UTILIZING ACOUSTIC RECORDERS TO INVESTIGATE THE MIGRATORY BEHAVIOR OF SOME SPARROW AND WARBLER SPECIES ALONG THE OHIO COAT OF LAKE ERIE

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The current study utilizes passive acoustic recording of nocturnal flight calls to determine if during active migration 5 species of songbirds respond differently to Lake Erie when reaching the narrow and island-filled Western basin compared to the more open water topography of the Central basin. Overall, migrants were more likely to fly over the western basin compared to the central basin. Seasonal analyses revealed that Savannah Sparrows (Passerculus sandwichensis), White-throated Sparrows (Zonotrichia albicollis), and Double-banded Up Group (Nashville (Vermivora ruficapilla), Tennessee (Oreothlypis peregrina), Black-throated Green (Dendroica virens), and Orange-crowned (Vermivora celata)) warblers demonstrated a higher propensity to cross in the Western basin. Chipping Sparrows (Spizella passerina) and American Redstarts (Setophaga ruticilla) showed no difference in their tendency to cross the Western basin compared to the Central basin. Examining single nights, a similar pattern emerged, but further revealed that the propensity of birds to cross varied between species and prevailing wind direction. Notably, a greater abundance of calls was observed over water in the Western basin under seasonally opposing north winds. Although there are some potential confounds in interpreting the data, the results generally support the conclusion that, as previously reported, Western Lake Erie is more amenable for migratory lake-crossings.
This Thesis and all the hard work it entailed is dedicated to my parents. Without their support and motivation none of this would have been possible.

"The truth of the matter is, the birds could very well live without us, but many, perhaps all of us would find life incomplete, indeed almost intolerable without the birds."

-Rodger Tory Peterson
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INTRODUCTION

Bird Migration

Migration in birds can primarily be defined as a two way seasonal movement between breeding and non-breeding or wintering areas. Why do some bird species migrate? Most theories of proximate causation focus on food availability, temperature and photoperiod. Ultimate causation is believed to include a decreased risk of predation, increased incubation and nestling periods. Quite simply, during summer months there is more food available at more extreme North/South latitudes due to seasonal changes. During summer months day light time is longer than at equatorial latitudes, allowing for nearly 15 hours of daylight in Ohio at the summer solstice. This increase in day length allows for increased opportunity to forage and feed offspring. Migration, however, is time and energy consuming. Nevertheless, each year countless numbers of birds migrate from tropical regions north in order to take advantage of seasonal fluctuations of food resource availability. These birds often display a set of characteristics known as migration syndrome. Migration syndrome can involve evolutionary changes in morphology, the acquisition of orientation and navigation skills and behavioral adjustments in relation to ecological and external factors (Dingle 1996, Piersma et al 2005, Hendenstrom 2008). Migratory birds are faced with the arduous task of crossing thousands of kilometers in a race to procure the best resource and breeding territories.

Migration through the Great Lakes

The Lake Erie coastline of Ohio has become an important stopover site for birds migrating through the Eastern United States. The Great Lakes represent a potentially large geographical barrier to birds, covering nearly 250,000 km$^2$ of open water and stretching 1,400 km east to west. Previous work has documented that evolution changes over time may have enabled birds to survive extended trips across harsh terrain (Biebach 1995). However, the
behavior of migratory birds over the Great Lakes is poorly understood (Hussell et al. 1992). To complicate matters, different sexes, ages and taxa likely respond differently when confronted with coasts and other geographic barriers during migration (Dorst 1962; Dunn and Nol 1980). Radiotracking work around Lake Michigan has revealed that *Catharus* thrushes, such as the Veery (*Catharus fuscescens*) or Swainson’s thrush (*Catharus ustulatus*); often engage in open crossing over Lake Michigan (Cochran et al. 1967, Cochran 1972). Recent work utilizing weather radars and locally deployed radar systems have been able to map movements of birds across the Great Lakes. Utilizing radar reflectivity, researchers are able to record movement of birds as they reach the coast and can determine potential open water paths that birds take to cross the Great Lakes. This research has shown that nocturnally migrating landbirds do cross the Great Lakes (Figure 1) including Lake Erie (Figure 2), but radar alone tells nothing of which species specifically are crossing open water (Diehl et al. 2003). Weather or Doppler Radars operate by sending out concentrated sweeps of radio waves traveling near the speed of light that strike objects and return to the receiver as an echo. Based on the time, direction and strength of the returning radio waves or echo the receiver can calculate the distance and size of the object (NWS 2010). Reflectivity measured in dBZ (decibels of Z or reflectivity) is a measurement of the amount of reflected radio waves that return to the receiver from rain drops, hail or birds.

Knowing that birds routinely migrate across the Great Lakes raises perhaps more interesting questions about differences in species propensities to cross the Lakes. Until we have studied and know which families and species of birds are actively crossing, it is difficult to determine how to go about conservation measures in the future. As stated above, most methods currently in use for tracking migration of birds are limited and surely no one method will reveal every aspect of bird migration. Recently, the use of Autonomous Recording Units or ARUs have
allowed researchers the opportunity to deploy preprogrammed acoustic recording equipment into the field to monitor avian flight calls produced during migration.

Importance of Great Lakes for Migration

The coastal wetlands on the southern coast of Lake Erie provides exceptional habitat for stopover migrants, providing ample resources to refuel between migratory events. These coastal wetlands of Lake Erie contain many important stopover habitats that seasonally observe high abundances of migrant songbirds. Compared to other Great Lakes areas, the southern coast of Lake Erie sees significantly higher numbers of stopover migrations (Shieldcastle et al. 2004). The coastal habitats provide a massive food resource vital to refueling during migration. Many studies have shown that insect larvae such as midges contribute significantly to the diet of many migratory songbirds including American Redstarts and Black-throated Green Warblers (Smith et al. 1998 and Smith 2005). However, this region also contains many ecological barriers that might impact the behavior of migrating songbirds such as, large agricultural areas, cities, rivers and lakes. The impact of factors such as wind on orientation errors often increases when migrants face ecological barriers during migration (Alerstam 1990). How species and individuals behave when confronted with ecological barriers remains largely unknown. There are more potential risks to migration than the lake itself. For example, offshore wind turbine development has long been discussed as an eventuality in the Southern Lake Erie region. Few concrete studies have been done to determine the effect that these wind farms may have on migratory birds. Huppop et al (2006) concluded that almost half of the birds observed (aloft over the South-eastern North Sea) fly at ‘dangerous’ altitudes, in the height region of turbine blades. They also demonstrated that, especially under poor visibility, birds are attracted to illuminated offshore objects and some species, passerines most frequently, risk collision (Huppop et al 2006). However, large gaps still remain in our knowledge of how and which species of birds take on such potentially dangerous lake crossings.

Monitoring Techniques
Enormous numbers of birds migrate each year, yet large gaps still remain in our understanding of where birds choose to breed, stopover and overwinter (Robinson et al 2009). Though countless taxa of organisms migrate, birds are among the most often studied migratory animals (Robinson et al 2009). Understanding not only the behaviors observed at breeding and overwintering grounds, but also behavior exhibited en route during migration, are fundamental to conservation and management of all migratory animals including birds (Robinson et al 2009). Though a wide variety of emerging technologies exist for the tracking of migratory birds, such as PTT radio tags (high frequency telemetry), geolocators, satellite telemetry and historically, radar imaging, all have their inherent uses and limitations. Radio tags are able to pinpoint an individual animal’s locations in space but are often too large for small birds and can influence behavior (Cochran et al. 2004, Thorup et al. 2007). Geolocators, which were primarily used in seabirds but have become small enough for medium sized passerines, require recapture in order to retrieve and access data (Burger and Shaffer 2008). Satellite telemetry is often too expensive to access data and accuracy can be low unless combined with GPS information. The minimum size of satellite telemetry tags are around 8 grams and GPS tags are around 22 grams, too large for even the largest warblers of around 18 grams (Berthold 2001). Radar uses broad sweeps or pulses to measure speed, intensity and direction of migration but species identification is completely absent and low flying birds might be missed (Gauthreaux and Belser 2003). Still other laboratory techniques such as using genetic markers or chemical isotope analysis exist. Utilizing genetic markers can be costly and often too little genetic variation exists within a species (Lovette et al. 2004). Chemical analysis of isotopes in the tissues or feathers of birds provides at best a rough estimation of location, but environmental isotopes vary greatly with elevation. Furthermore, North America isotope differences provide better North-South resolution than East-West. Finally, although historical isotope maps of North America are well
documented, many other regions are less complete or absent (Hobson and Wassenaar 2008). Birds too small to carry tracking devices are generally monitored as they pass through observational fields created by portable radars, thermal cameras, or microphone arrays (Robinson et al. 2008). Acoustic recording can also be used to monitor nocturnal migration. Acoustic recording combines the fields of bioacoustics and ornithology to record, isolate and interpret the wide variety of calls produced by birds during their migration. Even this technology, is not without its limitation, and only recently has it been possible to identify species more accurately by spectral analysis. Also, acoustic targets are prone to masking from outside interference such as wind, weather and other non-focus organisms. The field of bioacoustics, nevertheless, is growing rapidly, and as the technology improves, vocalizations may play a larger role in understanding behavior.

Bioacoustics

Bioacoustics is the study of the production, detection and interpretation of sounds by biological organisms (Evans and Mellinger 1999). Animal sounds vary widely in their characteristics and functions. Elephants are well known to communicate using very deep, low frequency, infrasonic (0 Hz - 16 Hz) tones, whereas bats that utilize echolocation produce calls that range above 20 kHz. Bird vocalizations such as songs and calls are generally found within the audible range of humans between 20 Hz - 20 kHz. Bioacoustics and monitoring of avian nocturnal flight calls has been around for more than century. Orin G Libby is credited as among the first to quantify nocturnal flight calls of migrating song birds, at the University of Wisconsin in 1899 (Libby 1899). It wasn't until the 1950's that technology allowed for the passive recording of nocturnal flight. This work done by Graber and Cochran (1957) involved recording every night and playing back the audio tapes the following day. Species level identification of flight calls based solely on audio playback, however was difficult and required intensive training
Evans 2005). New advances over the past few decades have allowed researchers to place smaller, discrete and self-contained acoustic recording devices into the field in order to capture sounds produced by various animals. The sensors utilize microphones in order to capture sound waves and convert them into electrical signals that are then stored electronically for future extraction. The extraction can involve the use of interpreting software that can process the electrical signals and display them visually as spectrograms. Spectrograms are graphical representations that map the spectral density, both frequency and amplitude, as a function of time (seconds).

Avian Vocalizations and Flight Calls

Bird vocalizations encompass a wide array of songs and calls, each used in a specific context. Songs are generally the most complex of bird vocalizations; they are almost exclusively observed in the order Passeriformes (song birds), but also occur in hummingbirds (Apodiformes). Songs are normally reserved for territory marking, family identification and most commonly courtship and breeding. Songs generally consist of notes or elements, syllables and phrases composed in a hierarchical structure where single notes can combine to form syllables and multiple syllables make up phrases (Brenowitz et al 1997). Typically song birds are highly social, and as such utilize a variety of songs and calls for specific purposes (Thorpe 1961).

Birds generally have 5 to 14 distinct calls that often overlap in their contextual functions (Thorpe 1961; Armstrong 1963). Among those types of calls are included social, injury, aggressive, alarm (various threat levels), active courtship and flight calls. Flight calls are defined as the primary vocalization given during sustained avian flight, most commonly during prolonged periods such as migration (Evans and O’Brien 2002). Flight calls are generally believed to be utilized for the purpose of flock coordination and cohesion during diurnal and nocturnal flights, though they have been observed during foraging and breeding times (Marler
2004). Many birds, including but not limited to passerines, produce these vocalizations, which are usually short in duration (usually less than a second and frequently less than half a second), high in frequency (in the 2-10 kHz range for most passerines), and produced while migrating at night (Ball 1952, Graber and Cochran 1959, Evans and Mellinger 1999). Flight calls are easily distinguishable and distinct from other types of short call notes such as “chips” or alarm calls (Farnsworth 2005). However not all species of birds produce flight calls, and those that are known and recorded for reference are generally from diurnal flights because they must be positively identified by sight (Evans 2005). Although flight calls are brief in duration, they are still strikingly varied, generally species-specific and vary greatly in their rise and fall of frequency, duration and repetition. These aspects make flight calls well suited for the study of some aspects of bird migration. For many avian groups changes in vocal frequencies correlate with changes in body mass or bill length. Inverse or negative relationships have been found between body mass or bill length and song/call frequencies (Wallschlager 1980, Palacios and Tubaro 2000). As such, species with a smaller mean body mass and shorter bill length generally have a higher frequency flight calls. Warblers and sparrows for example, produce calls between 6-9 kHz, while larger passerines such as thrushes produce calls between 2-4 kHz. For examples, Figure 3 displays the flight call of a White-throated Sparrow (*Zonotrichia albicollis*).

**Applications for Flight Calls**

A large number of ornithological studies have utilized flight calls to investigate behavior and migration. Flight calls have been used extensively in discerning differences among taxa (Mundinger 1979, Farnsworth and Lovette 2005). Flight calls may also be used to help provide insight on habitat preference (Groth 1993). There are also potentially useful applications of monitoring flight calls for describing species level nocturnal movements (Ball 1952; Graber and Cochran 1960; Evans 1994). Studies utilizing flight call counts can be useful in determining the
abundance of birds aloft as well as relative proportions of species on different nights (Larking et al 2002; Farnsworth 2005). Local topography has an influence on the amount of calls observed; features such as mountain, hills and coastlines all appear to concentrate flight calls (Evans and Mellinger 1999). Several relationships exist between flight call counts and atmospheric conditions. Counts increase with increasing cloud cover, at boundaries between opposing air masses, and with seasonally appropriate tail winds (Cochran and Graber 1958, Evans and Mellinger 1999, Peterssen 1956, and Graber and Cochran 1960). The largest gap in our understanding of migration around the Great Lakes and Lake Erie remains, which routes are species taking through this geographical area and how do they come to occupy specific stopover habitat (Diehl 2003). Nocturnal flight calls can be effectively used to discern the movement of birds through a regional geographic landscape.

Study Goals and Assumptions

The intent of the study was to determine if the likelihood of different migrant species/group crossing Lake Erie was higher near the Western basin compared to the open water flight of the Central basin. We assumed (but see Discussion) that migrants reach Lake Erie from the south from different source populations represented by our land recording sites, and that the likelihood of a lake crossing could be assessed by comparing the seasonal and nightly ratio of the number of birds recorded at the over-water site compared to the over-land site for each basin. The expectation was that for at least some species/group the ratios would be higher in the Western basin where the topography is more conducive for a crossing to occur.
HYPOTHESES

The proximity of the Western basin to the Lake Erie Island chain and its shorter between coast distance renders this basin more accessible as a Lake Erie crossing than the Central basin. If true, a higher ratio in the number of calls detected at the over-water site compared to the over-land site is expected in the Western basin compared to the Central basin. Not all species will respond in the same way to the differences in the Western and Central basins, and ratios are also expected to be influenced by wind direction and speed as these will influence the costs of a more extensive over-water flight.
METHODS

Data Collection

To record nocturnal flight call activity of migrating passerines, four Autonomous Recording Units (ARUs), Wildlife Acoustic Song Meters (model: SM2+; Wildlife Acoustics Inc., Concord, MA, USA) were deployed at four sites along the Southern Lake Erie Coast during Spring 2012 and Spring 2013. All four ARUs were equipped with SMX-NFC Night Flight Call microphones (model: SMX-NFC; Wildlife Acoustics Inc., Concord, MA, USA). The microphones are specially designed to record sounds originating from above the instrument in a 125 degree arc. The design of the microphone creates a pressure zone that provides an up to a 10 decibel increase in amplitude of sounds originating from above the microphone over those emanating from the sides and below. The recorders were set to factory specifications for a gain +48 dB, and high pass filter to additionally attenuate low frequency signals. The units house an internal memory supply of flash memory or SD format cards, with up to four usable card slot per recorder. Depending on location ample memory was supplied in each recorder to help ensure no loss of recording nights between servicing recorders. Power was supplied by either four internal D-cell batteries on land or through an external six volt battery at water sites to provide extended unit life. Recordings were sampled at 22 kHz to ensure all calls up to 10 kHz were adequately recorded. The SMX-NFC microphone is designed to operate only through a single channel and
as such can record only in mono meaning only one signal is being recorded. Recordings were made at each site from 0.25 hours post civil twilight, approximately 20:45 local DST, to 8 hours post, approximately 4:45 local DST or 0.25 hours prior to civil twilight. Recorders were left to record from late April to early June to coincide with peak songbird migration. Microphones were leveled to ensure uniform vertical detection at each site.

Study Sites

Four sites were utilized in this study, two at the Western basin of Lake Erie and two at the Central basin of Lake Erie, with each basin pair consisting of one over-water and one over-land site (Figure 4). For the Western Basin over-water site, the recorder was located on West Sister Island, part of Ottawa National Wildlife Refuge, located 12.8 km from the Ohio coast at coordinates (41°44′21″N 83°6′20″W). The over-land site was the Ottawa National Wildlife Refuge's headquarters near Oak Harbor, Ohio, and was located approximately 3.2 km from the coast (41°36′24″N 83°12′42″W). The over-water site for Central basin was the Cleveland Municipal Water District Intake Crib located 7.0 km from the shoreline and within sight of Cleveland (41°32′54″N 81°45′0″W). The over-land site was French Creek Nature Center in Sheffield Village, Ohio situated 3.5 km from the coast (41°27′37″N 82°5′57″W).

Feature Extraction

Recordings were visualized as spectrograms using Wildlife Acoustics Song Scope v4.1.1 software (Wildlife Acoustics Inc., Concord, MA, USA) at 22050 Hz, 256 fast Fourier transform (FFT), 1/2 FFT overlap and a one second background filter. Spectrograms were visually screened for nocturnal flight calls and assigned to a species or species groups (see below) by utilizing known species examples provided by William R. Evans (Old Bird Inc., Ithaca, NY, USA). Intraspecific calls were screened by counting only a single call per 30 second time window; this is elaborated further in the discussion section. For the seasonal analysis, data from
recording nights in which rain was present at any one recording site were excluded due to the inability to identify flight calls. For the seasonal analysis, data were also excluded for nights in which one recorder failed due to loss of battery power or malfunction. Of the nights used in the seasonal data analysis, 5 hours of recording data were processed at each site from 3 hours post civil twilight, approximately 23:45 local DST, to 8 hours post, approximately 4:45 local DST or 0.25 hours prior to civil twilight. The data were broken down by the number of individuals of each species/group recorded for each of the four recording sites for each recording night.

Study Species

Species and species groups recorded in this study are all common biannual passerine migrants (Figure 5). Two families of birds are represented in the study: Emberizidae (sparrows) and Parulidae (warblers). These species/group were chosen based on ease of detectability. All species or species groups in this study have specific flight calls easily distinguishable from other species/group specific flight calls. The Emberizids consisted of regionally common Savannah Sparrows (*Passerculus sandwichensis*), Chipping Sparrows (*Spizella passerina*), and White-throated Sparrows (*Zonotrichia albicollis*). The Parulids consisted of American Restart (*Setophaga ruticilla*) and the Double-banded Up Group (DbUp). The Double-banded Up Group consisted of four species, the regionally common Nashville (*Oreothlypis ruficapilla*), Tennessee (*Oreothlypis peregrina*), and Black-throated Green (*Setophaga virens*) Warblers, and the rarer Orange-crowned Warbler (*Oreothlypis celata*). Crucially, what unites the five species and species groups is that they all emit easily identifiable and distinctive flight calls (see inter-observer reliability analysis below). The larger species group characterized by the "zeep" call complex was not analyzed because the group consists of eight species of warblers, which we considered too robust to draw any informative species-sensitive conclusions. Thrushes (family *Turdidae*) were also not analyzed due to gull activity at both over-water sites. The presence of
nocturnally calling gulls masks the lower frequency end of Thrush flight calls, making isolation and identification of their calls difficult.

Data Analysis and Statistics

For the seasonal analysis, for each species or group the ratio of bird calls sampled at the water site over the number sampled at the corresponding land site was computed for each basin. Recall, the seasonal data were only taken from nights when all four recorders were operational and no rain was present. As an illustrative, fictional example, 215 Savannah Sparrow calls were recorded at West Sister Island and 258 recorded at Ottawa NWR in the Spring of 2012. The resulting calls sampled would result in a calculated ratio of 0.83. To compare the ratio between basins for each species/group, and indirectly assess differences in how the species/group responded when they reach the lake at the Western and Central basin, a chi-square test was used to calculate whether a significant difference was observed. All calculations were performed using SPSS v17, Significance was set at $p < 0.05$.

To supplement the seasonal analysis, An ANCOVA was carried out to further understand the potential effects of basin, wind direction and wind speed on the ratio. Ratio scores for a species/group used in the ANCOVA were taken from single nights when a minimum of 10 total flight calls were recorded from one site and at least one call for the same species/group from its basin-companion site. All possible nights were included in the ANCOVA regardless of activity at the other basin. Wind direction was determined by averaging the prevailing wind direction at a basin every hour for five hours during the period of data collection. Wind directions were determined separately for each basin, from recorded data by the National Weather Service (Toledo, Ohio/Western Basin, Cleveland, Ohio/Central Basin). For the ANCOVA, wind directions were coded categorically based on cardinal direction, North 315 to 45 degrees, East 45 to 135 degrees, South 135 to 225 degrees and West 225 to 315 degrees, and were each given a
nominal value of 1,2,3 and 4, respectively. Wind speed was again determined by averaging wind velocity (m/s) every hour for five hours during data collection from the same National Weather Service monitoring stations. Wind Speeds were input into the ANCOVA as a scalar covariate. Basin and Species were both coded categorical and given nominal values to represent basin, West and Central, and species, Savannah Sparrow, Chipping Sparrow and Double-banded Up Group (too few White-throated Sparrows and Redstarts were recorded to be included in this analysis). The ANCOVA, was carried out using SPSS v17. Significance was again set at $p < 0.05$.

Inter-observer Reliability

The validity of our study is dependent on accurate assignment of recorded flight calls to species/group. To test the reliability of our identification protocol, a flight-call identification trial was carried out with a second observer. After training to visually identify the flight calls of our 5 species/groups, the control observer was asked to identify 105 sound files with respect to which species/group they belonged to. As foils, the sample presentation also consisted of flight calls from birds not included in our study and background or other non-avian biotic noises. The sample consisted of 60 sound files from the study’s species/group and 45 sound files of bird calls from other species and noise. Each sound file was then scored by the control observer as specifically one of our species/group, e.g., Redstart, other species bird call or noise, and those selections were compared to my identification of the same 105 sound files. The short audio files were visualized at the same settings as above (see Feature Extraction) and displayed visually using GlassofFire software (Old Bird Inc., Ithaca, NY, USA). Calls were identified visually by cross-referencing against a set of known call spectrograms. The inter-observer reliability score recorded between myself and the control scorer was 95.3%, demonstrating that the calls of the
species/groups used in our study were easily discriminable in a way that varied little across observers.

Recorder Sensitivity and Species/Group Detectability

All four recorders were tested to ensure uniform flight-call detectability for all four microphones and recorder sets. A terrestrial horizontal test was conducted on all four setups simultaneously using sample calls from all five species/group used in this study. Spectrograms for each setup were created from sample calls played at a distance of 100 meters from the microphone array. Figure 6 displays the spectrograms recorded from all four setups for all the call groups used in the study. It is clear that all four recorders displayed a similar degree of sensitivity and consistency across recorders.
RESULTS

All Bird

Summarized in Table 1 are the flight call data for all species/group during the two field seasons. Figure 7 shows the water to land ratio of all birds, regardless of species/group, observed for each basin and year. In Spring 2012, the frequency of calls recorded over water and over land was significantly ($\chi^2 (1)=50.38$, $p<0.001$) different with regard to basin. Fewer birds were recorded in 2013, and no significant effect of basin was found ($\chi^2 (1)=0.778$, $p=0.378$), although the ratio of water to land birds was still higher over the Western basin. The data are in general agreement with the hypothesis that upon reaching the Lake Erie coast more migrants continue over the lake at our observation point in the Western basin compared to the Central basin observation point, and are consistent with courser scale analyses of radar observations showing the same pattern (Diehl 2003).

Emberizidae

Savannah Sparrow

Figure 8a shows the water to land ratios recorded from Savannah Sparrows. As would be expected, fewer birds were recorded over the lake deployment sites compared to the land sites. For both years, the frequency of birds observed over water and over land differed with respect to basin. The Western basin saw more birds continuing over water compared to the Central basin (2012, $\chi^2 (1)=8.75$, $p<0.05$; 2013, $\chi^2 (1)=5.04$, $p<0.05$). The higher relative number of Savannah Sparrows observed crossing our observation point in the Western basin indicates that Savannah Sparrows are one species whose in-flight behavior is influenced by differences in topography along and in Lake Erie. This statistical relationship is reinforced in the pooled data across both seasons ($\chi^2 (1)=12.84$, $p<0.001$).
**Chipping Sparrow**

Figure 8b shows the water to land ratios recorded from Chipping Sparrows for Spring 2012 and 2013. Like the Savannah Sparrows, more birds were recorded over the deployed sites compared to the water sites. However, for both years, the ratio was only slightly higher in the Western basin, and in neither year was a significant difference found (2012, $X^2 (1)=0.295$, $p=0.587$); 2013, $X^2 (1)=0.074$, $p=0.785$). Even when pooling the data across both seasons, there where no significant difference between the Western and Central basins ($X^2 (1)=0.375$, $p=0.540$). Unlike the Savannah Sparrows, Chipping Sparrows seemed to respond similarly to the topography of the Western and Central basins.

**White-throated Sparrow**

Figure 8c shows the water-to-land ratios observed for White-throated Sparrows from Spring 2012 and 2013. While for both years the ratio at the Western basin was higher (although very few White-throated Sparrows were recorded in 2013), the counts themselves demonstrate an unexpected phenomenon. The ratio at the Western basin exceeds a ratio of 1 revealing that more birds were observed over-water than over-land. 2012 was associated with a significant difference between Western and Central basins ($X^2 (1)=54.96$, $p<<0.0001$). No significant difference was recorded in 2013 ($X^2 (1)=2.213$, $p=0.137$), but this is not surprising given the low number of birds recorded and the general conclusion is supported by a chi-square applied to the pooled data ($X^2 (1)=80.903$, $p<<0.0001$). In some sense then, the White-throated Sparrows seem to be responding to differences in the topography of the Western and Central basin similar to the Savannah Sparrows. However, they clearly differ from every other species/group studied in that more birds are actually being recorded at our Western basin recording site. However, it is noteworthy that on one night, May 7th 2012, the recorded calls were greater over the Western basin water site than the control land site. However, even when this night is removed from the
analysis, the ratio over the Western basin still approaches 1, and a significant between-basin difference remains (2012; $X^2 (1)=172.27$, $p<<0.0001$).

**Parulidae**

*American Redstart*

Figure 9a shows the water to land ratios of American Redstart calls observed at each site by basin and year. Again as expected, fewer birds were recorded over water compared to over land control sites. Acknowledging that Redstarts were recorded less than any other species/group, no general trend can be observed in the data between Spring 2012 and Spring 2013. As can be intuited from Figure 10a, no differences in the frequency of birds observed between basins were found in 2012 ($X^2 (1)=0.236$, $p=0.627$), 2013 ($X^2 (1)=0.748$, $p=0.387$), nor was a difference found when the data are pooled across both seasons ($X^2 (1)=0.020$, $p=0.888$). Redstarts appear indifferent to the differences associated with the topography associated with our Western and Central basin recording sites.

**Double-banded Up Group**

Figure 9b shows the water to land ratio for the Double-banded Up group (DbUp) of birds for each basin and year. Generally, the DbUp group displayed the expected pattern of more birds recorded over land compared to over water. However, the Western basin in Spring 2012 had a ratio of 1.04 indicating a similar number of birds recorded over land and water. The Spring 2012 season was associated with a significantly different ratio of birds over the Western basin compared to the Central basin ($X^2 (1)=16.48$, $p<0.001$). Fewer birds were recorded in Spring
2013, but enough were observed for us to conclude that the lack of statistical difference between the Western and Central basin ($X^2 (1)=0.277, p=0.599$) was an accurate reflection of what was occurring in the field in 2013. Pooling the data from the two seasons resulted in a significant difference between basins ($X^2 (1)=64.147, p<0.001$). Overall, the ratio pattern for the DbUp group is complex, but at least under some conditions some species in this group were responding to topography differences between the Western and Central basin recording sites.

Factors Explaining the Night-to Night Variation in Ratio Scores: Analysis of Covariance

The data presented above are based on the whole-season pooling of data for the species/group. However, they say nothing about how factors such as wind speed and wind direction may interact to influence the basin-ratio pattern on single nights. To assess the night-to-night variation in ratio pattern, we carried out an ANCOVA using the two species, Savannah Sparrows and Chipping Sparrows, and the Double-banded Up group that had enough nights with at least 10 birds recorded at one recording site and at least 1 bird recorded at its companion basin site; i.e., the two recording sites at the Western basin or the two recording sites at the Central basin. The ratio on a given night served as our dependent variable and species, basin, wind direction and wind speed as our independent variable (see Methods).

Summarized in Table 2 are the results of the ANCOVA. Rather than summarize the entire analysis, we have chosen to discuss what we believe are the most interesting, significant interactions (significant main effects were found for species and basin (Table 2), which was expected given the whole season analyses analysis, but also wind direction).
**Basin-Wind Direction-Species Group Interaction**

The nightly analyses demonstrated a main effect of basin (p<0.001), with clearly higher ratios recorded in the Western basin compared to the Central basin. The ANCOVA also revealed a significant wind direction-basin interaction (p<0.001). Post-hoc analyses revealed that for all ratios recorded, a significant difference exists among nights in the Western basin on nights with seasonally-opposing northerly winds compared to southerly winds (p<0.001), with northerly winds associated with higher ratios (Figure 10a). In the Central basin no significant difference was found between nights with northerly and southerly winds (Figure 12b; p=0.586).

Figure 10a suggests that on single nights with a larger number of migrants aloft, Chipping Sparrows were most influenced by the interaction of wind and topography of the Western basin recording sites, DbUps were also clearly affected by this interaction and Savannah Sparrows were affected the least; an impression supported by the ANCOVA. A significant basin-wind direction-species/group interaction was revealed by the ANCOVA (Table 2; p<0.01). Post-hoc analysis could not be carried out due to the low number of nightly ratios present under certain conditions, however a few trends are evident in Figure 10. Figure 10a suggests that all three species/group are reacting differently to changes in topography around the Western basin with opposing northerly winds. Figure 10b suggests in the Central basin all three species/group are unaffected by local topography and prevailing wind direction.

One curious finding from the single night analysis is that on the three nights when Chipping Sparrows and DbUps were counted in large numbers (>10) in the Western basin under northerly winds, they showed considerably higher ratios (12.0, 7.0 and 1.75) than they did overall for the season. This observation suggests that whatever factors promote a large migration
DISCUSSION

The Relationship between Basin and Flight Call Ratio

The current study provides evidence of behavioral differences among some common species in how they respond to Lake Erie during migration. During spring migration, an overall higher ratio of birds from our sampled species/group was observed actively crossing the Western basin compared to the Central basin of Lake Erie (Figure 7). More generally, the study reveals a greater propensity to cross Lake Erie in some species/group in the narrower and island-filled Western basin compared to the Central basin of Lake Erie. Broken down by species, Savannah Sparrows, Chipping Sparrows, White-throated Sparrows, and the Double-banded Up Group warblers all showed a higher ratio in the Western basin compared to the Central basin for both spring seasons. Savannah Sparrows were the only species to show a significantly (p<0.05) higher ratio in the Western basin both years, White-throated Sparrows and DbUps in Spring 2012 only. Chipping Sparrows did not show a significant basin difference in ratios, but a trend toward higher ratios in the Western basin can be detected in the seasonal numbers. The ratio differences are consistent with the hypothesis that individuals from these species/group behave differently when confronted with the Western basin compared to the Central basin during migration. The higher seasonal ratios exhibited in the Western basin suggests (but see below) a higher proportion of individuals from these species are actively undertaking lake crossings. American Redstarts were the only species to show no indication of a ratio difference between the two basins, although a higher ratio was observed in the Western basin in 2012 while a higher ratio was observed in the Central basin in 2013. In fact, the ratio of Redstarts in the Western basin
were not significantly different between 2012 and 2013 ($z=1.149, p=0.2579$). The ratio of Redstarts in the Central basin approached significance between 2012 and 2013 ($z=1.776, p=0.0869$). This suggests that more factors than basin topography are impacting the propensity of Redstarts to undertake lake crossings.

Recent radar research in the Lake Erie region has also suggested that there is a correlation between landscape topography and migrant bird numbers. Bonter et al. (2008) demonstrated a positive correlation between forested, residential and urban landscape and migrant activity, as well as revealing a negative correlation between migrant activity and agricultural landscape. Based on the findings of Bonter et al. (2008), we expected an unequal frequency of calls at the two land sites; an expectation confirmed by our results. Looking at both seasons, more calls were recorded in the heavily forested area at French Creek (450) compared to the more agricultural area surrounding Ottawa NWR (329). Moon-watching studies by Lowery and Newman (1966) suggests that large differences can occur in the abundance of migrants between spatially-close observation sites, providing further evidence for the idea that migrants are not uniformly distributed along a broad front as they approach Lake Erie.

**Observations with Ratios above 1**

A paradox, however, presents itself when examining the White-throated Sparrow data. The Spring 2012 ratio for White-throated Sparrows in the Western basin was above 1. Assuming that our reference land sites served as the source population of birds for the over-water sites, a ratio above 1 would imply that more birds were recorded at the over-water site than were actually present in the source locations. Clearly this assumption is invalid for White-throated Sparrows. Similar occurrences with a ratio exceeding 1 were also observed in the nightly analysis (discussed further below). This anomalous finding was unlikely to have been caused by measurement errors. Rather, local conditions, wind or weather likely drew in additional
individuals from neighboring source populations to the recording site. Conditions present in the Western basin could have created a situation where birds were recruited from a broad area and drawn towards West Sister Island. Perhaps, as Huppop et al (2006) describe, under poor visibility conditions passerines are attracted to illuminated offshore objects, in this case the visual beacon atop West Sister lighthouse. The night of May 7th, 2012 was predominately overcast with intermitted light rain and a light opposing northerly wind 1.75 m/s; these conditions would have likely reduced the visibility of migrant birds aloft over the Western basin. That night the ratios of three species/group recorded were above 1 (Chipping Sparrow 12.0, White-throated Sparrows 25.0 and DbUps 7.0). One possible explanation of the data is that birds were migrating in a direction opposite to the overall seasonal directionality. Reverse migration is common in migratory songbirds. Komenda et al (2002) estimate that around 5% of the migratory population will engage in reverse movements every night. Reverse movements in birds can result from a number of different conditions; adverse weather, appearance of ecological barriers, orientation errors by juveniles and search for appropriate stopover habitat (Komenda et al 2002). Reverse migrations observed in the Northeast US during Fall migration were more common on nights with high cloud cover and poor visibility (Richardson 1982). Observations made by Cochran and Graber (1958) note that migrant birds often fly against the lights of lighthouses and regularly collide resulting in bird fatalities. The color and type of beacon, whether red or white light and either flashing or fixed had little impact on the number of fatalities observed (Cochran 1958). If this lighted beacon is indeed attracting migrants under previously described conditions in the Western basin, then that raises questions for conservation of migrants in the area (discussed further below). Another possibility is that under such poor visibility conditions, birds were unable to judge the distance of the lake and were ultimately conflicted as to continue or make landfall. Observations made by Bruderer and Liechti (1998) demonstrate that birds will
often reverse their migration and return to coastlines when faced with a barrier of unknown dimensions.

Impact of Nightly Conditions on Flight Call Ratio

The results of the ANCOVA provide some insights into the topographical and weather factors that can influence the likelihood of an overwater crossing once migrants encounter Lake Erie. That is, factors such as species, basin (local topography), wind direction, and their interactions, seemingly impact the night-to-night ratio of birds being observed crossing Lake Erie. This finding parallels Diehl et al (2003) which showed a higher abundance of birds aloft around the Western basin compared to the Central basin. The significant basin-wind direction interaction observed in the ANCOVA demonstrates that, depending on basin and by inference local topography, wind direction had an impact on the ratio of birds observed over-water compared to over-land. This result is not without precedent, as previous studies have concluded that night-to-night variability in migration might simply reflect the fact that different species select different wind directions to initiate migration depending upon their ultimate destination (Evans 1966, Nisbet and Drury 1967). The coding resolution for wind direction in the ANCOVA was admittedly coarse, but the results are generally consistent with the findings of Nibset and Drury (1967). Wind has always been a major factor in explaining migratory behavior (Alerstam 1976), and migration intensity is often strongly correlated with wind direction and speed (e.g., Gauthreaux and Able Nature paper). Typically birds prefer to migrate in light or tail winds (Richardson 1978, 1990).

Our results indicate that wind direction is having an impact on the ratio of birds observed, however this significant main effect is largely due to the heightened ratio of relatively few species/group in the Western basin. Like the White-throated Sparrows discussed above, a similar phenomenon could be occurring as birds are recruited from a broader area than what is sampled
at the land-recording site and attracted to West Sister Island as described above. The significant basin-wind direction-species/group interaction demonstrated in the ANCOVA shows that certain species/groups are behaving differently under varying wind directions across the different basins. Based on trends observed in Figure 10, Chipping Sparrows and DbUps in the Western basin, under presumptively opposing northerly winds, regularly demonstrate higher than normal ratios. Why Savannah Sparrows do not show the same pattern could be due to differences in prey availability. Unlike Chipping Sparrows, Savannah Sparrows prey extensively on Grasshopper populations (Miller and McEwan 1995). Schaub and Jenni (1999) suggest that differences in food availability can explain differences in organization (duration of stopover, nightly distance, and pathways) of migration.

The covariate wind speed in our ANCOVA did not have any significant impact alone on the nightly ratio of birds recorded crossing Lake Erie. Based on our limited sample, the data suggests factors such as wind direction is having a greater impact on nightly ratio than wind speed. The overall ANCOVA, however, represented by the corrected model (Table 2) suggests that wind speed is having an impact on nightly ratios when combined with the remaining main effects (basin, wind direction, species/group). It is worth mentioning that one should be cautious when discussing wind data alone as birds will often take flight regardless of winds when urgency to reach their destination increases (Akesson and Hedenstrom 2000). Nonetheless, strong evidence from other studies show that birds take into account wind direction and speed when departing on migratory flights (Akesson and Hedenstrom 2000).

Implications in Conservation

Stopover sites along the Western basin of Lake Erie are recognized globally as significant staging areas for bird migration all across the Eastern United States (Ewert et al 2005). Specifically the open waters encompassing Maumee Bay, Ohio and Ottawa National Wildlife Refuge and
surrounding property have all been named important stopover sites by The American Bird Conservancy (Chipley et al. 2003). Approximately 5% of the original 121,000 ha (1210 km²) of coastal wetlands remain in Northwestern Ohio (Bookhout et al. 1989). There are, however, few quantitative studies that have investigated the ecology and distribution of migrating landbirds, especially species-specific distributions in the Western basin of Lake Erie (Ewert et al. 2005). The current study provides insight into the migration patterns of some sparrow and warbler species along the Southern coast of Lake Erie during spring migration. Furthermore, we believe that while the landscape topography of Northwestern Ohio is less favorable for migrant passerines (Bonter et al. 2009), the Southwestern coast of Lake Erie is an important staging area for potential lake crossing by migrant landbirds. Higher relative abundances of birds were observed crossing the narrower and island-filled Western basin compared to the more open water topography of the Central basin. Furthermore, whether a bird is more or less likely to cross Lake Erie is heavily influenced by factors such as species, topography and wind direction. In conclusion, discovering species-specific distributions of migrating passerines is important for implementing conservation strategies. The current study provides evidence of the viability of utilizing acoustic recorders to examine the behavior of migrant passerines along the Ohio coast of Lake Erie.
REFERENCES


Figure 1: NEXTRAD WSR-88D weather radars track bird movement across the Great Lakes area. The relatively flat topography surrounding the region and the number of radars allows for clear scanning to create an almost complete panoramic view of the entire Great Lakes area. The black dots represent radar sites; the reflectivity spectrum shows densities of birds. The “bulls-eye” like appearance around each station is attributed to the angle of projection from the radar and corresponds to the height of the birds as they fly through that beam (Diehl et al 2003).
Figure 2: Reflectivity of radars positioned at Cleveland, OH and Buffalo, NY showing movements of birds across Lake Erie along the Lake Erie Island Chain and along Long Point in Canada for the night of September 18, 2000. Much of the orange to red color around Pelee Island is attributed to the movement of birds across the lake. Much of the green north of Cleveland is believed to not have been caused by birds. (Diehl et al 2003).
Figure 3: Nocturnal flight call of White-throated Sparrow recorded May 5th 2012 over French Creek Nature Center Sheffield, Ohio. Spectrogram visualized using Raven Pro© Software. Frequency in kHz is measured on the Y-axis against time in seconds on the bottom axis.
Figure 4: Satellite map of study sites (Google Earth, 2013). Sites are labeled in red, latitudinal and longitudinal transects are displayed in white.
Figure 5: Sample spectrograms illustrating the structural flight call characteristics of the species and species groups used in the study. Left hand column displays an image of each bird species or member of species group; the right-hand column displays a representative spectrogram of a flight call for that species/group (frequency kHz vs. time seconds) Photos copyright Cornell Lab of Ornithology.
Figure 6: Detection capabilities for SM2+ microphone setups. Listed from left to right are each species/group used in the study: Savannah Sparrow, Chipping Sparrow, White-throated Sparrow, American Redstart and Double-banded Up Group. Displayed in each column from top to bottom are spectrograms of the sample flight calls followed by spectrograms extracted from each recorder (identified by serial number).
Table 1: Total Night Flight Call Counts for each species/call group by site and year

<table>
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<th>Species / Call Group</th>
<th>2012</th>
<th>2013</th>
<th>Year and Deployment Site</th>
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<tr>
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<td>1ONWR</td>
<td>2WSI</td>
<td>3FCNC</td>
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<tr>
<td>Savannah Sparrow</td>
<td>77</td>
<td>51</td>
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<tr>
<td>5Double-banded Up Group</td>
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1ONWR=Ottawa National Wildlife Refuge  
2WSI=West Sister Island  
3FCNC=French Creek Nature Center  
4CWIC=Cleveland Water Intake Crib  
5Double-Banded Up Group consists of 4 species Tennessee, Nashville, Black-throated Green, Orange-crowned Warblers

Table 1: Total number of recorded flight calls by species/group for each deployment site and year. The data are based on 28 observation nights, 14 from Spring 2012 and 14 from Spring 2013. Each night was analyzed from 3 hours post civil twilight, approximately 23:45 local DST, to 8 hours post, approximately 4:45 local DST or 15 minutes prior to civil twilight.
Figure 7: Water to land ratios pooled across all species/group for the Western and Central basin by year. Numbers on top of each bar represent total number of recorded birds. *** = p<0.001.
Figure 8: Species specific water to land ratios for three Emberizidae species for each basin and year. a) Savannah Sparrow (*Passerculus sandwichensis*), b) Chipping Sparrow (*Spizella passerina*), c) White-throated Sparrow (*Zonotrichia albicollis*). Numbers over each column represent total number of recorded birds. * = p<0.05, ** = p<0.01, *** = p<0.001.
Figure 9: Species specific water to land ratios for member of the family Parulidae for the Western and Central basin by year. a) American Redstart (*Setophaga ruticilla*) b) Double-banded Up Group consisting of Tennessee (*Oreothlypis peregrina*), Nashville (*Vermivora ruficapilla*), Black-throated Green (*Dendroica virens*) and Orange-crowned (*Vermivora celata*) warblers. Numbers on the top of each column represent total number of birds recorded. *** = p<0.001.
Table 2 ANCOVA Results of Main and Between Subject Effects for Crossing Ratio

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Table 2: Results of ANCOVA showing main effects and interactions. Statistics calculated utilizing SPSS.
Figure 10 a) Mean nightly ratio for each species/group in the Western basin by wind direction. b) Mean nightly ratio for each species/group in the Central basin by wind direction. Symbols show mean ratios calculated for each species/group from nights included in the ANCOVA analysis. Numbers outside the parentheses identify number of nights with ratios for a species/group-wind direction condition and in the parentheses is the standard error of the mean. Note; no nights with suitable data were recorded with easterly or westerly winds.