relationships between acoustic monitoring and banding. I reported highly significant positive relationships between the date of passage of 10th, 50th, and 90th percentiles of the populations of up to 25 groups of passage migrant species as detected through acoustics and banding. These correlations in the timing of migration in both spring and fall suggest that acoustic monitoring is an effective tool for monitoring the seasonal timing of migrants in the western basin of Lake Erie. When I examined the migration timing of six distinctly identifiable species, I discovered subtle differences between peak detections via acoustic monitoring and banding data in the fall migration season for several species. The lag in

peak acoustic detections behind banding detections may be attributable to age-based differential migration patterns.

Understanding the seasonal distribution of migrants on a small geographic landscape is important for making land use decisions, particularly in Important Bird Areas (IBAs) where concentrations of migrants are known to occur. In my second data chapter (Chapter 3), I used acoustic monitoring to study birds in active migration over the western basin of Lake Erie during their bi-annual migrations. I evaluated whether Lake Erie is a significant ecological barrier for migratory birds along a major North American flyway. Thousands of night flight calls from an array of seven recording stations revealed significantly more night flight calls on Pelee Island than on the mainland, which suggests that many individuals cross Lake Erie in the spring and fall and that Lake Erie does not stand as an impassable barrier to migration. I found no evidence that any species or species-group avoids cross Lake Erie. In spring migration, the average first arrival dates for 48 species or species-groups of migrant birds were significantly earlier on Pelee Island than on mainland Ontario. These data on acoustic monitoring of migrants over the western basin of Lake Erie indicates the importance of islands during migration.

Taken together, these results confirm that acoustic monitoring of nocturnal migrants can play an important role in monitoring migratory birds. An important next step in this research is to widen the scope of comparison data, to investigate the relationship between acoustic monitoring and other techniques for migration monitoring, such as daily visual count data and radar data. As a migration monitoring technique, mist-netting has limitations in that only birds within the immediate vicinity of the mist nets can be sampled, and it is a time-intensive monitoring strategy. Comparison to other techniques might better ground-truth bioacoustic

recordings as a migration monitoring strategy, and reveal the value of using multiple alternative approaches to migration monitoring (see Milliken 2005; Peckford 2006).

For acoustic monitoring to become an efficient technology for monitoring migration, continued effort should be directed towards developing automated call detection software and call classification software. As is typical of bioacoustic research projects, it is easy to acquire very large datasets quickly, but analysis becomes the limiting step. Automated detection software would be very advantageous for processing night flight call recordings, as it has been in other wildlife monitoring programs with very large datasets (Swiston and Mennill 2009).

Unfortunately, the nature of flight calls (very short and sometimes obscured by environmental noise) makes automated pattern recognition very challenging. To date, there has been no processing break-through that allows reliable, automated detection of night flight calls, and this is an important priority for future investigators. Until such a break-through occurs, identification resources and standardized monitoring and reporting methods would continue to benefit night flight call monitoring across North America with the current, manual approach to detection and classification. Research that collects example flight calls with confirmed species identification will help us to understand the inter- and intraspecific species variation that is thought to exist but is poorly characterized to date (Lanzone et al. 2009).

With increasingly fragmented habitats along migration routes, as well as increasing urban sprawl and light pollution around the globe, a better understanding of how birds use night flight calls can inform conservation and management plans. Night flight call monitoring has already been used as a technique for assessing migrant bird distribution in relation to wind turbine development, offshore oil platforms, and aircraft sites (see Evans 2000, Farnsworth and Russell 2005, Farnsworth et al. 2009). In light of this, additional research on using flight call monitoring to assess environmental effects of anthropogenic development on migratory species

or species-at-risk would be worthwhile. There is a growing understanding that ambient light affects night flight call detection (Evans 2007), which may have influenced the data I collected here. It is important to quantify the effect of anthropogenic light on the migration paths of birds, and its effect on night flight call monitoring, to ensure that artificial lights do not confound future migration monitoring studies. The use of passive acoustic technology to estimate animal population density an emerging field but being able to estimate “cue rates” for migrant bird species in relation to environmental and endogenous influences is fundamental to being able to estimate density of migratory flocks using this technique (Marques et al. 2013).

While much of the current research in this field has focussed on acoustic recording of nocturnal songbirds (Evans 2005, Farnsworth 2005) this technique may be an important opportunity to further the field of shorebird, rail, and heron migration ecology. Further investigation as to the accuracy of identification and accuracy in monitoring these taxa could be important for monitoring in regions across the globe that are important for shorebird passage. Additionally, determining the sensitivity of the recording equipment and an investigation into what distance birds are using flight calls to communicate across is also prudent to furthering this field, both for passerines and other avian taxa (Farnsworth 2005). This will allow us to better understand the range of animals being sampled, which will help us to gain insight into the usefulness of the technique at a landscape scale. Simultaneous radar and acoustic studies would help to elucidate some of these questions.

Continued broad-scale acoustic studies over multiple seasons will validate patterns of geographic and temporal differences in migrant distribution in Essex County, Ontario that I have described in this thesis. Acoustic monitoring studies of migrant birds beyond the Great Lakes system would play a significant role in revealing whether the patterns I described are paralleled

in other ecosystems and may help to clarify the role of acoustics for monitoring birds in migration globally. Through this research, I have shown that there is undoubtedly an opportunity for a more broad scale use of acoustic monitoring in avian migration monitoring, which is widely recognized as an important conservation priority (Kirby 2011).

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VITA AUCTORIS

Claire E. Sanders

Place of Birth: Edmonton, Alberta

Education:

2011-2013 MSc., University of Windsor, Windsor, ON

1995-1999 BSc., University of Alberta, Edmonton, AB

Work Experience:

2011-2013 Graduate Teaching Assistant, Biological Diversity, University of Windsor, ON

2010-2011 Supply Teacher, Grades K-8; Pelee Island Public School, Pelee Island, ON

2006-2012 Executive Director, Pelee Island Bird Observatory, Pelee Island, ON

2004-2006 Director, Saskatchewan Burrowing Owl Interpretive Centre, Moose Jaw, SK

2002-2004 Research Assistant, University of Arizona, WA, USA

2003 Environmental Educator, Mountain Trail Outdoor School, NC, USA

2001 Research Assistant and Naturalist, Creston Valley Wildlife Management Area, BC

1997-2000 Research Assistant, Department of Anthropology, University of Alberta, AB

Conference Presentations:

2012 Sanders, C., M. Watson, and D.J. Mennill. 2012. Poster Presentation: Acoustic monitoring of migrants over Lake Erie. North American Ornithological Conference (NAOC), Vancouver, BC

Volunteer Positions:

2013 Bird Bander, Holiday Beach Migration Observatory, ON

2013 Director, Essex County Field Naturalists Board of Directors, Windsor, ON

2009-2011 Secretary of the Board of Directors, Pelee Island Artworks, Pelee Island, ON

2005-2006 Secretary of the Board of Directors, Nature Saskatchewan, Regina, SK

2005-07 Director, Moose Jaw Tourism Board of Directors, Moose Jaw, SK