

The spring reverse migration of landbirds in the Pelee region: 2010-2012

by

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Author's Declaration

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

I understand that my thesis may be electronically available to the public.

Abstract

The spring reverse migration of landbirds (i.e., birds flying in the direction opposite to be expected), within the Great Lakes region is controversial because it is not understood if the extent or reversal of flight direction in spring is truly a change in migratory patterns or a brief anomaly. It is also not clear what the fitness and community level impacts are. My objective was to determine what and how weather influences reverse migration and to determine which species and families of birds participate the most frequently in this form of flight. I examined species which are participatory (and those that are not) as well as the impacts of specific weather covariates on the abundance of landbirds and focused explicitly on the putative reverse migration of landbirds.

Field sites were located at the extreme southern tip of Fish Point, Pelee Island (2010-2012) and Point Pelee National Park (2012), where my field assistant and I visually recorded the total number of birds observed to be reverse migrating, while identifying all birds to species or family as best possible. This study was conducted over 97 days during April 26 – May 20, in 2010-2012. Information pertaining to potential reverse migration has only been formally documented twice in the Great Lakes region, most recently in 1951.

I undertook a descriptive analysis to compare the numbers of individuals of bird species and families. Temperate and neotropical migrants were examined, compared, and divided into sub-sets based on their geographic ranges. I identified species at risk and vagrants which I observed during reverse migrations. Based on provincial population estimates, I determined the proportion of all reverse migrants where ≥ 200 individuals were observed. A descriptive analysis was undertaken to determine differences between sites (i.e., Point Pelee and Fish Point) in the final year of surveys (2012). Species and abundance were comparatively differentiated between each site and subsequently compared.

While very few birds were observed flying anything but south, a total of 61,677 birds of 80 species was documented flying south. My results indicate temperate migrants vastly outnumbered neotropical migrants (as much as 4:1) and numbers of birds varied between study sites. Temperate migrants were noted to be more common (in the final study year) at Point Pelee compared to Fish Point, while neotropical migrants were more numerous at Fish Point than Point Pelee. Despite the fact that most migrant species participated in reverse migrations (i.e., of the species regularly occurring in the Pelee region at this time of year), complete absences were noted, most notably in *Catharus* thrushes, while species such as Rose-breasted Grosbeak and Scarlet Tanager, and families such as Tyrant Flycatchers, Vireos and Sparrows were observed to be less prevalent than anticipated. Species at risk and vagrants were noted relatively frequently during this study, suggesting that these surveys are an efficient and

potentially important tool for migration monitoring in this region. Diurnal migrants, most notably Blackbirds, were observed to engage in reverse migration in higher numbers than nocturnal migrants, such as Wood Warblers.

Seven weather covariates were measured and modeled with the total number of birds detected using R to determine which covariates explain the most amount of variation of the total number of birds during my surveys. I used an AIC_c approach to select the best model for each hypothesis. After selecting the top weather covariates with time lags according to the best (lowest) AIC_c values, I built general models by comparing all possible combinations of the covariates identified in the top models for each hypothesis. I included a random effect intercept for study site to discern any site difference or similarities between Point Pelee and Fish Point and specified a Poisson distribution (log-link function as implemented in the LMER package) because the data set was continuous (time-series) and count oriented.

My adjusted time lag results show that most migrants tend to migrate during and ahead of inclement weather and/or periods of south winds. I also found that all identified covariates influence reverse migration to some degree. Wind direction and barometric pressure were the most significant of the covariates examined ($\beta = 0.718$ and -0.213 , respectively). Specifically, wind direction is the most important covariate in explaining reverse migration, with days of south winds dramatically increasing the probability of higher numbers of birds during surveys. Low barometric pressure is also important for explaining the number of observed reverse migrants; therefore, days with lower barometric pressure have a greater likelihood of increased bird observations.

Based on my observations and results I theorized that while reverse migration pertains to a distinct form of flight, it is likely not an actual form of migration. This form of flight at its simplest is likely a form of reorientation, whereby migratory birds take advantage of local weather conditions by flying south for extended distances. I anticipate that this form of flight must have serious consequences for the fitness levels and life-cycles of migratory birds.

Studies looking at reverse migration provide a useful tool for migration monitoring, particularly as it is an underexplored phenomenon. Observations of thousands of birds, many of which are either species at risk or vagrants, collected in an efficient manner are vital for determining population trends related to migratory birds. Continuing this study would aid on-going monitoring programs assessing bird populations passing through the lower Great Lakes region. These studies will also help us understand the impacts of climate and climate change on migratory birds.

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I extend my unconditional gratitude to my family, particularly my parents James and Carol and my brother Michael for their ongoing love and support – without this I would not be where I am today. Thanks to Richard and Felicity Pope for your continued support, interest and friendship. Thanks also to the Pelee Island Bird Observatory (Graeme, Sumiko and Claire) for your generosity, friendship and support; to Parks Canada and Ontario Parks for permitting me to conduct research within Fish Point Provincial Nature Reserve and Point Pelee National Park; to Josh Vandermeulen, my field assistant, stationed at Point Pelee National Park in 2012 whose work was vital to the success of this project. And finally, special thanks to my advisors, Dr. Stephen Murphy and Dr. Bradley Fedy, to whom I offer my sincere appreciation for their commitment, time, encouragement, and friendship throughout my M.E.S.

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Prologue

Reverse migration¹ refers to spring migrant landbirds flying, diurnally, in a southerly direction instead of northwards (i.e., in the direction opposite to what one would normally expect of a spring migrant in North America). Defined and previously studied by Lewis (1939) and Gunn (1951), reverse migration has seldom been studied in the Great Lakes region and North America. Observations of thousands of birds flying southwards has been regularly observed, yet very few birds flying anything but south during these flights have been documented. Published accounts of reverse migration as a whole have only been documented at a few locations throughout the World, and generally concern migration occurring adjacent to large bodies of water (Richardson 1978). While reverse migration has been shown to occur in the fall in the Atlantic Maritimes (Richardson 1982, McLaren et al. 2000), Cape May, NJ (Weidner et al. 1992), and in Fennoscandia (Alerstam 1978, Lindstrom and Alerstam 1991, Akesson 1999), within the Great Lakes region it has been observed only in the spring (Lewis 1939, Gunn 1951, Burrell 2013). While reverse migration is a known phenomenon, the implication is still not completely understood and should be carefully delineated. This form of flight, though known as ‘reverse migration’, should most likely be understood as a ‘reorientation/correction flight’.

Two studies (one peer-reviewed and one PhD thesis) have attempted to look specifically at this phenomenon in the Pelee region (Figure 1 and 2), both during the spring (Lewis 1939, Gunn 1951). Species which are common during reverse migration become increasingly uncommon to completely absent in days following intense reverse migration (Lewis 1939). Flights have generally been found to occur between one and four hours after sunrise, and are most intense in May (Gunn 1951). Increased abundance of migrants during reverse migrations has been linked to approaching inclement weather, and it has been noted that birds commonly fly into the wind (Gunn 1951). Blackbirds (*Icteridae*), Wood Warblers (*Parulidae*) and Pipits (*Motacillidae*) appear to be common participants during reverse migration events (Gunn 1951).

There is fairly extensive literature demonstrating that birds will fly in the direction opposite to what one would expect (Haartman 1945, Haartman et al. 1946, Evans 1968, Richardson 1978). Overall, reverse migration of nocturnal migrants has been shown to account for 5% of all migrants - a substantial number

¹ While reverse migration is the term used most widely in relation to this phenomenon, this thesis does not make any assumption that this phenomenon is an actual ‘reverse migration’. Based on my observations, it is my understanding that this phenomenon is in essence a reorientation flight, whereby birds, due to localized events (e.g., weather events and/or habitat type) undergo reorientation flights to benefit from these localized events. However, given that most, if not all, research pertaining to this phenomenon regards it as and calls it a ‘reverse migration’, I have also decided to employ this term as a way to create uniformity and continuity within the literature on this topic. Be this as this may, hereafter, reverse migration, should yield to the term reorientation flight.

(Komenda-Zehnder et al. 2002). Baseline information pertaining to reverse migration shows that several factors influence this type of migration, particularly: location, habitat selection, wind speed and direction, age structure and vagrancy patterns.

Reverse migration has been shown to occur entirely at coastal locations, generally due to ecological barriers, such as large lakes (Akesson 1999). Several studies show that birds along coasts are generally younger and more likely to be disoriented, and to use the coast as a geographical reference for their migration (Alerstam 1978, Ralph 1978). While birds have a great deal of knowledge based on instinct, a large amount of knowledge is gained through experience. Young birds have been shown to be more prone to vagrancy and mortality as compared to older birds (Alerstam 1990, Alerstam 1991, Jenni and Schaub 2003, Thorup 2010). While birds at coastal locations are more likely to be younger and, therefore, less experienced migrants, it is presumed these birds are looking for suitable stopover sites to rest or forage (Komenda-Zehnder et al. 2002). Sites at coastal locations generally have lower insect availability compared to inland locations (Alerstam 1978) and birds leaving these areas may be in search of food or shelter (Alerstam 1978, Akesson 1999). Lindstrom and Alerstam (1986) found that finches (Fringilidae) on the coast in Sweden regularly flew inland to find their preferred food and habitat before crossing large bodies of water and continuing their migration. Alerstam (1978) also found that birds which reverse migrate generally have lower body fat reserves and must re-fuel before continuing with their migration. Another study revealed similar findings that birds which participate in reverse migration do so because it is advantageous for them in terms of decreased energy expenditures (Akesson 1999).

While site location and habitat are significant factors for affecting birds and bird migration, weather is another significant factor influencing bird migration. Wind speed has been shown to have significant impacts on bird migration (Richardson 1978). Zehnder et al. (2001) found that intense movements of birds were associated with weak winds and that regardless of the wind direction birds would fly in the same direction. While wind speed has significant impacts on migration, wind direction has been shown to be more significant (Richardson 1978, McLaren et al. 2000).

Observing and documenting reverse migrations fill important gaps in the knowledge pertaining to and surrounding landbirds (e.g., general population indices, trends and behaviour), climate and the overall integrity of the environment (i.e., increases in the resilience of the environment). Studies on reverse migration provide first-hand information about the abundance of migrant landbirds. Conducting long-term reverse migration studies in conjunction with other monitoring programs will potentially determine if species are declining (or increasing). Reverse migration studies could potentially act the same way that mist-netting at bird observatories do in regard to monitoring migrant bird populations as well as changes

in climate. With dramatic declines noted in a large proportion of neotropical species (e.g., Cerulean Warblers *Setophaga cerulea* have declined on average 3% per year over the last 40 years; Smith et al. 1996, Hamel 2000, Stutchbury 2007), understanding species at risk and species on the verge of becoming at risk is vital for future bird conservation. A study of this scope could provide novel baseline information on migrant bird populations as well as attempt to discern patterns and correlations in bird migration and weather.

Understanding the impact of weather on various taxa is an issue that needs to be understood better, particularly as anthropogenic impacts increasingly alter the environment. With global temperatures increasing, the arrival and breeding dates of several species of birds have already been advanced and affected (Askeyev 2008). It is important to understand the effects of climate change on the flora and fauna of the world in order to enact policies contributing to biological conservation. Conducting studies on reverse migration makes it possible to monitor temporal and spatial shifts in species movements (along with documenting significant numbers).

Several methods have been used to measure the occurrence and intensity of bird migration. Radar has been used extensively for the last fifty years (Hassler et al. 1963, Richardson 1982). While radar allows for remote detection, it is able to detect only large movements of birds and is not capable of identifying species precisely. Despite this, it is fairly easy to use and is likely the most common method for quantifying migration patterns of birds (Larkin et al. 2002, Farnsworth et al. 2004). Though relatively easy to use, radar is rather costly. Banding recoveries have also been widely used in the Great Lakes region to study and document bird migration (McNicholl and Cranmer-Byng 1994, Bird Studies Canada 2011). Banding recoveries between the Pelee Island Bird Observatory and the Black Swamp Bird Observatory (located on the north of Lake Erie in Ohio) provide a viable method for detecting reverse migration; however, actual recoveries between the two stations are too few to be of any significance (e.g., there have been <10 recoveries between the stations; Graeme Gibson the younger, pers. comm.).

My study used visual counts of the total numbers of landbirds diurnally migrating south from Fish Point, Pelee Island and the tip of Point Pelee National Park, while also identifying birds to species or family. This method is the easiest and most pragmatic approach for a study of this scope. Several studies and bird observatories documenting reverse migration and migration in general use visual observations for estimating total numbers of landbirds (Long Point Bird Observatory 2005, Wojnowski et al. 2010). Studies conducted in the Atlantic Maritimes and northern Europe have also used visual observations for estimating the total number of reverse migrants (Nisbet and Drury 1967, Alerstam and Ulfstrand 1971, Wiedner et al. 1992, Akesson 1999, McLaren et al. 2000, Thorup 2010). Two studies conducted in the

Pelee region on reverse migration used visible observations to document and analyze this phenomenon (Lewis 1939, Gunn 1951).

Methodology

Study Site Selections

This study was conducted at Fish Point Provincial Nature Reserve and Point Pelee National Park. Studies conducted at Fish Point, Pelee Island were undertaken at the southern tip of the island (41.4° N., 82.40° W.) during spring (April-May) from 2010-2012. Studies conducted at Point Pelee National Park were also undertaken at the extreme southern tip (41.5° N., 82.30° W.), though only in the final year of this study (2012). The study sites are separated by 24.5km and located within Essex County, Ontario (Figure 1 and 2).

Fish Point is located 33km southwest of Leamington, Ontario (Figure 1 and 2) and situated within the western Lake Erie basin. Pelee Island is part of the Pelee archipelago and is the largest island within the basin (Henson et al. 2010). Fish Point is a provincial nature reserve, located on the southwestern tip of Pelee Island within the Carolinian life-zone (Ontario Parks 2008). Fish Point is approximately 110 ha. and lies on a limestone bed overlaid by a shallow sand-plain (Ontario Parks 2008).

Point Pelee National Park is 6km southeast of Leamington, Ontario and situated at the tip of the Pelee Peninsula (Figure 1 and 2). Located in the Carolinian life-zone, Point Pelee is the largest ‘green’ space within Essex County and serves as an important refuge for migratory birds (Figure 1 and 2; O’Neill 2006). Point Pelee was founded in 1918 as a national park and is world-renowned for the numbers and diversity of migratory birds passing through the park and adjacent areas annually (Goodwin 1995, Hince 1999, O’Neill 2006). Because of this distinction, thousands of birders visit the park every year (Hvenegaard et al. 1989); yet despite this, relatively few migratory bird studies have taken place within the park (Sarah Rupert pers.comm.).

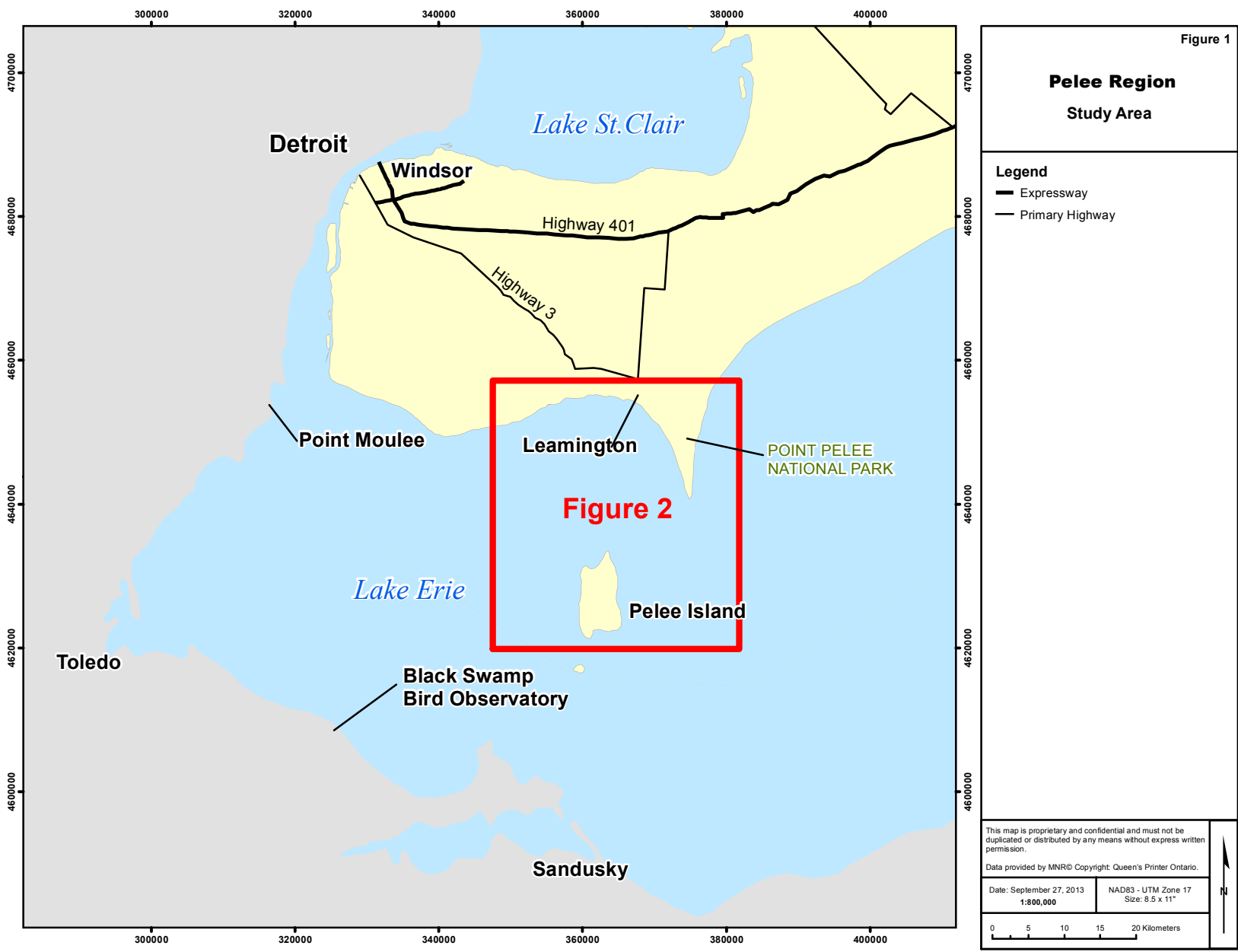
Fish Point and Point Pelee were selected as suitable sites for this study because of their historic role in research on this topic and for logistical reasons, namely their geographic location and proximity to one another. Two prominent studies pertaining to reverse migration in the spring have examined this phenomenon at these locations (Lewis 1939, Gunn 1951). Fish Point and Point Pelee are geographically situated in a similar aspect to one another, both on a north-south axis, identified as sandpits, and surrounded by the waters of Lake Erie. Fish Point and Point Pelee were selected because of their geographic importance to bird migration in the lower Great Lakes. Both sites lie within two migrant flight paths – the Mississippi and Atlantic (Kerlinger 1995, Weidensaul 2000). These locations offer suitable sites to explore reverse migration as birds are abundant here during spring migration.

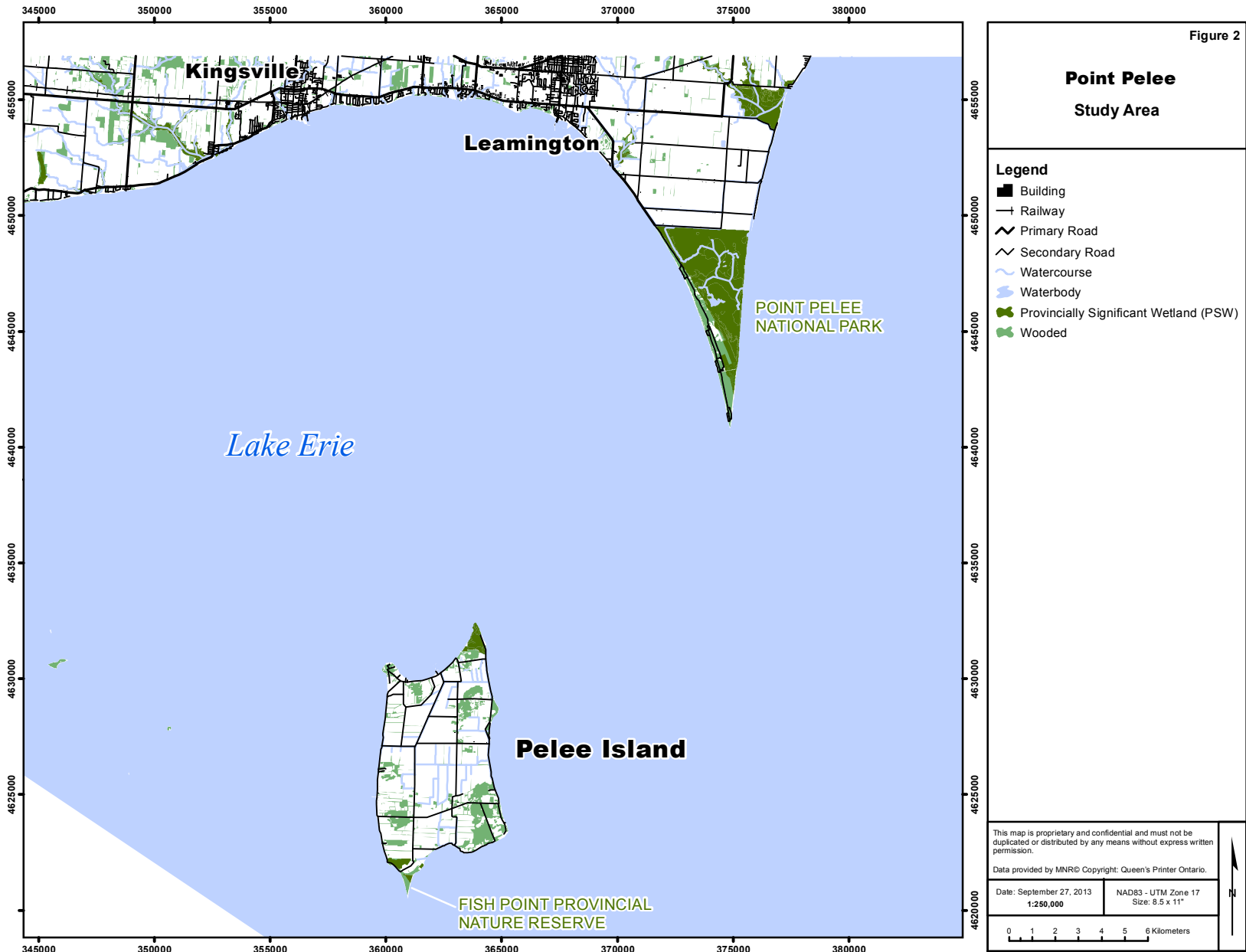
Data collection

I developed a standardized survey based on the migration monitoring protocols of the Long Point and Thunder Cape Bird Observatories (Long Point Bird Observatory 2005, Wojnowski et al. 2010), while also taking into account the methods of Lewis (1939), Gunn (1951), and Wiedner et al. (1992). Daily visual observations were noted from April 26-May 20 at Fish Point during all study years (2010-2012; $n = 73$), while observations were conducted at Point Pelee April 26-May 20 in the final study year (2012; $n = 24$).

My field assistant and I situated ourselves at the tip of Fish Point and Point Pelee, along the edge of the last vegetated land. This allowed for an unobstructed view of the sky, while putting us close enough to identify individual birds. Bird observations were collected during the first three hours (approximately 06:00-09:00) following sunrise and sometimes longer if the volume of flight warranted more observation.

We recorded all birds flying in a persistent southerly direction over Lake Erie. Observations were conducted by experienced surveyors at each site. Birds were identified to species when possible, otherwise each individual bird was assigned an identification as close to species level as possible (e.g., Blackbird species). Songbirds [Passeriformes; excluding Swallows (Hirundinidae)], as well as Doves (Columbidae), Hummingbirds (Trochilidae), and Woodpeckers (Picidae) were counted as these species have been shown to reverse migrate in higher abundance (Lewis 1939, Gunn 1951, Burrell 2013). Swallows were excluded because they are aerial insectivores and can range quickly over large areas, making it difficult to properly record accurate numbers of individuals (Kerlinger 1995, Faaborg 2002) and to determine whether they are settled individuals or migrants engaging in reverse migration.





Chapter 1: Flight Participants: Species-specific Analysis

Introduction

Long-distance bird migration (i.e., birds travelling thousands of kilometres bi-annually) represents one of the most astounding and challenging phenomena known in the natural world (Beauchamp 2011). This form of migration occurs virtually worldwide and throughout all times of the year (Rappole 1995, Weidensaul 2000). Long-distance migration is common for many birds, evolving as a strategy for species to take advantage of temporal changes in food resources and their availability (Cox 1968, 1985, Alerstam and Enckell 1979, Rappole 1995, Bell 2000). In southern Ontario, the first long-distance spring migrant songbirds (e.g., Horned Larks *Eremophila alpestris*) generally arrive in mid-February, while other species continue migrating through the region until as late as early- to mid-June (e.g., Alder Flycatchers *Empidonax alnorum*); however, peak migration is generally between mid-April and the end of May (Goodwin 1995, Hince 1999, Ridout 2010, eBird 2013).

Most songbirds migrate during the night, as this offers several advantages (Kerlinger and Moore 1989). Nocturnal migration results in lower predation and requires less energy expenditure in comparison to diurnal migration (Kerlinger and Moore 1989, Lank 1989, Alerstam 2009). Predation risks are higher during diurnal periods, as more predators are active (Kerlinger and Moore 1989, Lank 1989, Alerstam 2009). Weather conditions are generally less intense during nocturnal periods, with calmer wind speeds and cooler temperatures (Kerlinger and Moore 1989, Alerstam 2009), allowing migrant birds the opportunity to expend less energy during these periods.

Despite being more costly in terms of increased predation and energy expenditures, diurnal migration is a common and relevant component of bird migration (Weidensaul 2000, Alerstam 2009). Diurnal migration has considerable literature devoted to it, examining species composition and abundances involved during these events (Alerstam 2009). Hawks (Accipitridae; e.g., Swainson's Hawk *Buteo swainsoni*) and to a lesser extent Cranes (Gruinae; e.g., Sandhill Crane *Grus canadensis*), and Herons (Ardeidae; e.g., Great Blue Heron *Ardea herodias*) are widespread and common participants in diurnal migrations (Tacha et al. 1992, Bechard et al. 2010, Vennesland and Butler 2011). Millions of birds of prey migrate diurnally on an annual basis through Mexico (e.g., Veracruz) and the southern United States (e.g., Texas and Florida; Bildstein 2006, Smith et al. 2008), allowing for excellent opportunities to monitor populations, in turn providing important information for conservationists.

In addition to birds of prey, various other songbirds, particularly Swallows (Hirundinidae) also migrate by day (Winkler et al. 2011). Historical and present-day population estimates throughout eastern North America have in some cases been broadly based on single-day counts (e.g., Tree Swallows *Tachycineta*

bicolor; Lowery 1955, Winkler et al. 2011), establishing the importance of diurnal migration counts for future conservation initiatives. Other common diurnal migrants include Crows and Jays (Corvidae), Blackbirds and Finches (Yasukawa and Searcy 1995, Dawson 1997, Peer and Bollinger 1997, Tarvin and Woolfenden 1999, Knox and Lowther 2000, McGraw and Middleton 2009). The north shore of Lake Erie appears to be an important area for diurnal migrants such as Blue Jays (*Cyanocitta cristata*) and Blackbirds, particularly Red-winged Blackbirds (*Agelaius phoeniceus*) and Common Grackles (*Quiscalus quiscula*), where single-day counts exceeding one hundred thousand birds have been noted in late fall and early spring (Mackenzie and Ridout 2008, eBird 2013, Mackenzie 2013). Finches also appear to be strong diurnal migrants, with counts of Common Redpolls (*Carduelis flammea*), Pine Siskins (*Spinus pinus*), and American Goldfinches (*S. tristis*) being well-represented throughout the Great Lakes region at known migratory hotspots (e.g., Point Pelee and Long Point, ON and Whitefish Point, MI; Mackenzie and Ridout 2008, eBird 2013). It is clear that migrant landbirds commonly engage in diurnal migrations; however, the direction of flight these birds undertake has not been well-studied and the few studies have focused on flights in the expected direction, given the location and time of year (Lewis 1939, Gunn 1951).

I visually examined species known to engage in reverse migration, as well as species expected to engage in reverse migration (i.e., which were not subsequently observed during my surveys). I tried to determine which species participate in reverse migration and to what extent. Lewis (1939) and Gunn (1951) noted Pipits, Wood Warblers, and Blackbirds in abundance during their surveys. Based on these results, I predicted Wood Warblers and Blackbirds would be the most abundant families observed during my surveys. Furthermore, I predicted that neotropical migrants would be well-represented as these species are common during the same time period in southern Ontario (Goodwin 1995, Hince 1999, Ridout 2010, eBird 2013).

Based on population estimates throughout eastern North America, temperate migrants (i.e., species known to migrate between breeding and wintering grounds, within the continental USA and Canada; Weidensaul 2000) are more common and widespread compared to neotropical migrants and have not declined on the same scale (Cadman et al. 2007, Stutchbury 2007). Based on current population estimates I predicted temperate migrants would be observed in higher abundance than neotropical migrants.

According to the Ontario Field Ornithologists (2012), 487 species of birds have been recorded and documented within Ontario, while 291 species have bred. As of 2013, 34 of the 487 species of birds known to breed or spend considerable time in Ontario are designated as at risk and afforded protection (Government of Ontario 2007, Committee on the Status of Endangered Wildlife in Canada 2012, Ontario Field Ornithologists 2012, Ontario Ministry of Natural Resources 2013b). Based on prior observations

(pre-2010), I predicted species at risk would be observed during my surveys; however, given the status of these species I did not expect them to be observed in great numbers. Therefore, I predicted species at risk would account for a small proportion (<3%) of the total number of birds, and between 5-10% of the total species observed.

Based entirely on my previous personal observations, vagrant species (e.g., Summer Tanager *Piranga rubra* and Dickcissel *Spiza americana*; Figure 2 and 3) have been documented relatively frequently during reverse migration events, in spite of their status and overall rarity. I therefore predicted vagrant species would account for a small fraction of all birds (1-3%), much higher than observations of these species by ordinary bird-watching observations. I predicted that Summer Tanagers and Dickcissels would be observed on a disproportionate number of reverse migration surveys in comparison to regular bird-watching sightings.

The north shore of Lake Erie is an area where thousands of diurnal migrants have consistently been observed during both spring and fall migrations (eBird 2013). Based on this observation, I predicted that diurnal migrants, such as Blackbirds and Finches, would engage more heavily in reverse migration in comparison to nocturnal migrants, such as Wood Warblers and Vireos.

While Fish Point and Point Pelee are similar to one another from several standpoints (e.g., flora and fauna, climate, and proximity to one another), their migration dynamics and flight patterns are different, as Point Pelee is located on a mainland, while Fish Point is located on an island. While not well-documented in relation to landbirds such as songbirds, habitat preference and large bodies of water can represent significant barriers for many species (e.g., Hawks, Cranes and Herons; Tacha et al. 1992, Bechard et al. 2010, Vennesland and Butler 2011). Based on differences in island and mainland sites, I theorized that there would be distinct differences in the composition and abundance of birds participating in reverse migrations between the two study sites.

Methods

Data Analysis

A descriptive analysis was conducted to compare the number of individuals of bird species and families. Bird families which were observed to be common during my surveys were examined, including: Woodpeckers (Picidae), Tyrant Flycatchers (Tyrannidae), Vireos (Vireonidae), Crows and Jays (Corvidae), Wood Warblers (Parulidae), Sparrows (Emberizidae), Cardinals and Allies (Cardinalidae), Blackbirds (Icteridae) and Finches (Fringillidae). Individual species comparisons of Wood Warblers and

Blackbirds were made due to their observed abundance among species participating in reverse migrations. Temperate and neotropical migrants were examined and divided into sub-sets based on geographic ranges according to Sibley (2000) and Dunn and Alderfer (2011).

Using the lists of species at risk from the Ontario Ministry of Natural Resources (2013b) and the Committee on the Status of Endangered Wildlife in Canada (2012), I identified all species at risk, which I observed during reverse migrations. Vagrants were identified as species which do not regularly (or ever) breed in Ontario, or breed at such low levels in the province that they are likely to be out of range (Goodwin 1995, Sibley 2000, Cadman et al. 2007, Dunn and Alderfer 2011). Vagrant records of Summer Tanagers and Dickcissels from Pelee Island and the Point Pelee area were noted from *North American Birds* and eBird (Wormington 2010, 2011, 2012, eBird 2013) from each study year to compare the number of reverse migrants for these species as opposed to species observed from these areas as a whole (i.e., during ‘normal’ birdwatching).

I analyzed the proportion of reverse migrants to determine if particular species engaged in reverse migration proportionally or disproportionately to their estimated provincial population, using the most recent population estimates from Blancher and Couturier (2007). Species were only analyzed if ≥ 200 individuals (equating to roughly 0.5% of the total identified number of birds; $n = 38,337$) were observed. The total number of observed individuals was divided by the provincial population estimate to ascertain what species engage in reverse migrations and whether they do so proportionately or disproportionately to their population.

A descriptive analysis was undertaken to determine differences between study sites (i.e., Point Pelee and Fish Point) in the final year of surveys (2012). Species and abundance were comparatively differentiated between each site location and subsequently compared.

Results

Eighty species, comprising 61,677 birds, were observed participating in reverse migrations over the study duration (2010-2012; Table 1). Very few birds were observed to fly in the direction of anything but south during my observations. Totals of reverse migrants varied according to study site and year (Table 1 and Figure 5), while 2012 served as the best year for study site comparison (due to there being two study sites for comparison). Fish Point’s mean count of 16,422 was substantially higher than Point Pelee’s 2012 count ($n = 12,412$), although 2012 appeared to be a low season in terms of the number of birds observed during reverse migration surveys (i.e., lowest observed counts in comparison of all study years). The

average daily counts also varied between sites, with Fish Point being substantially higher than Point Pelee ($n = 675$ and 517 respectively).

Most expected species were observed, with Wood Warblers and Blackbirds being the most common participants ($n = 10842$ and 42686 respectively), accounting for 87% of all reverse migrants. Pipits were relatively scarce, with just 136 individuals (0.22% of all reverse migrants) noted over the study duration (Table 1). Twenty-seven species of Wood Warblers and nine of Blackbirds were noted, respectively (Table 1). Individuals of Woodpeckers ($n = 58$), Tyrant Flycatchers ($n = 300$), Vireos ($n = 166$), Crows and Jays ($n = 1113$), Wood Warblers ($n = 10842$), Sparrows ($n = 226$), Cardinals and Allies ($n = 847$), Finches ($n = 1230$), and Blackbirds ($n = 42686$) were all well represented over the study duration (Figure 6). *Catharus* Thrushes (Turdidae) were absent in all surveys, while Tyrant Flycatchers, Vireos and Sparrows were present, albeit in lower than anticipated numbers compared to observations on the rest of Pelee Island and Point Pelee (eBird 2013, pers.obs.). Rose-breasted Grosbeaks and Scarlet Tanagers were also noted in lower numbers than expected, given their relative (perceived) abundance in southern Ontario during this time period (Goodwin 1995, Blancher and Couturier 2007, Cadman et. al 2007, eBird 2013, pers.obs.).

Neotropical migrants were well-represented, representing over half the total number of species noted ($n = 42$), however, temperate migrants outnumbered neotropical migrants almost 4:1, largely as a result of the high numbers of Blackbird observations (Figure 7).

Species at risk and vagrants were noted throughout all study years and study sites. Nine species at risk were noted, comprising two endangered, four threatened, and two species of special concern, amounting to 313 individuals (Table 2). Several vagrant species such as: Kirtland's Warbler, Lark Sparrow, Blue Grosbeak, and Yellow-headed Blackbird were noted during surveys (Table 3). Reverse migrant Dickcissels and Summer Tanagers were noted among 33% (9/27 occurrences) of all sightings from Pelee Island and Point Pelee, while observations (during our surveys and regular bird-watching observations) were taken during the study period (Wormington 2010, 2011, 2012, eBird 2013).

Based on provincial population estimates, Blackbirds appear to disproportionately engage in reverse migrations - more so than any other family (Table 4). Baltimore Orioles (0.93), Red-winged Blackbirds (0.38), and Common Grackles (0.22) engaged disproportionately to their provincial populations, more so than almost all other species or families, with the exception of Indigo Bunting (0.26). Identified Wood Warblers, such as Magnolia (0.002), Palm (0.005), and Nashville Warblers (0.005) appear to engage to the lowest proportion in relation to their provincial population estimates. Common species engaging in reverse migrations do not likely represent substantial proportions of their population being affected as

their populations are high (i.e., in the millions); however, species at risk, such as the Kirtland's Warbler, a globally endangered songbird, maybe disproportionately affected by these reorientation flights due to their low population sizes.

In the final study year Fish Point had more observed neotropical migrants, such as Wood Warblers and Cardinals and Allies (e.g., Yellow-rumped Warbler and Indigo Bunting), while Point Pelee consistently had many more temperate migrants (e.g., Mourning Dove, Blue Jay, American Robin, Cedar Waxwing and American Goldfinch; Table 1).

Discussion

Most migrant landbirds participate in varying abundance in reverse migrations; however, their involvement varies among family and species. Temperate migrants appear to participate in these flights much more frequently in comparison to neotropical migrants (as per the abundance results; Table 1). Wood Warblers and Cardinals and Allies are the most abundant neotropical participants during reverse migrations, while among temperate migrants, Blackbirds are by far the most abundant participants in these flights. Neotropical migrants have declined at alarming rates, particularly interior forest species, aerial insectivores, and grassland bird species (Robbins et al. 1989, Cadman et al. 2007, Stutchbury 2007, North American Bird Conservation Initiative Canada 2012). These migrants have declined in part because of their use of and reliance on different habitats during their life-stages and because of their increased range sizes, therefore increasing their susceptibility to diverse and increasing anthropogenic pressures (e.g., agriculture, deforestation, water pollution, etc.; Stutchbury 2007, Cadman et al. 2007, North American Bird Conservation Initiative Canada 2012). These pressures possibly accounted for the observed differences in the abundance of reverse migrants during my study.

Approximately thirty-eight species of Wood Warblers are regularly present in Ontario on an annual basis (Goodwin 1995, eBird 2013). My surveys noted twenty-seven species, accounting for 17.5% of all reverse migrants ($n = 10,842$), indicating that these surveys documented a large proportion of the possible species present in Ontario. My results agreed with Wiedner et al. (1992), where Wood Warblers accounted for a large proportion of the identified species participating in reverse migrations. Nine Blackbird species were observed (out of a total of eleven regularly occurring species; Goodwin 1995, eBird 2013), totaling 69% of all reverse migrants ($n = 42,686$). Blackbirds are known to be strong diurnal migrants (Lewis 1939, Gunn 1951, Yasukawa and Searcy 1995, Jaramillo and Burke 1999), and the large numbers of this family observed indicate similar findings. Wood Warblers, while not nearly as strong fliers as Blackbirds, have evolved to undertake dramatic migratory flights, and in the case of the

Blackpoll Warbler lengthy oceanic flights, flying from the U.S.A. east coast south over the Atlantic Ocean to northern South America without rest (Hunt and Eliason 1999, Weidensaul 2000, eBird 2013). Based on the analysis of species observed participating in these flights, reverse migrants appear to be partially through their spring migration, though still substantial distances from their breeding grounds (e.g., birds breeding in the boreal forest, such as the Nashville and Yellow-rumped Warblers). Our observed results illustrate that Wood Warblers, possibly due to their adaptive migratory behaviour of performing exhaustive cross-oceanic flights are still strong participants during reverse migration, despite being largely nocturnal migrants.

While temperate and neotropical migrant diversity was high, several species and families were conspicuously absent. Most notably *Catharus* thrushes were completely absent, despite being relatively abundant in areas adjacent to Fish Point and Point Pelee during study years (eBird 2013, pers.obs.). Weidner et al. (1992) found similar results pertaining to *Catharus* thrushes, where they accounted for 0.01% of all identified neotropical migrants (among a sample size of 24,378). *Catharus* thrushes are largely nocturnal migrants (Mack and Yong 2000, Lowther et al. 2001, Rimmer et al. 2001), and my results confirm they do not seem to be common diurnal reverse migrants. *Catharus* thrushes may not reverse migrate as these species are strong nocturnal migrants (compared to Wood Warblers and Blackbirds), and able to perform their migrations to a higher degree of accuracy resulting in fewer travel days during their migrations. Determining how these species orient themselves before undertaking nocturnal migration will be vital to understanding why these species do not engage in reverse migrations. *Catharus* thrushes are also primarily forest interior species and the habitat associated with the tips of Fish Point and Point Pelee may not be suitable for this genus.

Several species were observed in lower numbers than anticipated given their abundances (Goodwin 1995, eBird 2013). Fewer than expected Rose-breasted Grosbeaks ($n = 43$), Scarlet Tanagers ($n = 111$), Vireos ($n = 166$), Sparrows ($n = 226$), and Tyrant Flycatchers ($n = 300$) were noted. These species and families are all noted to be primarily nocturnal migrants (Lanyon 1997, Middleton 1998, Mowbray 1999, Cimprich et al. 2000, Wyatt and Francis 2002) and common in Ontario (Cadman et al. 2007); however, they do not appear to be common participants in diurnal spring reverse migration in the Pelee region. It is possible nocturnal migrants such as these species are able to perform their migrations to a higher degree of accuracy, needing less room for reorientation. The decline of neotropical migrants has had serious impacts on the populations of breeding birds across eastern North America as well as Ontario. The small number of observations of Scarlet Tanagers, Rose-breasted Grosbeaks, and Vireos may in part be due to this observed decline (in neotropical migrants); however, more research relating to these species and families is needed, particularly as they relate to reverse migration.

Species at risk and vagrants were noted throughout the duration of this study in varying numbers ($n = 313$ and 14, respectively; Table 2 and 3). Cumulatively, species at risk and vagrants accounted for 0.83% of all identified individuals ($n = 38,337$), representing relatively high numbers for particular species (e.g., Red-headed Woodpecker *Melanerpes erythrocephalus*, Prothonotary Warbler *Protonotaria citrea*, and Bobolink *Dolichonyx oryzivorus*; Figure 8 and 9). Based on the high numbers of species at risk and vagrants that I observed, my results indicate reverse migration surveys could be a useful tool in conjunction with other monitoring programs for monitoring migratory bird species, particularly species at risk (and species on the verge of becoming at risk) and vagrants. Reverse migration surveys appear to be an efficient tool for monitoring large populations of landbirds and could potentially be used in conjunction with mist-netting observations towards answering population-trend related questions. Using standardized long-term datasets pertaining to reverse migrants will potentially allow researchers to track declines (and increases) of migratory species effectively.

While Wood Warblers are one of the most abundant family groups in Ontario (Blancher and Couturier 2007, Cadman et al. 2007), they do not appear to engage as abundantly in reverse migration as Blackbirds. While Blackbirds are strong diurnal migrants (Jaramillo and Burke 1999), Wood Warblers are almost exclusively nocturnal (Curson et al. 1994, Dunn and Garrett 1997), likely resulting in fewer Wood Warblers participating in (diurnal) reverse migrations. That said, Blackbirds, largely a family of diurnal migrants (Jaramillo and Burke 1999), engage disproportionately in higher numbers during reverse migration than any other family group.

It is likely that larger landbirds which flock, such as Blackbirds, maybe better adapted for diurnal migration and in particular diurnal spring reverse migration than other birds (e.g., Wood Warblers or Vireos). Birds which flock are generally better adapted for identifying predators and alerting other birds to their whereabouts (Thompson et al. 1974, Lazarus 1979, Cresswell 1994), translating into fewer mortalities.

While Indigo Buntings are prevalent nocturnal migrants, the high proportion observed during reverse migrations maybe attributed to preferred habitat (e.g., edges or clearings; Lanyon 1981, Payne 2006), in addition to their behaviour of actively calling while flying (Payne 2006, pers.obs.), likely allowing for greater rates of detection.

The proportion of Orchard Orioles observed was not calculated; however, it is likely given their small provincial population size (Woodliffe 2007), that the proportion of participation would be very high, similar in proportion to other observed Blackbirds (e.g., Red-winged Blackbird and Baltimore Oriole).

Distinct study site differences were noted between Fish Point and Point Pelee during surveys in 2012. Temperate migrants outnumbered neotropical migrants by a substantial margin at Point Pelee, while the opposite was true at Fish Point. I theorize that the amount of vegetative cover and the island versus mainland dynamic are primary differences for the numbers and diversity of species at the study sites. As Point Pelee has a substantially larger vegetative cover in comparison to Fish Point and Pelee Island, the surveys indicate that as vegetative land cover increases, so does the number of birds in the entire vicinity (i.e., the area experiences migrant saturation), thus increasing competition between migrants and therefore increasing the likelihood for increases in the number of reverse migrants to be noted. Water crossing is also a significant difference between study sites, with Point Pelee being located on the mainland, while Fish Point is on Pelee Island. Willingness to fly over open water poses a major challenge, depending on the species. These surveys indicate that migrants who are primarily diurnal migrants appear to prefer the mainland (over islands), possibly due to risks associated with drowning, while there appears to be no difference between site preference for neotropical migrants.

While reverse migration affects a wide range of species and individuals, differences in site location and species participation varies markedly. It is also postulated that short- and long-distance migrants are impacted and affected by different migratory cues (e.g., photoperiod and weather) and therefore participate at varying intensities within reverse migrations. Implications of this study highlight the importance for continued data collection for monitoring species at risk, as well as species on the verge of becoming at risk. This study in conjunction with other monitoring programs allows researchers the ability to monitor bird populations unobtrusively. While reverse migration is an observed phenomenon, the implications and repercussions of this flight are still not clearly understood. The study of reverse migration warrants more research, particularly in observing reverse migrations (i.e., gathering data), while also trying to determine where reverse migrants go, using new technologies (e.g., satellite transmitters, isotope analysis).

Chapter 1 Tables and Figures



Figure 3. Reverse migrant, first-alternate male Summer Tanager *Piranga rubra*. May 21, 2011 Point Pelee National Park. Plumage terminology follows Humphrey and Parkes (1959). Copyright Alan Wormington. Note: this individual was not recorded or counted as part of this study.



Figure 4. Reverse migrant, definitive alternate male Dickcissel *Spiza americana*. May 3, 2012 Fish Point Provincial Nature Reserve. Plumage terminology follows Humphrey and Parkes (1959). Copyright Brandon R. Holden.

Table 3. Total number of observed reverse migrants throughout the study duration (2010-2012). Species are in taxonomic order, according to the American Ornithologist Union's 7th edition (53rd supplement). Totals are delineated by species, study site and year. FP denotes Fish Point, Pelee Island, ON; PP denotes Point Pelee National Park, ON; ¹ denotes a species at risk; and ² denotes a vagrant bird species.

Common name	Latin name	2012 PP Total	2012 FP Total	2011 FP Total	2010 FP Total	Species total
Rock Pigeon	<i>Columba livia</i>	1	0	0	0	1
Mourning Dove	<i>Zenaida macroura</i>	26	4	9	7	46
Ruby-throated Hummingbird	<i>Archilochus colubris</i>	16	20	35	61	132
Red-headed Woodpecker ¹	<i>Melanerpes erythrocephalus</i>	9	7	11	17	44
Red-bellied Woodpecker	<i>Melanerpes carolinus</i>	0	6	0	3	9
Northern Flicker	<i>Colaptes auratus</i>	2	0	1	2	5
Eastern Wood-Pewee	<i>Contops virens</i>	0	2	1	1	4
Least Flycatcher	<i>Empidonax minimus</i>	0	0	1	0	1
Eastern Phoebe	<i>Sayornis phoebe</i>	1	0	0	2	3
Great Crested Flycatcher	<i>Myiarchus crinitus</i>	0	4	4	0	8
Eastern Kingbird	<i>Tyrannus tyrannus</i>	6	13	156	107	282
Yellow-throated Vireo	<i>Vireo flavifrons</i>	0	1	5	1	7
Blue-headed Vireo	<i>Vireo solitarius</i>	0	0	8	0	8
Warbling Vireo	<i>Vireo gilvus</i>	3	24	21	20	68
Philadelphia Vireo	<i>Vireo philadelphicus</i>	0	2	9	0	11
Red-eyed Vireo	<i>Vireo olivaceus</i>	0	0	16	2	18
Blue Jay	<i>Cyanocitta cristata</i>	439	101	220	349	1109
American Crow	<i>Corvus brachyrhynchos</i>	0	0	0	2	2
Horned Lark	<i>Eremophila alpestris</i>	0	1	4	0	5
Blue-gray Gnatcatcher	<i>Polioptila caerulea</i>	36	10	8	31	85
Ruby-crowned Kinglet	<i>Regulus calendula</i>	0	0	5	0	5
Eastern Bluebird	<i>Sialis sialis</i>	0	2	3	0	5
American Robin	<i>Turdus migratorius</i>	215	52	151	147	565
Gray Catbird	<i>Dumetella carolinensis</i>	0	1	0	0	1

European Starling	<i>Sturnus vulgaris</i>	581	238	362	502	1683
American Pipit	<i>Anthus rubescens</i>	26	16	11	83	136
Cedar Waxwing	<i>Bombycilla cedrorum</i>	482	128	116	33	759
Ovenbird	<i>Seiurus aurocapillus</i>	0	0	2	0	2
Northern Waterthrush	<i>Parkesia noveboracensis</i>	0	1	0	0	1
Golden-winged Warbler ¹	<i>Vermivora chrysoptera</i>	0	1	0	0	1
Blue-winged Warbler	<i>Vermivora cyanoptera</i>	1	4	1	0	6
Black-and-white Warbler	<i>Mniotilta varia</i>	0	0	25	0	25
Prothonotary Warbler ¹	<i>Protonotaria citrea</i>	1	1	1	1	4
Tennessee Warbler	<i>Oreothlypis peregrine</i>	0	6	11	1	18
Orange-crowned Warbler	<i>Oreothlypis celata</i>	0	1	2	0	3
Nashville Warbler	<i>Oreothlypis ruficapilla</i>	28	119	626	58	831
Hooded Warbler ¹	<i>Setophaga citrine</i>	0	0	1	0	1
American Redstart	<i>Setophaga ruticilla</i>	0	3	53	0	56
Kirtland's Warbler ^{1 2}	<i>Setophaga kirtlandii</i>	0	0	1	0	1
Cape May Warbler	<i>Setophaga tigrina</i>	0	6	11	3	20
Northern Parula	<i>Setophaga americana</i>	0	0	28	0	28
Magnolia Warbler	<i>Setophaga magnolia</i>	2	1	286	0	289
Bay-breasted Warbler	<i>Setophaga castanea</i>	0	0	32	0	32
Blackburnian Warbler	<i>Setophaga fusca</i>	2	3	68	3	76
Yellow Warbler	<i>Setophaga petechia</i>	133	166	129	153	581
Chestnut-sided Warbler	<i>Setophaga pensylvanica</i>	0	1	136	2	139
Blackpoll Warbler	<i>Setophaga striata</i>	0	0	8	0	8
Black-throated Blue Warbler	<i>Setophaga caerulescens</i>	0	0	33	0	33
Palm Warbler	<i>Setophaga palmarum</i>	16	56	268	11	351
Pine Warbler	<i>Setophaga pinus</i>	1	3	1	0	5
Yellow-rumped Warbler	<i>Setophaga coronata</i>	19	1618	404	236	2277
Black-throated Green Warbler	<i>Setophaga virens</i>	0	11	44	11	66
Canada Warbler ¹	<i>Cardellina canadensis</i>	0	0	6	0	6
Wilson's Warbler	<i>Cardellina pusilla</i>	0	0	7	0	7
Chipping Sparrow	<i>Spizella passerina</i>	1	19	3	40	63

Clay-colored Sparrow	<i>Spizella pallida</i>	0	0	1	0	1
Field Sparrow	<i>Spizella pusilla</i>	0	1	2	1	4
Lark Sparrow ²	<i>Chondestes grammacus</i>	0	0	0	1	1
Savannah Sparrow	<i>Passerculus sandwichensis</i>	0	0	5	0	5
Summer Tanager ²	<i>Piranga rubra</i>	0	0	2	1	3
Scarlet Tanager	<i>Piranga olivacea</i>	0	0	101	10	111
Northern Cardinal	<i>Cardinalis cardinalis</i>	8	1	0	0	9
Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>	5	13	24	1	43
Blue Grosbeak ²	<i>Passerina caerulea</i>	1	0	0	0	1
Indigo Bunting	<i>Passerina cyanea</i>	117	228	188	255	788
Dickcissel ²	<i>Spiza americana</i>	0	1	4	1	6
Bobolink ¹	<i>Dolichonyx oryzivorus</i>	40	33	126	42	241
Red-winged Blackbird	<i>Agelaius phoeniceus</i>	6398	3584	2498	2553	15033
Eastern Meadowlark ¹	<i>Sturnella magna</i>	0	0	1	1	2
Yellow-headed Blackbird ²	<i>Xanthocephalus xanthocephalus</i>	1	0	0	0	1
Rusty Blackbird ¹	<i>Euphagus carolinus</i>	8	0	3	2	13
Common Grackle	<i>Quiscalus quiscula</i>	2288	1574	1400	949	6211
Brown-headed Cowbird	<i>Molothrus ater</i>	143	287	831	388	1649
Orchard Oriole	<i>Icterus spurius</i>	68	116	24	58	266
Baltimore Oriole	<i>Icterus galbula</i>	491	644	634	1014	2783
Purple Finch	<i>Carpodacus purpureus</i>	0	0	1	0	1
House Finch	<i>Carpodacus mexicanus</i>	0	5	12	0	17
Pine Siskin	<i>Spinus pinus</i>	0	0	21	0	21
American Goldfinch	<i>Spinus tristis</i>	401	160	188	442	1191
House Sparrow	<i>Passer domesticus</i>	0	0	2	2	4
Crow sp.	<i>Corvus sp.</i>	2	0	0	0	2
Flycatcher sp.	<i>Tyrannidae spp.</i>	0	0	0	2	2
Vireo sp.	<i>Vireo sp.</i>	4	0	28	22	54
Warbler sp.	<i>Parulidae sp.</i>	172	1378	4277	148	5975
Sparrow sp.	<i>Emberizidae sp.</i>	2	91	12	47	152

Meadowlark sp.	<i>Sturnella sp.</i>	1	0	0	0	1
Blackbird sp.	<i>Icteridae sp.</i>	215	0	6553	9718	16486
Small Bird Sp.	<i>Passeriforme spp.</i>	0	0	546	122	668
	Total	12412	10768	20828	17669	61677

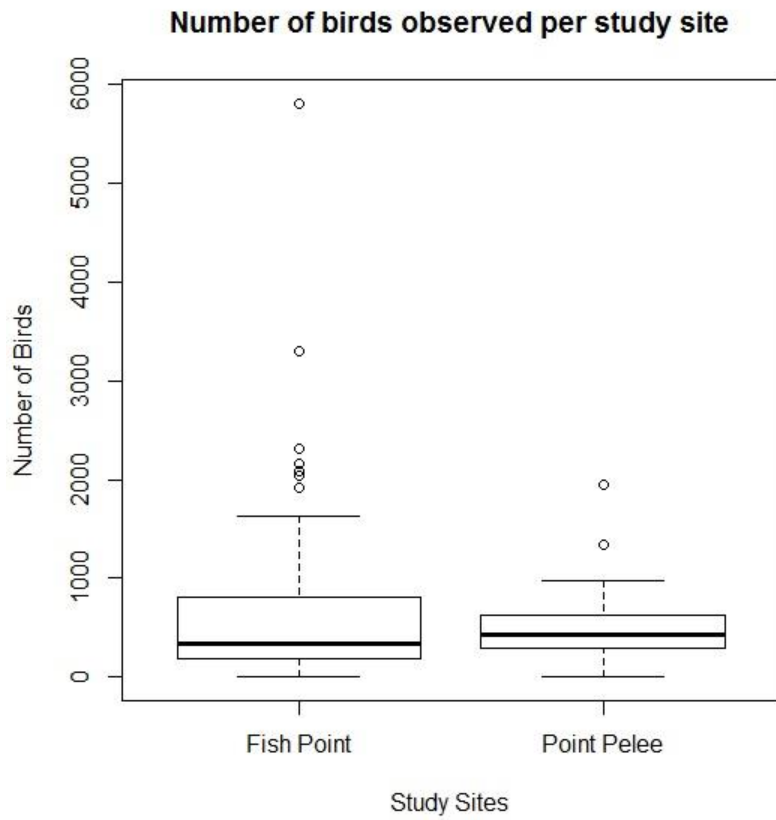


Figure 5. Box plot comparing the two study sites in relation to the number of birds observed during reverse migrations. The solid black bar denotes the mean; the open circles denote outliers.

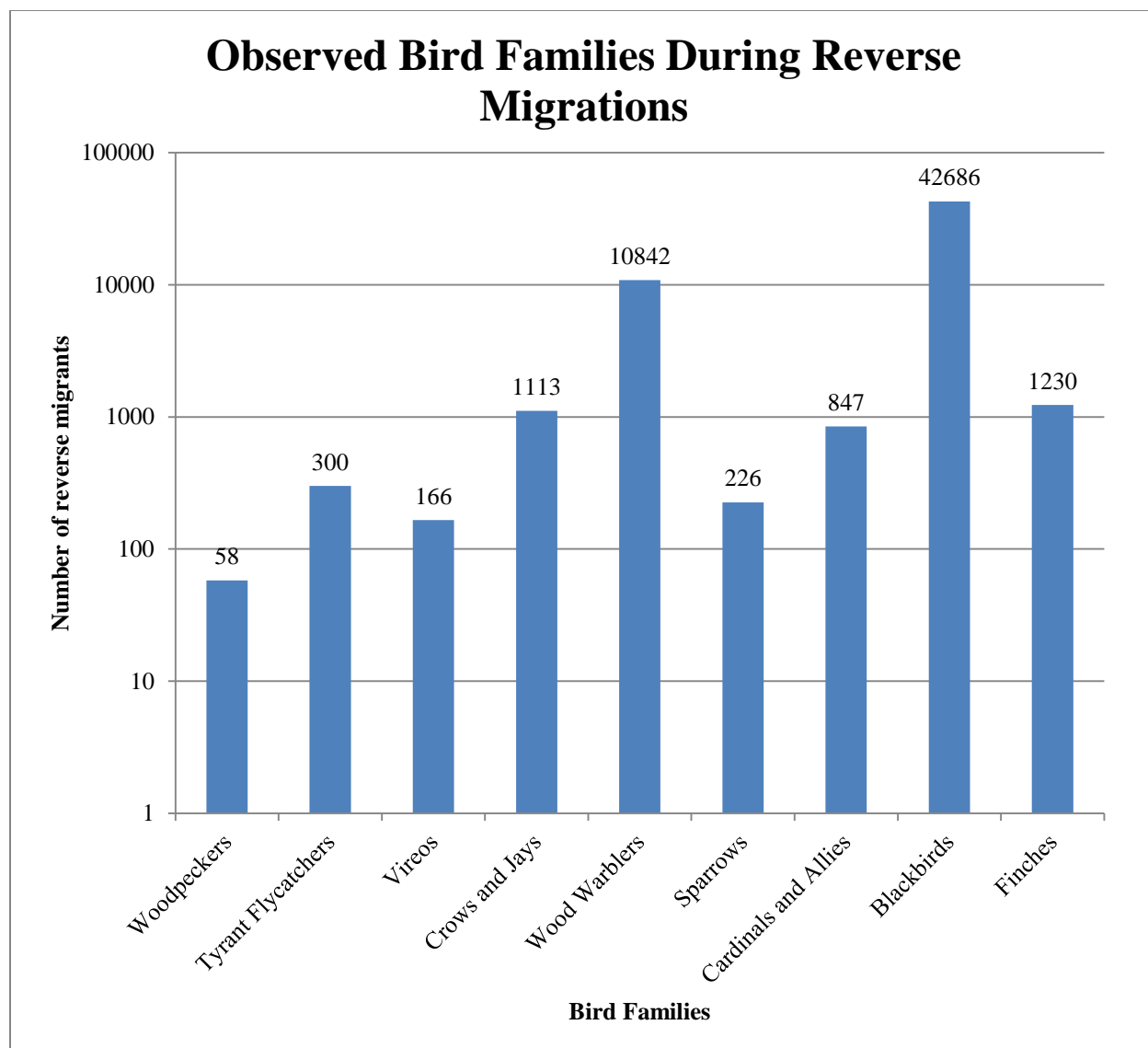


Figure 6. Comparison of abundant bird families observed. All bird families are in standard taxonomic order and labeled according to the American Ornithologist Union's 7th edition (53rd supplement). Numbers pertain to the actual number of observed birds in each family. This subset of observations accounts for 94% ($n = 57468$) of all bird observations during the entire study (2010-2012).

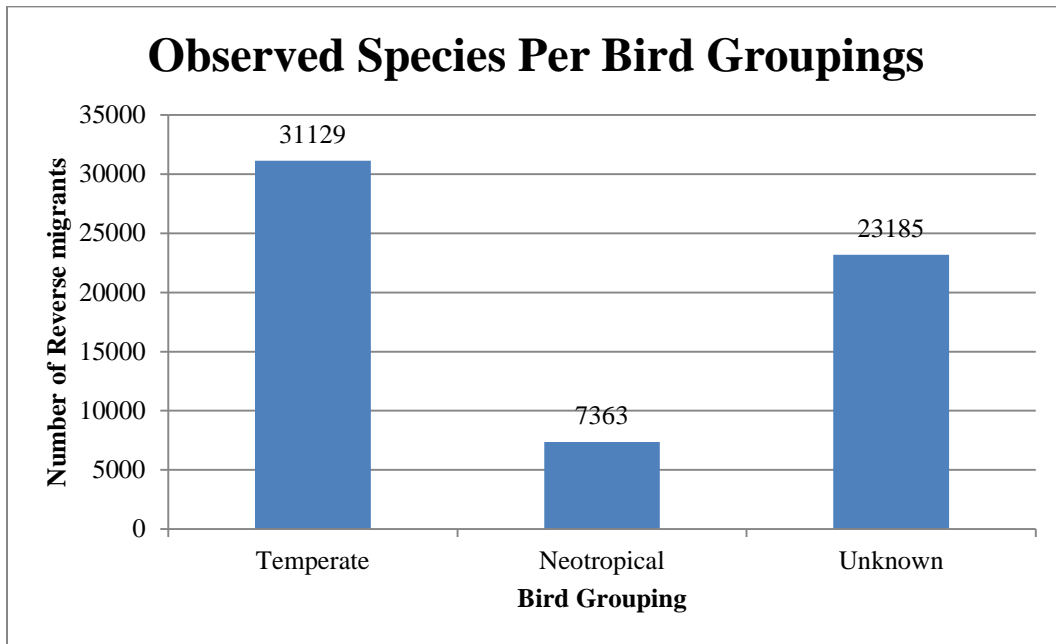


Figure 7. Comparison of temperate and neotropical migrants (and unknowns) observed during reverse migrations (2010-2012). Numbers pertain to the observed number of individual birds. Temperate denotes bird species spending all life-cycles within the continental United States and Canada; Neotropical denotes bird species spending parts of their life-cycles in Central and/or South America (and the continental United States and Canada); and Unknown denotes species not identified during reverse migration surveys.

Table 4. Species at risk noted participating in reverse migrations. All species at risk are designated by the Ontario Ministry of Natural Resources and Environment Canada. COSEWIC pertains to the Committee on the Status of Endangered Wildlife (federal: Environment Canada). SARO pertains to the Species at Risk in Ontario List (provincial: Ontario Ministry of Natural Resources). END denotes an endangered species in Ontario; THR denotes a threatened species in Ontario; SC denotes a special concern species in Ontario; and NAR denotes not-at-risk.

Species	COSEWIC	SARO	Observed Reverse Migrants
Red-headed Woodpecker	THR	SC	44
Golden-winged Warbler	THR	SC	1
Kirtland's Warbler	END	END	1
Prothonotary Warbler	END	END	4
Hooded Warbler	THR	SC	1
Canada Warbler	THR	SC	6
Bobolink	THR	THR	241
Eastern Meadowlark	THR	THR	2
Rusty Blackbird	SC	NAR	13
Total Number Of Noted Species at Risk			313

Endangered: a wildlife species facing imminent extirpation or extinction.

Threatened: a wildlife species likely to become endangered, if limiting factors are not reversed.

Special Concern: a wildlife species that may become a threatened or endangered species because of a combination of biological characteristics and identified threats.

Not at risk: a species that has been evaluated and found to be not at risk (Ontario Ministry of Natural Resources 2013a).

Table 3. Vagrant species noted participating in reverse migrations. All species noted as vagrants are species which do not regularly breed in Ontario (Cadman et al. 2007). The term, “reverse migrants” denotes species observed during reverse migration surveys. Numbers in parentheses () denote the total number of selected species and individuals observed in the Fish Point (Pelee Island) and Point Pelee region during the survey periods as per Wormington (2010, 2011, 2012) and eBird (2013).

Species	Reverse migrants
Kirtland’s Warbler	1
Summer Tanager	3 (21)
Lark Sparrow	1
Blue Grosbeak	1
Dickcissel	6 (6)
Yellow-headed Blackbird	1



Figure 8. Reverse migrant, definitive basic/alternate Red-headed Woodpecker *Melanerpes erythrocephalus*. May 3, 2012 Fish Point Provincial Nature Reserve. Plumage terminology follows Humphrey and Parkes (1959). Copyright Brandon R. Holden.



Figure 9. Reverse migrant, alternate female Prothonotary Warbler *Protonotaria citrea*. May 3, 2012 Fish Point Provincial Nature Reserve. Plumage terminology follows Humphrey and Parkes (1959). Copyright Brandon R. Holden.

Table 4. Proportion of species observed reverse migrating in correlation to the estimated provincial population. All provincial estimates are according to Blancher and Couturier (2007). Species are listed taxonomically if ≥ 200 individuals were observed, equating to 0.5% of the identified individual birds throughout this study ($n = 38,337$).

Species	Cumulative Study Observations	Provincial Estimate (circa 2007)	Proportion Observed (%)
Eastern Kingbird	282	300,000	0.094
Blue Jay	1,109	700,000	0.16
European Starling	1,683	4,000,000	0.042
Cedar Waxwing	759	4,000,000	0.019
Nashville Warbler	831	15,000,000	0.006
Magnolia Warbler	289	12,000,000	0.002
Yellow Warbler	581	4,000,000	0.015
Palm Warbler	351	7,000,000	0.005
Yellow-rumped Warbler	2,277	12,000,000	0.019
Indigo Bunting	788	300,000	0.26
Bobolink	241	800,000	0.030
Red-winged Blackbird	15,033	4,000,000	0.38
Common Grackle	6,211	3,000,000	0.21
Orchard Oriole ^a	266	N/A	N/A
Baltimore Oriole	2,783	300,000	0.93
American Goldfinch	1,191	4,000,000	0.029

^a Orchard Oriole does not have an estimated provincial population (Blancher and Couturier 2007). The Orchard Oriole, a southern species, extending its range only into extreme southern Ontario (Woodliffe 2007, eBird 2013) was not recorded frequently enough on Point Counts to statistically model a population estimate; therefore no ‘Proportion Observed’ has been identified for this purpose.

Chapter 2: Impacts of Weather on Reverse Migration

Introduction

Migration is an extensively studied aspect of avian ecology, particularly in comparison to the study of other taxa (Berthold and Terrill 1991, Dingle 1996). There is general agreement on the evolutionary advantages of migration, such as increased food and reproductive success (Levey and Stiles 1992, Runge and Marra 2005); however, there are considerable costs associated with bird migration (Richardson 1978, Bairlein et al. 2012). The most direct of these costs is the high rate of mortality associated with making long-distance flights (Hassler et al. 1963, Jehl and Henry 2010). Migration is physically demanding from an energy perspective, as migrants must fuel their muscles over prolonged periods of time (Nilsson et al. 2006, Delingat 2008). The energy costs associated with migration can change significantly depending on environmental conditions (Monteith et al. 2011), so it is important for individual birds to make their migrations under the most favourable (i.e., least energetically costly) weather conditions possible (Gauthreaux and Able 1970, Kerlinger and Moore 1989). Because of energy perspectives, birds crossing large bodies of water are particularly sensitive to favourable weather conditions (Kerlinger and Moore 1989, Moore and Aborn 1996).

Mechanistically, bird migration is an instinctual process, appearing intuitive to the casual observer; however, it has taken decades to formally explicate. Bagg et al. (1950), Lack (1960) and Pyle et al. (1993) found that warm fronts in the spring are conducive to bringing birds north in larger numbers, as increases in food supply correlate with temperatures increases. Conversely precipitation can reduce migration intensity (i.e., abundance of birds), perhaps because it chills birds (Richardson 1978), as well as causing more flight resistance in the form of increased body weight (Gessaman and Nagy 1988, Norberg 1995). Wind speed and direction can also have significant impacts on migration intensity (Bloch and Bruderer 1982). Increased wind speeds can create resistance and thus increased energy expenditures, while wind direction with headwinds increases resistance and energy requirements (Bloch and Bruderer 1982). Despite the apparent positive influence of tail-winds on migratory birds, birds will fly in their desired direction despite any perceived positive or negative gain (Bloch and Bruderer 1982, Zehnder et al. 2001).

Wind speed has been shown to have significant negative impacts on migration. Zehnder et al. (2001) found that intense (i.e., higher abundance) movements of birds were associated with weak winds and that regardless of the wind direction birds would fly in the desired direction. While wind speed has significant effects on migration, wind direction has also been shown to dramatically influence bird migration, particularly in regards to reverse migration (Gunn 1951, Richardson 1978, McLaren et al. 2000). Gunn

(1951) noted inclement weather as a driver for reverse migration, particularly with drops in barometric pressure.

By modeling the visual observations of the total number of birds (reverse migrants), I tried to determine which weather covariates are able to explain the most variation for predicting reverse migration as well as the number of birds observed. I also wanted to see how the sampled weather influences bird numbers during reverse migrations. I framed hypotheses pertaining to each weather covariate sampled and how it might influence this form of flight.

Increases in temperature in the spring positively correlate to increases in birds (Bagg et al. 1950, Pyle et al. 1993, Both et al. 2005). I theorized that with higher temperatures observed during visual watches, the higher the total number of birds would be. Higher humidity is directly associated with precipitation and indirectly with inclement weather. Heavy flights (i.e., higher numbers) of reverse migrants have been documented during and ahead of inclement weather events (Lewis 1939, Gunn 1951, Burrell 2013). I predicted that days with higher humidity readings would see a positive correlate to the number of birds. Gunn (1951) found that approaching inclement weather was a predictor for increases in the number of birds observed reverse migrating. Because of Gunn's (1951) work, I predicted that days with high cloud cover would similarly see more birds reverse migrating.

Wind direction has been found to have significant impacts on bird migration during both fall and spring migration (Bloch and Bruderer 1982, Richardson 1978, McLaren et al. 2000). While it would make sense that birds would fly with the wind, there is extensive literature to say otherwise (Evans 1968, Richardson 1978). Lewis (1939) and Gunn (1951) found during their reverse migration watches birds commonly flew into the wind. While no definitive documentation explains why birds fly into the wind, it is postulated that birds do so because it is advantageous for them, whether through increased food availability or due to localized weather events (Evans 1968, Richardson 1978, Komenda-Zehnder et al. 2002, pers.obs.). Based on Lewis (1939) and Gunn's (1951) work, I theorized that the total number of birds would increase during periods of south winds.

Wind speed has been found to have significant impacts on the intensity of spring and fall bird migration (Richardson 1978, Bloch and Bruderer 1982, McLaren et al. 2000). The higher the wind speed, the higher the cost in terms of energy expenditure is required for migrant birds. Zehnder et al. (2001) found that intense movements of birds were associated with weak winds. Based on the literature which has shown that wind speed has significant impacts on bird migration, I theorized that days which have low-moderate wind speeds would correlate to an increase in birds observed reverse migrating.

Substantial movements of reverse migrants have been linked to approaching inclement weather (Gunn 1951). During typical inclement weather events, the barometric pressure generally drops (along with an increase in precipitation, wind speed and strength, and cloud cover). I predicted that with lower barometric pressure, an increase of birds would take place. Extensive literature has shown that migrant landbirds are hampered when they come into contact with precipitation (Richardson 1978). I predicted that days with lower amounts of precipitation would have higher numbers of birds and vice versa. I also theorized that certain weather covariates would have higher impacts on the number of birds than others. Fittingly I theorized that wind direction and temperature would be the two most significant predictors to increases in the numbers of reverse migrants, as had been observed by others (Lewis 1939, Bagg et al. 1950, Gunn 1951, Lack 1960).

Methods

Data collection

Weather conditions were recorded twice daily (07:00 and 19:00) with the exception of precipitation (noted once daily), using Environment Canada's Historical Climate Data interface from Windsor, ON (http://climate.weatheroffice.gc.ca/climateData/canada_e.html; Environment Canada 2013). Windsor, ON was chosen because it was the closest Canadian city to the study sites of Fish Point and Point Pelee (54.6 and 64.7km respectively to Point Pelee and Fish Point) with a complete dataset appropriate for the scope of this study (Environment Canada 2012).

Seven weather covariates expected to influence migration were measured: temperature, humidity, cloud cover, wind direction, wind strength, barometric pressure, and precipitation (Table 6).

Data analysis

Time lags

Birds may reverse migrate in anticipation of inclement weather (Lewis 1939, Gunn 1951, Burrell 2013). Therefore, I tested the numbers of birds and how they responded to weather covariates at various time lags to these observations (i.e., comparing bird counts to different temporal periods). Five distinct temporal periods (time lags) were chosen. Each day consisted of weather observations twice per day (i.e., once in the AM and once in the PM). A maximum time lag of two days before and after was examined due to *a priori* circumstances involving the effect that approaching and passing weather has on migratory birds, as well as the phenology of spring migrants passing through the region, and because of previous

research from the Pelee Island Bird Observatory's recaptured data on spring migrant stopover durations (Table 7; Graeme Gibson the younger, pers. comm.).

Wind Direction

I transformed wind direction (degrees) into radians and then the subsequent values using the cosine transformation for my adjusted wind direction values.

$$\text{radians} = \text{wind direction} \left(\frac{\pi}{180} \right)$$

$$\text{transformation} = \cos(\text{radian}) * -1$$

Following the transformation, wind direction values were constrained to range between -1 and +1. Wind direction falling between 91°-269° generated a positive value; conversely wind direction falling between 271°-360°-89° generated negative values. Wind direction falling on 90° and 270° generated values of 0. Positive values indicated winds with a southern component, while negative values indicated winds with a northern component. Neutral values indicated winds from due east or west.

Outliers

Four outliers (dates) occurred, when disproportionate numbers of birds were observed in comparison to the mean. These four dates had exceptionally high numbers of reverse migrants, with >2,100 birds observed, comprising 22% of the total number of reverse migrants noted throughout the study ($n = 13,583$). These observations were examined with regards to removing from the general model; however, because no statistically different results were apparent and because the integrity of losing these valuable data points, these observations were not examined further.

Temporal Correlations

Time-series (and specifically weather) data represent observations that are continually built upon previous events (i.e., days). In response to these continually built observations from these previous values, there was concern the sampled covariates would be inherently correlated to one another. To properly account for potentially strong correlations, I used the autocorrelation function (ACF) to display trends between covariates in the time series (Zur et al. 2009, Crawley 2013). Two covariates (temperature and barometric pressure) affected the total number of birds disproportionately and subsequently displayed significant values above the 0.95 confidence-interval, while showing strong cyclic trends (Fedy and Doherty 2011, R Core Team 2013). To account for these values, first-differencing was used to mitigate the effects of the first observation and develop subsequent patterns of significance with these covariates (within the 0.95

confidence-interval; Zur et al. 2009, Fedy and Doherty 2011, Crawley 2013). As a result of first-differencing, the first observation within each covariate was deleted and the previous observation within the time-series was used as a way to mitigate the strong cyclic trends in the observations and display results within the 0.95 confidence interval. I then used the first-differenced values for temperature and barometric pressure in all subsequent modeling.

Spatial Correlations

Because two study sites were investigated, it was deemed prudent to explore any relations or correlations between the number of birds observed at each study site. I investigated the variation in the number of birds observed between the two study sites by examining box-plots and a Wilcoxon rank sum test (Zur et al. 2009, Crawley 2013). I used the Wilcoxon rank sum test as my dataset represented count-data, thus non-normal in distribution, while also being able to assess data with the presence of outliers, therefore being a more powerful test in comparison to t tests (Crawley 2013).

Selecting the top covariates among time lags:

Performing a univariate generalized linear model (LMER) enabled me to distinguish the top time lag for each covariate as a way to establish the best model statement (Broström and Holmberg 2011, Barton 2013). All covariates due to time lags surrounding real-time observations and the rate of daily sampling ($n = 2$) amounted to 10 observations, with the exception of precipitation. Precipitation was sampled once a day ($n = 5$ observations). To identify key weather covariates influencing the number of birds observed during reverse migration, I used an AIC_c approach to select the best model for each hypothesis within my limited (i.e., small) dataset for both the univariate and mixed-model approaches (Burnham and Anderson 2002, Fedy and Martin 2011). AIC_c allows for comparing the complexity of the statistical model with the relative goodness of fit, doing so by penalizing the log-likelihood (Crawley 2013). Although previous studies examining reverse migration have suggested that wind direction and barometric pressure are the key covariates influencing reverse migration (Lewis 1939, Gunn 1951), neither study examined the influence of weather using a quantitative approach. After selecting the top weather covariates with time lags, I built general models by comparing all possible combinations of the covariates identified in the top models for each hypothesis (Barton 2013). I included a random effect intercept for study site and specified a Poisson distribution (log link function as implemented in the LMER package; Broström and Holmberg 2011, Bates et al. 2012, Barton 2013, Pinheiro et al. 2013). Data were analyzed using ‘R’ Software, version 2.15.3 (R Core Team 2013).

Results

Eighty species comprising a total of 61,677 birds were observed participating in reverse migrations over the study duration (2010-2012; $n = 97$ days). The mean daily count was 636, varying by site (Fish Point's mean = 675, versus Point Pelee's mean = 517), however, 2012 provided the best year for comparison due to both Fish Point and Point Pelee being sampled simultaneously.

Spatial Correlations: Fish Point vs. Point Pelee

I used a box-plot and the Wilcoxon rank sum test to analyze differences in the number of birds observed from Fish Point ($n = 73$ days sampled) and Point Pelee ($n = 24$ days sampled) throughout the study's duration. Study site in relation to the number of birds observed varied (Wilcoxon rank sum test, $W = 843.5$ and $P = 0.79$) identifying each site as inherently different from the other (Figure 12). Subsequently, I modeled site as a random mixed-effect to specify a unique intercept for each site.

Temporal Correlations

Two covariates (temperature and barometric pressure) displayed results above the 0.95 confidence interval using the autocorrelation function (ACF; Figure 10). I first-differenced these covariates (temperature and barometric pressure) in order to reduce the values associated with the first observation and to develop patterns of significance. Subsequently the results of first-differencing displayed results below the 0.95 confidence interval (Figure 11). I then used the first-differenced results in all subsequent modeling.

Univariate LMER

Time lags were identified, with up to two days before and after surveys (i.e., having a range of time lags between -2A and +2B), with ten possible time lags. I used generalized linear mixed-models (LMER) including site as a random intercept to assess the relative performance of the selected time lags. I used an AIC_c approach to best determine the appropriate covariates with corresponding time lags (Table 8).

Following the results of the generalized linear mixed-model (LMER) for each univariate correlation, I determined the time lag with the best (lowest) AIC_c value. Time lags between 0A -- +2B (i.e., time compared to during and after surveys) were the top time lags for all covariates sampled, confirming that immediate and approaching inclement weather and/or periods of south winds are drivers behind reverse migration (Table 7).

My results indicated that all measured covariates were influential for predicting numbers of birds during reverse migration in some capacity; however, wind direction accounts for the most variation among all

covariates ($\beta = 0.732$, $SE = 0.006269$). Barometric pressure ($\beta = -0.088$, $SE = 0.0076$), temperature ($\beta = 0.097$, $SE = 0.0011$) and wind strength ($\beta = 0.029$, $SE = 0.00042$) were also important in explaining the variation of number of birds, while humidity, cloud cover, and precipitation were weak predictors for explaining the variation in the number of birds ($\beta = <0.02$, $SE = <0.00049$).

The top covariates and model statement:

Following the selection of the top time lags, I created a generalized linear mixed-model with a random-mixed effect of study site to test the selection using all possible combinations. I used an AIC_c approach to select the best models (Table 9).

I used the top models ($\Delta AIC_c \leq 8$) to select the candidate covariates inducing the number of birds observed during reverse migration (Table 9). Table 5 presents the weighted-averages of all coefficients from the top models ($w_i = \geq 0.37$).

Wind direction ($\beta = 0.72$, $SE = 0.0082$) and barometric pressure ($\beta = -0.21$, $SE = 0.0089$) account for a high proportion in the variation of the numbers of birds (Table 10).

Coefficients revealed positive associations with several covariates (temperature, humidity, wind direction and wind speed), suggesting that increases in temperature, humidity and wind speed correlate to increases in the number of birds. The positive coefficient for wind direction suggests that winds with a southerly flow have a positive influence on the number of birds observed. Three covariates revealed negative associations with their respective coefficients (barometric pressure, cloud cover and precipitation), indicating that the lower the barometric pressure, less cloud cover and precipitation respond to increases in the number of birds.

Discussion

My results indicate that of the sampled weather covariates, wind direction is the most important, followed by barometric pressure; however, all other (measured) covariates are influential to some degree. Time lags have influences on the number of birds observed, particularly how reverse migrants participate in these flights during or ahead of inclement weather. There appears to be variation between study sites, with Point Pelee exhibiting higher numbers of reverse migrants.

There are subtle yet distinct differences in the number of reverse migrants observed at Point Pelee and Fish Point. While both study sites are similar in their geography, climate and biology, numbers of reverse migrants at Point Pelee were slightly higher than at Fish Point, however, 2012 is the best year for

comparisons between sites, as the study was conducted at both locations simultaneously. Based on satellite imagery, Point Pelee offers a more continuous and extensive amount of natural cover compared to Fish Point and the rest of Pelee Island. Increased amounts of natural cover provide shelter and feeding opportunities for landbirds (Heikkinen et al. 2004). As there is more natural cover at Point Pelee, it is anticipated there would be more appropriate habitat for migratory birds than at Fish Point and thus more birds present - as my results indicate.

Some landbirds (e.g., Blue Jays, *Cyanocitta cristata*) prefer flying over land in comparison to open water (Tarvin and Woolfenden 1999). This behaviour would negatively affect the numbers of birds observed at Fish Point, as this location is completely surrounded by water. Birds that prefer to fly over land would more likely be in higher numbers at Point Pelee as it is on the Ontario mainland. I presume that the difference in natural cover is a key reason for the difference in the number of birds, while the mainland versus island dynamic potentially serves as a differentiating factor in the numbers of reverse migrants noted at the study sites in specific species.

The time lags that best suited all top covariates ranged from 0A – 2B (refer to Table 2). While these time lags varied for all covariates, this suggests that birds reverse migrate due to the immediate and approaching weather (i.e., inclement weather and/or periods of south winds) as observed by Gunn (1951) and Burrell (2013) and thus these flights appear to be a reorientation flight. Wind direction and temperature were the only covariates which displayed immediate responses to the weather (time lag = 0A), while all other covariates (barometric pressure, cloud cover, humidity, and precipitation) displayed an early response to approaching inclement weather (time lag = 1B-2B).

After testing the selection of all covariates using all possible combinations (Table 4 and 5), my results display that the top two models account for 0.99 of the variation in the number of birds observed during reverse migrations. All covariates examined (Table 1) are influential (in the top models), suggesting that reverse migration is driven by a combination of weather factors. Two covariates (wind direction and barometric pressure) displayed significant results from the β coefficients and the lowest values from the AIC_c approach. These covariates appear to be crucial in explaining reverse migration from a meteorological approach among the other covariates. My results indicate birds generally reverse migrate in higher numbers when winds are from the south or have a southerly component to their direction, and when there is a drop in barometric pressure. My results also suggest that as cloud cover and precipitation decrease, the number of reverse migrants increases. Conversely as temperature, humidity and wind speed increase, so too will the number of birds. Based on the results, my hypotheses were relatively accurate, except in relation to cloud cover. All covariates reacted in anticipated ways, as explained in my

introduction. My results correspond with those of 'normal' spring migration; as general increases in the number of birds are noted, so too are higher numbers of reverse migrants.

Chapter 2 Tables and Figures

Table 6. Covariate selection, including the range of values.

Covariate	Abbreviation	Description	Range
Temperature	temp	Air temperature measured in degrees Celsius (°C)	2.4°-28.8° C
Humidity	hum	Humidity measured using percent (%)	24-99%
Cloud Cover	cloud	Cloud cover was recorded to the nearest tenth percent, (e.g., cloudy = 100% cloud cover; and clear = 0% cloud cover)	0-100%
Wind direction	wdir	Direction of wind, measured in degrees (°) and transformed using radians and COS	0-360° -1 to +1
Wind strength	wspe	Strength of wind, measured in kilometres per hour (km/hr)	0-46km/hr
Barometric pressure	press	Barometric pressure, measured in kilopascals (kPa)	97.16-100.68kPa
Precipitation	precip	Amount of precipitation measured daily, using millimetres (mm).	0-30.4mm

Table 7. Recorded time lags associated with the weather sampled.

Numbers of days time lagged	Time Lag	Example*
Day of observation minus 2 days	-2A	Counts observed on April 25; weather correlated to April 23 in the AM
Day of observation minus 2 days	-2B	Counts observed on April 25; weather correlated to April 23 in the PM
Day of observation minus 1 day	-1A	Counts observed on April 25; weather correlated to April 24 in the AM
Day of observation minus 1 day	-1B	Counts observed on April 25; weather correlated to April 24 in the PM
Day of observation (0)	0A	Counts observed on April 25; weather correlated to April 25 in the AM
Day of observation (0)	0B	Counts observed on April 25; weather correlated to April 23 in the PM
Day of observation plus 1 day	+1A	Counts observed on April 25; weather correlated to April 26 in the AM
Day of observation plus 1 day	+1B	Counts observed on April 25; weather correlated to April 26 in the PM
Day of observation plus 2 days	+2A	Counts observed on April 25; weather correlated to April 27 in the AM
Day of observation plus 2 days	+2B	Counts observed on April 25; weather correlated to April 27 in the PM

*All weather readings in the AM were recorded at 07:00; conversely all weather readings in the PM were recorded at 19:00.

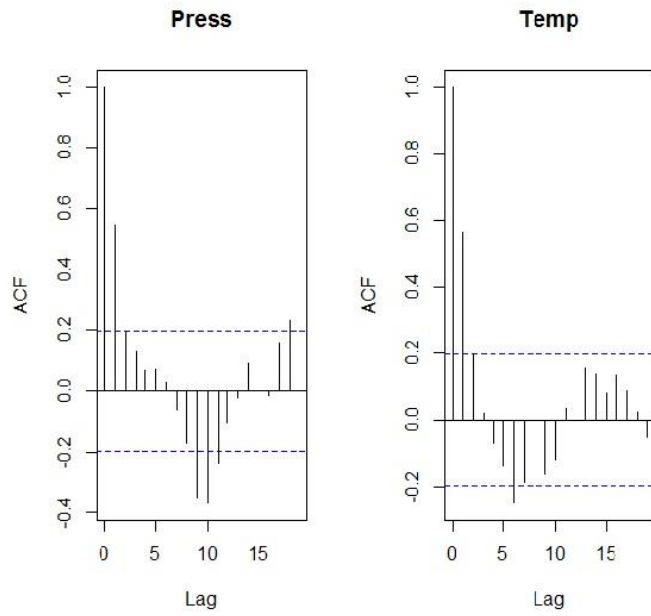


Figure 10. Autocorrelation plots of barometric pressure (Press) and temperature (Temp) over a time-series of the entire dataset. *Dotted line* denotes a confidence interval of 0.95 approximating significance.

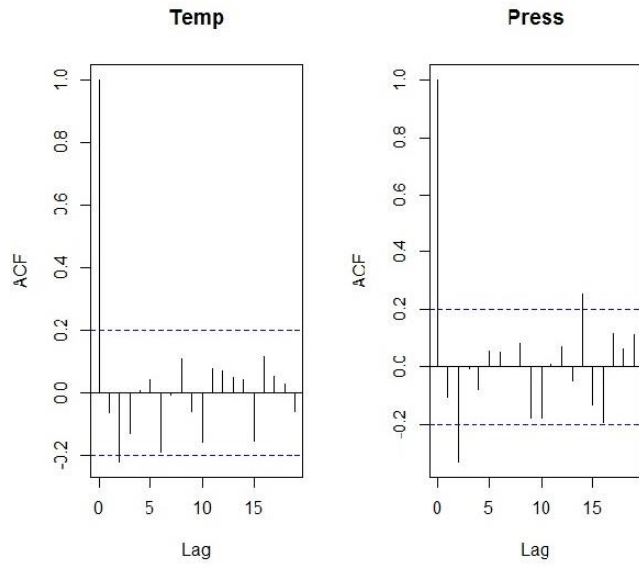


Figure 11. First-differenced autocorrelation plots of temperature (Temp) and barometric pressure (Press) displayed over a time-series of the entire dataset. *Dotted line* denotes a confidence interval of 0.95 approximating significance.

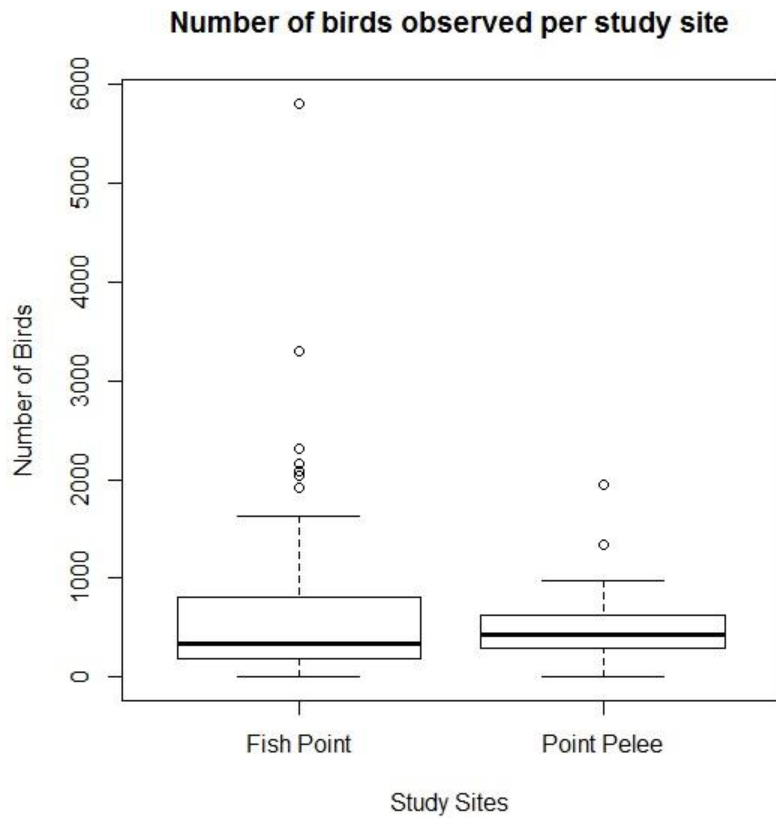


Figure 12. Box plots comparing the two study sites (Fish Point in 2010-2012 and Point Pelee in 2010) in relation to the number of birds observed during reverse migrations throughout the entire study. The solid black bar denotes the mean; the open circles denote outliers.

Table 8. Top time lags for each covariate using a univariate LMER. Notated time lags are identified in Table 7. Coefficient, β coefficient; SE, standard error; LL, log-likelihood; AIC_c , Akaike's information criterion adjusted for small sample size.

Covariate	Time lag	Coefficient	SE	LL	AIC_c
Temperature	0A	0.10	0.0016	-26097.49	52201
Humidity	+2B	0.010	0.00019	-28558.15	57122
Cloud Cover	+1B	0.0062	0.00013	-28529.76	57066
Wind Direction	0A	0.73	0.0063	-22985.94	45978
Wind Strength	+2A	0.029	0.00042	-27700.45	55407
Barometric Pressure	+2A	-0.087	0.0076	-29782.27	59571
Precipitation	+2A	0.019	0.00049	-29157.75	58321

Table 9. Summary of top models in a comparison of all possible combinations of models based on the top covariates identified in Table 7. Only models with a $w_i \geq 0.001$ are presented. Notation of model covariates are identified in Table 1. K , number of covariates in the model; Intercept, random-intercept of site; ΔAIC_c , difference in Aikake's information criterion (AIC_c); ΔLL , difference in log-likelihood; Rank, models rank within the set; w_i , model's weight within the set.

Model	K	Intercept	ΔAIC_c	ΔLL	Rank	w_i
cloud + hum + press + temp + wdir + wspe ^{a b}	6	5.80	0	0	1	0.63
cloud + hum + precip + press + temp + wdir + wspe	7	5.79	1.08	0.46	2	0.37
hum + press + temp + wdir + wspe	5	5.78	13.54	7.77	3	0.001

^a $AIC_c = 38329.8$

^b $LL = -19156.89$

Table 10. Model-averaged coefficients and standard errors for each weather covariate according to the top 2 models (see Table 9). Coefficient, β coefficient; SE, standard error.

Covariate	Coefficient	SE
Temperature	0.044	0.0014
Humidity	0.0032	0.0003
Cloud cover	-0.0059	0.0002
Wind direction	0.72	0.0082
Wind speed	0.029	0.0005
Barometric pressure	-0.21	0.0089
Precipitation	-0.0002	0.0006

Epilogue

Despite the regular occurrence of landbirds participating in reorientation flights, few migrants were noted flying anything but south. My results indicate that reverse migration occurs among many migratory landbirds found regularly in the Pelee region (therefore affecting a wide diversity of species; Goodwin 1995, Hince 1999, eBird 2013). Wood Warblers and Blackbirds are the most common participants in reverse migrations, while temperate migrants greatly outnumber neotropical migrants (as much as 4:1). Specific differences in abundance were noted among species and families. *Catharus* Thrushes were completely absent from my surveys, while fewer than expected of certain neotropical species were observed (e.g., Scarlet Tanager, Rose-breasted Grosbeak, Tyrant Flycatchers, and Sparrows). Species at risk and vagrants were noted relatively frequently (0.83% of all migrants), highlighting the importance of these surveys in conjunction with other surveys to monitor migrant landbird populations.

Disproportionately high numbers of Blackbirds and other diurnal migrants engage in reverse migrations, particularly compared to strong nocturnal migrants such as Thrushes and Wood Warblers.

Weather plays an integral role in influencing this form of flight. Of the studied weather covariates, wind direction appears to be the most important component to determining reverse migrations, and to a lesser extent, barometric pressure. Winds with a southern component correspond to dramatic increases in the number of birds, while drops in barometric pressure correspond similarly with increases in the number of birds. Overall my results indicate that birds reverse migrate during or ahead of inclement weather and/or periods of south winds.

While the elements of reverse migration pertain to a distinct form of flight, it is likely not truly a form of migration. This form of flight in its simplest is likely a form of reorientation, whereby migratory birds take advantage of local weather conditions by flying south for extended distances. I hypothesize that birds moving south during these 'reorientation flights' in the spring have either overshot their traditional 'stopover' site or presumed breeding territory and are trying to make a correction to get to these more favourable locations, or they are taking advantage of more propitious weather conditions (to the south). This form of flight is expected to have serious repercussions on the fitness levels and life-cycles of migratory landbirds.

Reorientation flights are expected to create significant delays in the migration phenology of landbirds as well as their breeding cycles. Songbirds delayed during stages in their life-cycle are expected to undergo increased stress, particularly on the birds physical and reproductive capabilities (Harrison et al. 2011). More importantly, reverse migration may also have more important consequences on the breeding success and cycles of birds later in the same year. Determining how reverse migration affects the breeding cycles

of songbirds is a novel concept this study may be able to address in the future. Determining how delays from reverse migration affect survivorship and reproduction is an aspect needing further exploring.

Studies looking at reverse migration provide a useful tool for migration monitoring. Observations of thousands of birds - many which are either species at risk or vagrants - in an efficient manner are important for helping to aid in determining population trends related to migratory birds in conjunction to migration monitoring activities currently being undertaken (e.g., mist-netting). Future conservation and research in this discipline will be greatly aided by increased knowledge pertaining to these issues. Studies examining reverse migration will be conducive for this area of research.

Short- and long-term studies of this nature will continue to develop our understanding of how weather affects and impacts bird migration (including reverse migration). This study in its simplest form offers a glimpse into the population index of landbirds. Continuing this study in conjunction with other programs will allow for a continual monitoring program to help assess landbird populations passing through the lower Great Lakes region in an effective and efficient manner.

Examining how short-distance migrants are impacted more so by weather in comparison to long-distance migrants being impacted by photoperiod is one aspect this study may be able to address in future studies. Time trends within seasons is another aspect needing to be examined further, particularly examining these spring flights both before and after this study was examined (i.e., early April and late May/early June). Anecdotal evidence suggests that large movements of reverse migrants may occur during periods of large increases in the number of birds, such as early or mid-April (pers.obs.). Future studies of this nature will also need to incorporate new technologies, such as radio telemetry and isotope analysis. These technologies will help determine where birds are coming from and going. Technological components will help address questions related to how reverse migration may impact the survival and reproduction of birds as well as the energetic costs associated with this form of flight. Monitoring populations will also help conservationists and policy-makers make informed decisions regarding the populations of species involved in these flights.

Bibliography

- Åkesson, S. 1999. Do Passerine Migrants Captured at an Inland Site Perform Temporary Reverse Migration in Autumn? *Ardea*, 87 (1): 129-137.
- Alerstam, T. 1978. Reoriented Bird Migration in Coastal Areas: Dispersal to Suitable Resting Grounds? *Current Bird Migration Research. Proceedings of a Symposium at Falsterbo, Sweden*. pp. 405-408.
- Alerstam, T. 1990. Ecological causes and consequences of bird orientation. *Experientia*, 46: 405-415.
- Alerstam, T. 1991. Bird flight and optimal migration. *TREE*, 6 (7): 210-215.
- Alerstam, T. 2009. Flight by night or day? Optimal daily timing of bird migration. *Journal of Theoretical Biology*, 4: 530-536.
- Alerstam T. and P.H. Enckell. 1979. Unpredictable Habitats and Evolution of Bird Migration. *Oikos*, 33(2): 228-232.
- Alerstam, T., and S. Ulfstrand. 1972. Radar and field observations of diurnal bird migration in south Sweden, Autumn 1971. *Ornis Scandinavica*, 3(2): 99-139.
- Askeyev, O.V., T. Sparks, and I.V. Askeyev. 2009. Earliest recorded Tatarstan skylark in 2008: non-linear response to temperature suggests advances in arrival dates may accelerate. *Climate Research*, 38: 189-192.
- Bagg, A.M., W.W.H. Gunn, D.S. Miller, J.T. Nichols, W. Smith, and F.P. Wolfarth, F.P. 1950. Barometric pressure-patterns and spring bird migration. *The Wilson Bulletin*, 62 (1): 5-19.
- Bairlein, F., D.R. Norris, R. Nagel, M. Bulte, C.C. Voigt, J.W. Fox, D.J.T. Hussell, and H. Schmaljohann. 2012. Cross-hemisphere migration of a 25g songbird. *Biology Letters*, 8: 505-507.
- Barron, G.D., J.D. Brawn, and P.J. Weatherhead. 2010. Meta-analysis of transmitter effects on avian behaviour and ecology. *Methods in Ecology and Evolution*, 1: 180-187.
- Barton, K. 2013. MuMIn: Multi-model inference. R package version 1.9.0. <http://CRAN.R-project.org/package=MuMIn>.
- Bates, D., M. Maechler, and B. Bolker. 2012. lme4: Linear mixed-effects models using Eigen and Eigenfaces. R package version 0.999999-0. <http://CRAN.R-project.org/package=lme4>.
- Beauchamp, G. 2011. Long-distance migrating species of birds travel in larger groups. *Biology Letters*, 7: 692-694.

- Bechard, M.J., C.S. Houston, J.H. Sarasola and A.S. England. 2010. Swainson's Hawk (*Buteo swainsoni*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: (<http://bna.birds.cornell.edu/bna/species/265>).
- Bell, C. 2000. Process in the evolution of bird migration and pattern in avian ecogeography. *Journal of Avian Biology*, 31: 258-265.
- Berthold, P., and S.B. Terrill. 1991. Recent advances in studies of bird migration. *Annual Review of Ecology and Systematics*, 22: 357-378.
- Bildstein, K.L. 2006. Migrating raptors of the world: their ecology and conservation. Cornell University Press Inc. Ithaca, NY.
- Blancher, P.A., and A.R. Couturier. 2007. Population Size Estimates for Ontario Birds, Based on Point Counts, pp. 655-657 in Cadman, M.D., D.A. Sutherland, G.G. Beck, D. Lepage, and A.R. Couturier, eds. Atlas of the Breeding Birds of Ontario, 2001-2005. Bird Studies Canada, Environment Canada, Ontario Field Ornithologists, Ontario Ministry of Natural Resources, and Ontario Nature, Toronto, xxii + 706 pp.
- Bloch, R., and B. Bruderer. 1982. The air speed of migrating birds and its relationship to the wind. *Behavioral Ecology Sociobiology*, 11:19-24
- Both, C., Bijlsma, R.G., and Visser, M. 2005. Climatic effects on timing of spring migration and breeding in a long-distance migrant, the pied flycatcher *Ficedula hypoleuca*. *Journal of Avian Biology*, 36: 368-373.
- Broström, G., and H. Holmberg. 2011. glmmML: Generalized linear models with clustering. R package version 0.82.1. <http://CRAN.R-project.org/package=glmmML>.
- Burnham, K.P., and D.P. Anderson. 2002. Model selection and multimodel inference. Springer, New York, NY.
- Burrell, K.G. 2013. Examining a large reverse migration off Fish Point, Pelee Island. *Ontario Birds*, 30(3): 140-147.
- Cadman, M.D., D.A. Sutherland, G.G. Beck, D. Lepage and A.R. Couturier (Ed). 2007. Atlas of the Breeding Birds of Ontario, 2001-2005. Bird Studies Canada, Environment Canada, Ontario Field Ornithologists, Ontario Ministry of Natural Resources and Ontario Nature. Toronto, ON. xxii + 706pp.

- Cimprich, D.A., F.R. Moore, and M.P. Guilfoyle. 2000. Red-eyed Vireo (*Vireo olivaceus*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: (<http://bna.birds.cornell.edu/bna/species/527>).
- Committee on the Status of Endangered Wildlife in Canada. 2012. Canadian Wildlife Species At Risk. Retrieved from: (http://www.cosewic.gc.ca/eng/sct0/rpt/csar_e.html).
- Cox, G.W. 1968. The role of competition in the evolution of migration. *Evolution*, 22: 180-192.
- Cox, G.W. 1985. The evolution of avian migration systems between temperate and tropic regions of the New World. *American Naturalist*, 126: 451-474.
- Crawley, M.J. 2013. The R Book: Second Edition. John Wiley and Sons Ltd. West Sussex, United Kingdom.
- Cresswell, W. 1994. Flocking is an effective anti-predation strategy in redshanks, *Tringa totanus*. *Animal Behaviour*, 47(2): 433-442.
- Curson, J., D. Quinn, and D. Beadle. 1994. Warblers Of The Americas: An Identification Guide. Houghton Mifflin Company. New York, NY.
- Dawson, W.R. 1997. Pine Siskin (*Spinus pinus*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: (<http://bna.birds.cornell.edu/bna/species/280>).
- Delingat, J., F. Bairlein, and A. Hedenström. 2008. Obligatory barrier crossing and adaptive fuel management in migratory birds: the case of the Atlantic crossing in Northern Wheatears (*Oenanthe oenanthe*). *Behavioral Ecology and Sociobiology*, 62 (7): 1069-1078.
- Dingle, H. 1996. Migration: the biology of life on the move. Oxford University Press, Inc. New York, NY.
- Dunn, J.L., and J. Alderfer. 2011. National Geographic Field Guide To The Birds of North America. National Geographic Society. Washington, D.C.
- Dunn, J.L. and K.L. Garrett. 1997. A Field Guide To Warblers of North America. Peterson Field Guides. Houghton Mifflin Company. New York, NY.
- Holder, M.L. 2002. Spring Migration: Ontario. *North American Birds*, 56 (3): 301-304.

- Hunt, P.D., and B.C. Eliason. 1999. Blackpoll Warbler (*Setophaga striata*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: (<http://bna.birds.cornell.edu/bna/species/431>).
- eBird. 2013. eBird: An online database of bird distribution and abundance [web application]. eBird, Ithaca, NY. Available: (<http://www.ebird.org>).
- Environment Canada. 2013. Historical Weather and Climate Data. National Climate Data and Information Archive. Retrieved from: (http://climate.weatheroffice.gc.ca/climateData/canada_e.html).
- Evans, P.R. 1968. Reorientation of passerine night migrants after displacement by the wind. *British Birds*, 61: 281-303.
- Faaborg, J. 2002. Saving Migrant Birds: Developing Strategies for the Future. University of Texas Press, Austin. Austin, TX.
- Farnsworth, A., S. Gauthreaux, and D. Van Blaricom. 2004. A comparison of nocturnal call counts of migrating birds and reflectivity measurements on Doppler radar. *Journal of Avian Biology*, 35: 365-369.
- Fedy, B.C, and K.E. Doherty. 2011. Population cycles are highly correlated over long-time series and large spatial scales in two unrelated species: greater sage-grouse and cottontail rabbits. *Population Ecology*, 165: 915-924.
- Fedy, B., and K. Martin. 2011. The influence of fine-scale habitat features on regional variation in population performance of alpine white-tailed ptarmigan. *The Condor*, 113(2): 306-315.
- Gauthreaux, S., and K. Able. 1970. Wind and the direction of nocturnal songbird migration. *Nature*, 228: 476-477.
- Gessaman, J.A., and K.A. Nagy. 1988. Transmitter loads affect the flight speed and metabolism of homing pigeons. *The Condor*, 90: 662-668.
- Gordo, O. 2007. Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. *Climate Research*, 35: 37-58.
- Goodwin, C.E. 1995. A Bird Finding Guide to Ontario: Revised Edition. University of Toronto Press Inc. Toronto, ON.
- Government of Ontario. 2007. The Endangered Species Act 2007. Retrieved from: (http://www.e-laws.gov.on.ca/html/statutes/english/elaws_statutes_07e06_e.htm).

- Gunn, W.W.H. 1951. Reverse migration of birds in the Pelee Region in relation to the weather. PhD Thesis. University of Toronto. Toronto, ON. 108 pp.
- Hamel, P.B. 2000. Cerulean Warbler (*Setophaga cerulea*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: (<http://bna.birds.cornell.edu/bna/species/511>).
- Harrison, X.A., J.D. Blount, R. Inger, D.R. Norris, and S. Bearhop. 2011. Carry-over effects as drivers of fitness differences in animals. *Journal of Animal Ecology*, 80: 4-18.
- Hassler, S.S., R.R. Graber, and F.C. Bellrose. 1963. Fall migration and weather: a radar study. *The Wilson Bulletin*, 75: 56-77.
- Henson, B.L., D.T. Kraus, M.J. McMurtry, and D.N. Ewert. 2010. Islands of Life: A Biodiversity and Conservation Atlas of the Great Lakes Islands. Nature Conservancy of Canada. 154 pp.
- Heikkinen, R.K., M. Luoto, R. Virkkala, and K. Rainio. 2004. Effects of habitat cover, landscape structure and spatial variables on the abundance of birds in an agricultural-forest mosaic. *Journal of Applied Ecology*, 41: 824-835.
- Hince, T. 1999. A Birder's Guide To Point Pelee (and surrounding Region). Preney Print and Litho. Windsor, ON.
- Hussell, D.J.T., and T.E. Quinney. 1987. Food abundance and clutch size of Tree Swallows, *Tachycineta bicolor*. *Ibis*, 129: 243-258.
- Hvenegaard, G.T., J.R. Butler, and D.K. Krystofiak. 1989. Economic values of bird watching at Point Pelee National Park, Canada. *Wildlife Society Bulletin*, 17: 526-531.
- Humphrey, P.S., and K.C. Parkes. 1959. An approach to the study of molts and plumages. *Auk*, 76: 1-3.
- Jaramillo, A. and P. Burke. 1999. New World Blackbirds: The Icterids. Princeton University Press. Princeton, NJ.
- Jenni, L. and M. Schaub. 2003. Behavioural and physiological reactions to environmental variation in bird migration: A review [in Avian Migration]. Springer-Verlag. Berlin, Germany.
- Jehl, Jr., J.R., and A.E. Henry. 2010. The Postbreeding Migration of Eared Grebes. *The Wilson Journal of Ornithology*, 122(2): 217-227.
- Kerlinger, P. 1995. How Birds Migrate. Stackpole Books. Mechanicsburg, PA.

- Kerlinger, P., and F.R. Moore. 1989. Atmospheric structure and avian migration. In: Power, D.M. (Ed.), *Current Ornithology*, vol. 6. Plenum Press. New York, NY. pp. 109-142.
- Knox, A.G., and P.E. Lowther. 2000. Common Redpoll (*Acanthis flammea*), *The Birds of North America Online* (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: (<http://bna.birds.cornell.edu/bna/species/543>).
- Komenda-Zehnder, S., F. Liechti, and B. Bruderer. 2002. Is reverse migration a common feature of nocturnal bird migration? An analysis of radar data from Israel. *Ardea*, 90 (2): 325-334.
- Lack, D. 1960. The influence of weather on passerine migration: a review. *Auk*, 77 (2): 171-209.
- Lank, D.B. 1989. Why fly by night? Inferences from tidally-induced migratory departures of sandpipers. *Journal of Field Ornithology*, 60: 154-161.
- Lanyon, W.E. 1981. Breeding birds and old field succession on fallow Long Island Farmland. *Bulletin of the American Museum of Natural History*, 168: 1-66.
- Lanyon, W.E. 1997. Great Crested Flycatcher (*Myiarchus crinitus*), *The Birds of North America Online* (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: (<http://bna.birds.cornell.edu/bna/species/300>).
- Larkin, R., W. Evans, and R. Diehl. 2002. Nocturnal flight calls of Dickcissels and Doppler radar echoes over south Texas in spring. *Journal of Field Ornithology*, 73: 2-8.
- Lazarus, J. 1979. The early warning function of flocking in birds: An experimental study with captive qulelea. *Animal Behaviour*, 27(3): 855-865.
- Lemke, P., J. Ren, R.B. Alley, I. Allison, J. Carrasco, G. Flato, Y. Fujii, G. Kaser, P. Mote, R.H. Thomas, and T. Zhang. 2007. Observations: Changes in Snow, Ice and Frozen Ground. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* [Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor, and H. L. Miller (eds.)]. Cambridge University Press Inc. Cambridge, United Kingdom and New York, USA.
- Levey, D.J., and F.G. Stiles. Evolutionary precursors of long-distance migration: resource availability and movement patterns in neotropical landbirds. *The American Naturalist*, 140(3): 447-476.
- Lewis, H.F. 1939. Reverse Migration. *Auk*, 56(1): 13-27.

- Lindström, Å. and T. Alerstam. 1986. The adaptive significance of reoriented migration of chaffinches *Fringilla coelebs* and bramblings *F. montifringilla* during autumn in southern Sweden. *Behavioural Ecology and Sociobiology*, 19 (6): 417-424.
- Long Point Bird Observatory. 2005. Migration Monitoring Protocol: 4th Edition. Bird Studies Canada. Port Rowan, ON. 67pp.
- Lowery, Jr., G.H. 1955. Louisiana birds. Louisiana State University Press Inc. Baton Rouge, LA.
- Lowther, P.E., C.C. Rimmer, B. Kessel, S.L. Johnson and W.G. Ellison. 2001. Gray-cheeked Thrush (*Catharus minimus*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: (<http://bna.birds.cornell.edu/bna/species/591>).
- Mack, D.E., and W. Yong. 2000. Swainson's Thrush (*Catharus ustulatus*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: (<http://bna.birds.cornell.edu/bna/species/540>).
- Mackenzie, S. 2013. Fall 2012 Migration Summary: A Fall for the Record Books! Long Point Bird Observatory E-news. Bird Studies Canada, Port Rowan, ON. 12 pp.
- Mackenzie, S., and R. Ridout. 2008. LPBO 2007 Fall Summary: A Fall Irruption. Long Point Bird Observatory E-news. Bird Studies Canada, Port Rowan, ON. 10 pp.
- McGraw, K.J., and A.L. Middleton. 2009. American Goldfinch (*Spinus tristis*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: (<http://bna.birds.cornell.edu/bna/species/080>).
- McLaren, I., B. Maybank, K. Keddy, P.D Taylor, and T. Fitzgerald, T. 2000. A notable autumn arrival of reverse-migrants in southern Nova Scotia. *North American Birds*, 54(1): 4-10.
- McNicholl, M.K., and J.L. Cranmer-Byng (eds.). 1994. Ornithology in Ontario. Ontario Field Ornithologists. Toronto, ON.
- Middleton, A.L. 1998. Chipping Sparrow (*Spizella passerina*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: (<http://bna.birds.cornell.edu/bna/species/334>).

- Monteith, K.L., V.C. Bleich, T.R. Stephenson, B.M. Pierce, M.M. Conner, R.W. Klaver, and R.T. Bowyer. 2011. Timing of seasonal migration in mule deer: effects of climate, plant phenology, and life-history characteristics. *Ecosphere*, 2, article 47.
- Moore, F.R., and D.A. Aborn. 1996. Time of departure by Summer Tanagers (*Piranga rubra*) from a stopover site following spring trans-Gulf migration. *Auk*, 113 (4): 949-952.
- Mowbray, T.B. 1999. Scarlet Tanager (*Piranga olivacea*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: (<http://bna.birds.cornell.edu/bna/species/479>).
- Nilsson, A., T. Alerstam, and J. Nilsson. 2006. Do partial and regular migrants differ in their responses to weather? *Auk*, 123: 537-547.
- Nisbet, I.C.T., and Jr., W.H. Drury. 1967. Orientation of spring migrants studied by radar. *Bird-banding*, 38(3): 173-186.
- Norberg, U.M. 1995. How a long tail and changes in mass and wing shape affect the cost for flight in animals. *Functional Ecology*, 9: 48-54.
- North American Bird Conservation Initiative Canada. 2012. The State of Canada's Birds, 2012. Environment Canada, Ottawa, Canada. 36pp.
- Ontario Field Ornithologists. 2012. Checklist of the Birds in Ontario. (Retrieved from: <http://www.ofo.ca/webapp/site/page/view/checklist.checklist>).
- Ontario Ministry of Natural Resources. 2013a. COSEWIC Status. Natural Heritage Information Centre. (Retrieved from: <http://nhic.mnr.gov.on.ca/MNR/nhic/glossary/cosewic.cfm>).
- Ontario Ministry of Natural Resources. 2013b. Species at Risk in Ontario (SARO) List. Retrieved from: (<http://www.mnr.gov.on.ca/en/Business/Species/2ColumnSubPage/276722.html>).
- Ontario Parks. 2008. Fish Point. Retrieved from (<http://www.ontarioparks.com/english/fish.html>).
- O'Neill, H.T. 2006. Birding at Point Pelee. James Lorimer and Company Ltd. Toronto, ON. 224pp.
- Pelee Island Bird Observatory. 2013. PIBO – About The Organisation. Retrieved from: (<http://pibo.ca/en/about-pibo/>).
- Peer, B.D., and E.K. Bollinger. 1997. Common Grackle (*Quiscalus quiscula*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: (<http://bna.birds.cornell.edu/bna/species/271>).

- Pinheiro, J., D. Bates, S. Debroy, D. Sarkar, and The R Development Core Team. 2013. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-108.
- Pyle, P., N. Nur, R. Henderson, and D. DeSante. 1993. The effects of weather and lunar cycle on nocturnal migration of landbirds at southeast Farallon Island, California. *Condor*, 95: 343-361.
- Ralph, C.J. 1978. Disorientation and possible fate of young passerine coastal migrants. *Bird-banding*, 49 (3): 237-247.
- Rappole, J.H. 1995. *The Ecology of Migrant Birds: A Neotropical Perspective*. Smithsonian Institution Press Inc. Washington, D.C.
- Richardson, W.J. 1978. Timing and amount of bird migration in relation to weather: A review. *Oikos*, 30: 224-272.
- Richardson, W.J. 1982. Northeastward reverse migration of birds over Nova Scotia, Canada, in autumn. *Behavioural Ecology and Sociobiology*, 10 (3): 193-206.
- Ridout, R. 2010. *A Birding Guide to the Long Point Area*. Bird Studies Canada. Port Rowan, ON. 146pp.
- Rimmer, C.C., K.P. McFarland, W.G. Ellison and J.E. Goetz. 2001. Bicknell's Thrush (*Catharus bicknelli*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: (<http://bna.birds.cornell.edu/bna/species/592>).
- Robbins, C.S., J.R. Sauer, R.S. Greenberg, and S. Droege. 1989. Population declines in North American birds that migrate to the neotropics. *Proceedings of the National Academy of Sciences of the United States of America*, 86: 7658-7662.
- Runge, M.C., and P.P. Marra. 2005. Modelling seasonal interactions in the population dynamics of migratory birds. *Birds of Two Worlds: The Ecology and Evolution of Migration* (eds. R. Greenberg and P.P. Marra), pp. 375-389. Johns Hopkins University Press Inc. Baltimore, MD.
- R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>.
- Sibley, D.A. 2000. *The Sibley Guide to Birds*. Alfred A. Knopf Inc. New York, NY.
- Smith, W. P., P. B. Hamel, and R. P. Ford. 1996. Mississippi Alluvial Valley forest conversion: implications for eastern North American avifauna. *Proceedings of the 1993 Annual Conference of the Southeast Association of Fish and Wildlife Agencies*, 47:460-469.

- Smith, J.P., C.J. Farmer, S.W. Hoffman, C.A. Lott, L.J. Goodrich, J. Simon, C. Riley, and E.R. Inzunza. 2008. Trends in autumn counts of migratory raptors around the Gulf of Mexico, 1995-2005. State of North America's birds of prey. *Series in Ornithology*, 3: 253-278.
- Stutchbury, B.J. 2007. Silence of the Songbirds: How we are losing the world's songbirds and what we can do to save them. Harper Collins Publishers Ltd. Toronto, ON.
- Sutherland, W.J., I. Newton, and R. E. Green. 2004. Bird Ecology and Conservation: A Handbook of Techniques. Oxford University Press Inc. New York, NY.
- Tacha, T. C., S. A. Nesbitt, and P. A. Vohs. 1992. Sandhill Crane (*Grus canadensis*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: <http://bna.birds.cornell.edu/bna/species/031>
- Tarvin, K.A., and G.E. Woolfenden. 1999. Blue Jay (*Cyanocitta cristata*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: (<http://bna.birds.cornell.edu/bna/species/469>).
- Thompson, W.A., I. Vertinsky, and J.R. Krebs. 1974. The survival value of flocking in birds: A simulation model. *Journal of Animal Ecology*, 43(3): 785-820.
- Thorup, K. 2010. Reverse migration as a cause of vagrancy. *Bird Study*, 51: 228-238.
- Vennesland, R.G., and R.W. Butler. 2011. Great Blue Heron (*Ardea herodias*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: (<http://bna.birds.cornell.edu/bna/species/025>).
- Weidensaul, S. 2000. Living on the Wind: Across the Hemisphere with Migratory Birds. North Point Press Inc. New York, NY.
- Wiedner, D.S., P. Kerlinger, D.A. Sibley, P. Holt, J. Hough, and R. Crossley. 1992. Visible morning flights of neotropical landbird migrants at Cape May, New Jersey. *Auk*, 109 (3): 500-510.
- Williams, H., I. Levin, D.R. Norris, A.E.M. Newman, and N.T. Wheelwright. 2013. Three decades of cultural evolution in Savannah sparrow song. *Animal Behaviour*, 85: 213-223.
- Winkler, D.W., K.K. Hallinger, D.R. Ardia, R.J. Robertson, B.J. Stutchbury and R.R. Cohen. 2011. Tree Swallow (*Tachycineta bicolor*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: (<http://bna.birds.cornell.edu/bna/species/011>).

- Wojnowski, J.K., G.C. Gibson, A.E. Heagy, B.J. Rodrigues, J. Woodcock, and D.J.T. Hussell. 2010. Field Protocol for Monitoring Bird Migration at Thunder Cape Bird Observatory. Bird Studies Canada. Port Rowan, ON. 40 pp.
- Woodliffe, P.A. 2007. Orchard Oriole, pp. 604-605 in Cadman, M.D., D.A. Sutherland, G.G. Beck, D. Lepage, and A.R. Couturier, eds. Atlas of the Breeding Birds of Ontario, 2001-2005. Bird Studies Canada, Environment Canada, Ontario Field Ornithologists, Ontario Ministry of Natural Resources, and Ontario Nature, Toronto, xxii + 706 pp.
- Wormington, A. 2010. Ontario. *North American Birds*, 64(3): 413-419.
- Wormington, A. 2011. Ontario. *North American Birds*, 65(3): 427-433.
- Wormington, A. 2012. Ontario. *North American Birds*, 66(3): 471-478.
- Wyatt, V.E., and C.M. Francis. 2002. Rose-breasted Grosbeak (*Pheucticus ludovicianus*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: (<http://bna.birds.cornell.edu/bna/species/692>).
- Yasukawa, K., and W.A. Searcy. 1995. Red-winged Blackbird (*Agelaius phoeniceus*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: (<http://bna.birds.cornell.edu/bna/species/184>).
- Zehnder, S., S. Åkesson, F. Liechti, F., and B. Bruderer. 2001. Nocturnal autumn bird migration at Falsterbo, South Sweden. *Journal of Avian Biology*, 32: 239-248.