

USING AUTOMATED RADIO-TELEMETRY TO ASSESS SPRING MIGRATORY  
ECOLOGY AND SURVIVAL OF IPSWICH SPARROWS  
(*PASSERCULUS SANDWICHENSIS PRINCEPS*)

by

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## ABSTRACT

Songbird behaviour during migration is consequential because it can affect survival and ultimately population size. Behaviour during spring migration may be particularly important because it affects condition and timing of arrival, which affects subsequent breeding. Population-level differences in behaviour can occur due to various factors. Intrinsic factors such as age and sex lead to differences in experience and sexual maturity. Extrinsic factors like landscape features such as ecological barriers can influence movement patterns and the spatial location of mortalities.

I used three years of radio-telemetry data to assess the behaviour and survival of a range-restricted songbird, the Ipswich Sparrow (*Passerculus sandwichensis princeps*), during spring migration. I tracked 153 sparrows migrating along the Atlantic Coast between wintering grounds in the eastern USA to breeding grounds on Sable Island, Canada, and used those data to evaluate how various intrinsic and extrinsic factors affected behaviour.

In Chapter 2, I assessed the temporal and spatial patterns of spring migration in the context of optimal migration theory to determine if sparrows followed a time- or energy-minimizing strategy. I found that sparrows followed an energy-minimizing strategy, travelling relatively slowly, making short nightly flights, and making frequent refueling stopovers. I found no evidence that strategy varied with age or sex.

In Chapter 3, I assessed behaviour at two overwater ecological barriers, the Gulf of Maine (GOM) and part of the Atlantic Ocean (AO). I also estimated daily survival probability in different spatial legs of the Atlantic Coast during migration. Sparrows both crossed and circumvented the GOM. Juveniles, in particular, also made non-migratory movements and abandoned flights before the AO but not elsewhere during migration, suggesting some difficulty crossing this barrier. Juvenile bearings to Sable Island were also less direct than adult bearings. There was no evidence that these behaviours varied with sex. Daily survival probability was variable across legs of the Atlantic Coast, being highest in the GOM and lowest in eastern Nova Scotia and crossing the AO to Sable Island.

Collectively, these results have conservation implications for the Ipswich Sparrow. There is a need for broad-scale protection of stopover sites that support the frequent refueling needs of sparrows along the coast. This may be especially important in Nova Scotia adjacent to the AO where non-migratory movements, abandoned flights, and low survival suggest that passing this barrier is a particularly challenging leg of migration.

These results also provide insight into how migratory behaviour develops across age and sex classes. By spring, the behaviour of juvenile sparrows is largely, but not completely, consistent with the behaviour of adults. This is likely attributable to individual learning by juveniles over the previous year. A lack of sex-related differences in behaviour suggest that males and females are under similar selection pressures or may be in similar condition during spring migration.

## LIST OF ABBREVIATIONS AND SYMBOLS USED

Abbreviation	Description
$\Psi$	transition probability between spatial states
$\beta$	Beta coefficient
AO	Atlantic Ocean
CI	confidence interval
CJS	Cormack-Jolly-Seber
d	day
dB	decibel
dBm	decibel relative to a milliwatt
g	gram
GLM	generalized linear model
GLMM	generalized linear mixed model
GOM	Gulf of Maine
h	hour
kHz	kilohertz
km	kilometer
lm	linear model
m	metre
min	minute
mHz	megahertz
NS	Nova Scotia
P	p-value
$p$	recapture (detection) probability
$S$	survival probability
s	second
SD	standard deviation
SE	standard error
VHF	Very High Frequency

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# CHAPTER 1: INTRODUCTION

## 1.1 Introduction

Animal migration is a globally observed behaviour that typically involves regular movements between breeding and wintering grounds. Migration is thought to confer several advantages to animals. It permits the exploitation of resources that are available during specific times of year (Dingle and Drake 2007; Somveille et al. 2019), allows animals to capitalize on favourable environmental conditions (Alerstam 2001; Pigot et al. 2010), facilitates the shedding of parasites (Slowinski et al. 2018), and can improve lifetime predator avoidance (Alerstam et al. 2003). All of these benefits can lead to increased annual survival (Lack 1968) and lifetime breeding productivity (Alerstam et al. 2003). Presumably as a result of these advantages, the behaviour has evolved across various taxa including insects, fish, reptiles, birds, and mammals.

Migration, however, can also be costly. Migrating animals must contend with unpredictable environmental conditions, inclement weather (Newton 2007), increased competition, and sometimes increased predation risk (Alerstam and Hedenström 1998). Animals must also accurately navigate to their migratory destinations, arrive in good condition, and arrive within a specific time frame (Alerstam 2009). The consequences of failing to manage these costs are significant. For instance, animals that finish migration in poor body condition or relatively late can have reduced breeding success or may not breed at all (Baker et al. 2004; Smith and Moore 2005; Crossin et al. 2012; Reed et al. 2015). The costs of migration must be outweighed by the benefits for this behaviour to evolve and persist in animal populations (Lack 1968; Alerstam et al. 2003).

### **Avian migrations and factors that influence migratory behaviour**

Birds are well-known for their seasonal migrations between breeding and wintering grounds, which are typically characterized by bouts of flight punctuated by stopovers to rest and refuel. There has been considerable study of the general patterns of where and when bird species migrate, but much less is known about migratory behaviour including the factors that drive individual behaviour during migration. This includes

timing, stopover frequency, flight speed, duration, and pathway selection (Alerstam et al. 2003).

Modern field studies have significantly advanced understanding of migratory behaviour (McKinnon and Love 2018). Contrary to earlier laboratory studies that suggested behaviour is under strict endogenous control (Gwinner 1996; 2003), field studies have revealed a suite of intrinsic factors that influence migratory behaviour within a population. Factors such as age and sex create differences in body size, experience, sexual maturity, social rank, and life history constraints, which in turn affect the costs of migration for individual birds and thus their behaviour (Cadahía et al. 2017; Verhoeven et al. 2018). For example, older and male individuals tend to arrive on wintering grounds earlier than younger and female individuals (Morbey et al. 2012). In contrast, younger and female birds spend more time at stopover sites (Moore et al. 2003; Kokko et al. 2006) than older and male individuals (although this pattern is less well documented). Similarly, adults may cross barriers quickly by taking more direct pathways past the barrier while juveniles may circumvent barriers (Hake et al. 2003; Handel and Gill 2010; Jorge et al. 2011; Crysler et al. 2016).

Migration appears to be a period of low survival in general for songbirds (e.g., Sillett and Holmes 2002; Rockwell et al. 2017) and may be particularly low at ecological barriers (Ward et al. 2018). Intrinsic factors that influence behaviour during migration also affect survival. Juvenile survival during migration can be lower than adult survival, and female survival lower than male survival (e.g., Stutchbury et al. 2009; Lok et al. 2015), though few studies have quantified survival by age and sex (Sillett and Holmes 2002). Therefore, how barriers and intrinsic factors drive survival differences during this period, and how these differences scale up from the individual to affect population size (Newton 2004; Calvert et al. 2009), are pertinent questions.

Migratory behaviour is also influenced by a variety of extrinsic factors including weather (Drake et al. 2014). Cloud cover, precipitation, and atmospheric pressure are closely tied to the timing of migratory flights in many species (Alerstam et al. 2003; Åkesson 2016; Dossman et al. 2016) and wind direction and speed can affect pathway selection (Able 1969; Deppe et al. 2015). Adverse conditions such as unseasonably low temperatures can force birds to stopover in unsuitable sites (Senner et al. 2015). Although

the evidence is limited, weather conditions may also affect behaviour by age and sex class. Adult Savannah Sparrows (*Passerculus sandwichensis*), for instance, selected more favourable conditions to begin migratory flights than juveniles (Mitchell et al. 2015).

### **Seasonal songbird migration**

Songbirds that breed in North America typically migrate in both spring and fall. These migrations are not simple reversals of each other because environmental conditions and selection pressures differ between seasons (Newton 2004; La Sorte et al. 2014; Horton et al. 2016). For instance, most songbirds fly at faster speeds and consequently have shorter migratory durations in spring compared to fall (Nilsson et al. 2013). This is presumably because of the strong pressure to arrive early to breeding grounds (Karlsson et al. 2012; Nilsson et al. 2014; La Sorte and Fink 2017). Further, because birds mature over the winter period, the gap in experience and sexual maturity is smaller in the spring than the fall, which can drive differences in movement by age and sex (Jorge et al. 2011; McKinnon et al. 2014). Thus, birds may behave differently during spring and fall migrations. Yet, bias towards breeding ground studies has produced disproportionate focus on fall migration when birds are departing from breeding areas (Faaborg et al. 2010). Subsequently, there is relatively poor understanding of behaviour during spring migration when birds are departing from wintering areas. There is also little known about how intrinsic factors such as age and sex influence individual behaviour and survival during this period (Stutchbury et al. 2009; Thorup et al. 2010; Marra et al. 2015).

The overarching objective of my thesis was to describe the behaviour and survival of a songbird, the Ipswich Sparrow (*Passerculus sandwichensis princeps*), during spring migration. I used automated radio-telemetry to assess behaviour during spring migration and to determine whether behaviour varies by age or sex. I also determined how behaviour and survival differed at ecological barriers compared to other legs of migration.

### **Study Species**

The Ipswich Sparrow is a small, range-restricted subspecies of Savannah Sparrow that has a migration distance typical of a short-distance migrant. Its wintering range is

limited to sandy dune habitat along the Atlantic Coast of North America, from Nova Scotia (NS), Canada to Florida, USA, which limits the scope of migratory movements (Stobo and McLaren 1971, 1975; Sullivan et al. 2014). It breeds exclusively on Sable Island, NS, a small (40 x 1 km) isolated sand island ~350 km east of the mainland of NS in the northern Atlantic Ocean (AO; Fig. 1.1).

The Ipswich Sparrow is an ideal model for studying the factors that affect behaviour and survival during migration. First, its range is spatially coincident with an automated radio-telemetry network, meaning the network can be used to track sparrows throughout migration and quantify individual behaviour. Second, restriction of breeding grounds to a small island means that the end of spring migration is clearly demarcated, all birds arriving on the island can be readily detected, and the population is closed to immigration and emigration. Third, sparrows must contend with two ecological barriers during migration, the Gulf of Maine (GOM) and the AO when flying from the mainland to Sable Island, allowing an assessment of whether survival differs at barriers compared to other legs of migration. Finally, the results of my study can be compared to research on the fall migration of Ipswich Sparrows (Crysler et al. 2016), allowing insight into how songbird behaviour changes as ageing and sexual maturation occur and how behaviour differs between the spring and fall migration.

### **Technology for studying small migratory birds**

Tracking small songbirds has been a challenge in migration studies due to a lack of lightweight devices with batteries powerful enough to last for a whole migration. The miniaturization and improvement of devices such as Very High Frequency (VHF) radio-tags used in this study have recently permitted the tracking of small songbirds during migration (Kenward 2001). Radio-tags transmit electromagnetic radio signals that are detected by receivers, which allow tracking of birds in locations where receivers are operating. Radio-tags have been used to collect a variety of data related to movement ecology. For instance, they have been used to determine weather conditions associated with migratory flights (Bolus et al. 2017), diel time of migratory flights (Sjöberg 2015), habitat use during stopovers (Woodworth et al. 2014), pathways at ecological barriers (Schmaljohann and Naef-Daenzer 2011), and post-fledging survival (Evans 2018).

The use of radio-tags in migratory studies has several clear benefits over other technologies. Tags transmit their signals, so birds do not need to be recaptured to obtain detections. This also means that data on movement can be collected from birds even if they do not survive migration. Tags are also relatively inexpensive compared to other technologies such as GPS tags, so large numbers can be deployed to increase sample sizes. Tag detections can be used to identify the exact date and time of movements at specific coordinates. Finally, the location of mortality events can be implied based on a cessation in tag detections (Murray 2006), although, this is confounded with tag loss and/or failure.

### *Tag effects*

The use of tracking devices on songbirds can, however, negatively impact behaviour and survival (Barron et al. 2010). These “tag effects,” are produced when the weight or drag of a device adds a significant energetic burden and reduces ability to maintain body condition, or, the attachment method constrains movement (Bowlin et al. 2010; Walker et al. 2012).

Complicating our understanding of tag effects is the reality that in many migratory studies, the effects of radio-tags on songbirds cannot be assessed. This is due to the difficulty of comparing the behaviour of tagged birds to an untagged control group, because studying the control group is what necessitates tags in the first place. As such, it is essentially impossible to study how tags impact some migratory behaviours such as pathway or the diel timing of flights (Barron et al. 2010; Geen et al. 2019). The evidence of tag effects on more easily studied behaviours during migration is mixed. Some studies report tagged individuals suffer increased energy expenditure or stress, or, reduced foraging duration or body mass (Nudds and Sjöberg 1989; Sykes et al. 1990; Godfrey et al. 2003; Suedkamp Wells et al. 2003). Other studies report no effects (Irvine et al. 2007; Gow et al. 2011; Townsend et al. 2012; Neudorf and Pitcher 2016; Bodey et al. 2018). Similarly, there is mixed evidence for tag effects on survival (e.g., Powell et al. 1998; Mattsson et al. 2006; Anich et al. 2009).

Generally, effects appear to vary by species and attachment method. Highly aerial birds such as swallows appear to be susceptible to tag effects because of the added energetic costs associated with tag weight and drag during flight (Pennycuick et al. 2012;

Costantini and Møller 2013), while ground-dwelling species do not appear to suffer comparable effects, presumably because they spend less time flying (Irvine et al. 2007; Rae et al. 2009; Costantini and Møller 2013).

Despite these limitations, it is generally accepted that the benefits of the data obtained from tags outweigh the risk of tag effects (Wilmers et al. 2015). These devices provide otherwise unobtainable information about movement and behaviour that has considerably advanced migratory theory (Bairlein et al. 2012; Lemke et al. 2013). Given the profound effect of the migratory period on the fitness and survival of songbirds and the significant unknowns regarding this period (Marra et al. 2015), it is difficult to understate the benefits of information derived from tags on bird conservation. This information must, however, be tempered by the fact that many studies cannot adequately examine tag effects, and so lack a clear understanding of the negative consequences of tags, and, how biological conclusions drawn from data could be biased by tags (Geen et al. 2019).

## **Thesis outline**

The goal of my thesis is to describe the spring migratory behaviour and survival of a songbird, using the Ipswich Sparrow as a model species. In Chapter 2, I examine the temporal and spatial parameters of spring migration. In Chapter 3, I examine behaviour at two migratory barriers and assess migratory survival. In both chapters I assess to what extent, if any, the intrinsic factors of age and sex affect behaviour. To meet these goals, I used three years of radio-telemetry data collected in 2013, 2018, and 2019.

## **1.2 Methods**

### **Tag deployments**

I captured wintering Ipswich Sparrows from 1–10 March 2018 and 26 February–10 March 2019 on beaches in the eastern USA (Fig. 1.1) at latitudes that support the highest densities of sparrows (Stobo and McLaren 1971; Horn and Dale 2007): Chincoteague National Wildlife Refuge (37.97°N, -75.29°W), Assateague Island National Seashore (38.19°N, -75.16°W), Fenwick Island State Park (38.49°N, -75.05°W),

Delaware Seashore State Park (38.66°N, -75.07°W), Cape Henlopen State Park (38.80°N, -75.10°W), Currituk National Wildlife Refuge (36.48°N, -75.86°W), and Pea Island National Wildlife Refuge (35.69°N, -75.48°W). Sparrows were also captured during spring migration from 12–18 April 2013 and 12–26 April 2019 at sites in eastern NS: Conrad’s Beach (44.64°N, -63.37°W) and Hartlen Point (44.59°N, -63.46°W). Habitat at all locations comprised sandy outer dune systems with the exception of Hartlen Point, which is a rock beach.

Sparrows were captured with mist nets and banded with US Fish and Wildlife Service aluminum leg bands, and a unique scheme of either two or four coloured leg bands. Standard measurements (wing, leg, and tail length; mass) were recorded.

In addition, I tagged sparrows with coded VHF radio-transmitters (Avian NanoTag, Lotek Wireless Inc.; hereafter “tags”) using a leg-loop backpack harness (Rappole and Tipton 1991; Table 1.1). Harnesses of nylon elastic cord were expected to degrade and fall off after ~100 d (Streby et al. 2015). Each tag transmitted uniquely coded electromagnetic radio pulses at 166.380 MHz and were registered within the Motus Wildlife Tracking System (Taylor et al. 2017). Tag models differed across years in weight and burst rate. Signal strength was consistent across models except in 2018 (Table 1.2; Lotek Wireless Inc., pers. comm., see below for details on 2018). Mean holding time for sparrows from capture to release was  $19.6 \pm 8.4$  min (range = 3–45 min).

The density of Ipswich Sparrows at winter sites is low (range = 0.11–0.87 sparrows/ha in occupied habitats, C Hines, Center of Conservation Biology, pers. comm.). Given this, and my need to deploy a large number of tags in a short time period, all sparrows were targeted for capture and all captured sparrows were tagged when the combined tag and harness mass did not exceed 4% of their body mass (mean body mass = 26.0 g; Barron et al. 2010). Tagging always occurred < 9 km from a telemetry receiver (mean =  $2.19 \pm 1.97$  km, range = 0.56–8.78 km) so the start of migration (i.e., departure from wintering grounds) would be documented by receivers. Receiver malfunction at one site increased this distance to 58.1 km for eight sparrows in 2018.

### **Ageing and sexing**

Sparrows were aged as ‘juvenile’ (< 1 year old) or ‘adult’ ( $\geq$  1 year old) using the colour and shape of the tail and upper primary covert feathers (Pyle 1997). I took and reviewed photographs of these feathers to ensure sparrows were aged correctly.

To sex sparrows, I removed up to 50  $\mu$ L of blood from the branchial vein by venipuncture, which did not exceed 1% body mass (Fair et al. 2010). Blood was transferred to FTA® card filter paper (Whatman Int. Ltd., UK) for preservation (Smith and Burgoyne 2004). Sex was determined from blood following methods in Griffiths et al. (1998) by extracting DNA from red blood cells, amplifying DNA using polymerase chain reaction, and separating products on agarose gel. Labs at Dalhousie and Acadia Universities conducted these analyses.

### **Automated radio-telemetry with the Motus Wildlife Tracking System**

To track the spring migratory movements of tagged Ipswich Sparrows, I used the Motus Wildlife Tracking System (hereafter “Motus”; [www.motus.org](http://www.motus.org); Taylor et al. 2017). This automated digital telemetry network is spatially coincident with the entire range of Ipswich Sparrows (Fig. 1.1). Motus receivers record the tag identity, signal strength, coordinates, radio frequency, and timestamp of all tag detections and have a range (when birds are in flight) of up to ~10–15+ km under ideal conditions (Taylor et al. 2017; but also see Crewe et al. 2019a). Each receiver has 1–6 directional 9-element Yagi antennas. There are two receiver types: SensorGnome receivers ([www.sensorgnome.org](http://www.sensorgnome.org)) simultaneously scan antennas for tags 24 h/d, and, SRX receivers (Lotek Wireless Inc.) scan between antennas on a prescribed schedule.

Although detectability likely varies with receiver type, I did not expect differences in receivers to cause systematic biases in my sampling. This is largely because receiver type is only one of a variety of factors, including atmospheric conditions, landscape features, and bird height that can affect detectability (Taylor et al. 2017; Crewe et al. 2019a). Although specific differences in detectability with receiver type are unknown, it is likely that interactions among the latter factors have an equal or larger effect on detectability than receiver type.



The number of receivers in the network along the Atlantic Coast varied by year. In 2018, there were 152 receivers and in 2019 the receivers were increased to 162 (Fig. 1.1). In 2013, receivers in NS were situated only along the eastern shore of the province so only movements in particular locations could be documented (Fig. 1.1). In 2013 only, three receivers were deployed on mobile supply vessels that serviced oil and gas platforms offshore NS and thus could detect sparrows flying overwater to Sable Island.

### **Manual telemetry and tag assessments on Sable Island**

I also used manual telemetry on Sable Island to document the presence of tagged Ipswich Sparrows at the end of migration, and to assess tag loss and tag failure. I conducted surveys from late May to early June when all sparrows that survived migration should have arrived on Sable Island.

I conducted three types of manual telemetry surveys. I used grid and line surveys to supplement detections at the three receivers on the island (Fig. 1.2), which can miss birds for various reasons (Taylor et al. 2017; Crewe et al. 2019a). I used grid and opportunistic surveys to assess tag loss and tag failure.

#### *Grid surveys*

I established a set of transects in the vegetated habitat used by the sparrows (Stobo and McLaren 1977) using a land cover atlas (AGRG 2011). The transects ran perpendicular to the main axis of the island and were spaced at 1 km intervals (Fig. 1.2). On each transect, an observer walked to the height of land and scanned for 2 min in each cardinal direction with the handheld telemetry antenna (5-element Yagi, range ~2.5 km, Lotek Wireless Inc.) and SRX600 receiver (Lotek Wireless Inc.). The identity, signal strength, coordinates, and timestamp of detected tags were recorded. When possible, detected sparrows were triangulated and visually assessed for tag retention (i.e., to ensure the tag was on a bird and not on the ground at the time of detection). I completed two surveys from 24 May–5 June in 2013 and one survey from 4–8 May 2018 and 24–28 May 2019.

#### *Line surveys*

In 2019, I walked though 15.3 km of Ipswich Sparrow habitat carrying an omnidirectional dipole antenna (range ~500 m) in a backpack attached to a SensorGnome

receiver. The identity, signal strength, coordinates, and timestamp of detected tags were recorded. I did this on 27–28 May and 1 June 2019. I could not do this survey in other years because of time restrictions.

### *Opportunistic surveys*

I assessed tag retention and tag functionality by examining tagged sparrows that were opportunistically observed on Sable Island. In these cases, I first observed the coloured leg bands on a sparrow and used these bands to identify if the sparrow had been previously tagged. If so, I visually determined if the tag had been retained and used handheld telemetry antenna (5-element Yagi, range ~2.5 km, Lotek Wireless Inc.) and SRX600 receiver (Lotek Wireless Inc.) to determine if the tag was functioning. I did this in May and June 2013 and 2019, and in May 2018.

With the combined data from receivers and surveys, I assumed that all tagged sparrows on Sable Island were detected. Data from these surveys also allowed me to assess if tags were retained and functional at the end of migration, an assumption of one analysis.

### **Tag data validation**

Radio-telemetry data contain false detections from random radio noise that appear similar to tag transmissions. Therefore, it is necessary to filter out false detections. I did this by following recommendations from Crewe et al. 2019b. In addition, I closely examined runs (series of consecutive tag bursts) where the mean frequency SD offset from 166.380 MHz was  $> 0.08$  kHz, and, runs where the mean burst slop (time difference between tag bursts) was  $> 0.20$  s from the expected tag burst rate (see Appendix A for additional details) to determine if they represented true detections.

In 2018, a relatively small number of detections on both the Motus network and during manual telemetry indicated an issue with tag transmissions. It was later determined that a manufacturing defect caused some tags to fail prematurely. I confirmed that four tags failed prematurely during manual telemetry surveys on Sable Island, and the true rate of premature tag failure was expected to be higher but impossible to confirm without re-locating every tagged bird. The signal strength of the tags deployed in 2018 was also less than half the expected strength, decreasing the tag detection distance and

reducing the likelihood that a tagged bird would fly sufficiently close to a receiver to be detected (Lotek Wireless Inc., pers. comm). Consequently, sample sizes from this year were small for some analyses.

## **Tag data processing**

### *Site interpretation*

In some instances, nearby receivers simultaneously detected tags (typically those < 25 km apart). Simultaneous detections do not represent repeated movement between receivers but rather a bird within the range of both receivers, which can produce errors in some calculations (e.g., impossible flight speeds). Consequently, in these situations I identified the location of the bird as the mid-point of the great-circle route distance (Vincenty 1975) between the two receivers.

### *Time of sparrows at receivers*

I determined the time a bird was at each receiver using signal strength (dB), which indicates proximity to a receiver. Because tags may be detected for a long time as a bird approaches and flies away from a receiver (Taylor et al. 2017), there is a need to isolate the exact time it was closest to each receiver for calculations such as flight speed. An increase in signal strength over time signifies approach, the highest strength indicates the closest point, and a decrease over time signifies movement away from a receiver. I therefore considered the time with the highest signal strength to be the time a bird was at a receiver (Mitchell et al. 2015). To confirm these times, I checked them against plots of signal strength by time (Fig. 1.3).

I also defined the first detection on a receiver as the arrival detection, the last detection on a receiver as the departure detection, and calculated the duration of time sparrows were at each receiver by subtracting the arrival detection from the departure detection (Mitchell et al. 2015; Smetzer et al. 2017). These durations were used to assess different movement patterns on receivers.

### *Direct and indirect flights*

To identify if flights between receivers were direct (i.e., sparrows did not make stopovers between detections on two receivers), or indirect (i.e., sparrows did make stopovers between detections on two receivers), I used the ground speed of movements

between receivers (Smetzer et al. 2017; Smetzer and King 2018). I identified flights as direct when the ground speed of flights between receivers was  $\geq 5$  m/s because there was a clear break in the data at this speed that suggested flights at this speed were direct (*sensu* Smetzer and King 2018), and, because this speed was close to the mean ground speed of nocturnally migrating songbirds (Nilsson et al. 2013). I identified flights as indirect when ground speed was  $< 5$  m/s.

*Definition of diel periods*

Day was defined as the period between sunrise and sunset (i.e., sun elevation  $< 0^\circ$  below the horizon) in all analyses.

### 1.3 Tables

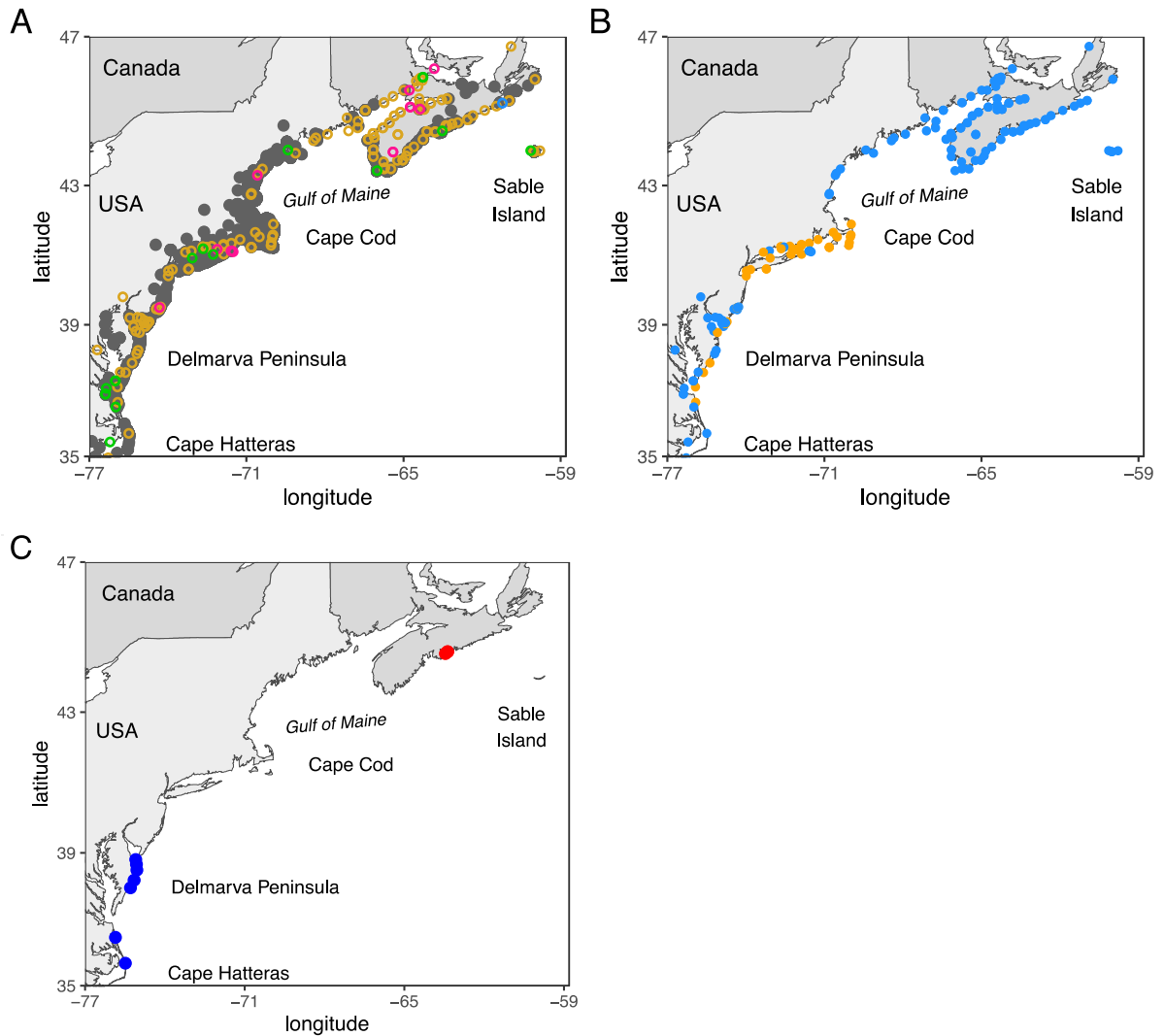
**Table 1.1** – Number of tagged Ipswich Sparrows by age and sex class. Location is USA states or Canadian provinces.

Year	Adult male	Adult female	Juvenile male	Juvenile female	Unknown age male	Unknown age female	Deployment	
							Location	Timing
2013	12	3	5	0	0	1	NS	migration
2018	20	7	19	13	0	0	DE, MD, VA	pre-migration
2019	2	5	31	26	3	2	DE, MD, VA, NC	pre-migration
2019	3	1	4	2	0	0	NS	migration
<b>TOTAL</b>	<b>37</b>	<b>16</b>	<b>59</b>	<b>41</b>	<b>3</b>	<b>3</b>		

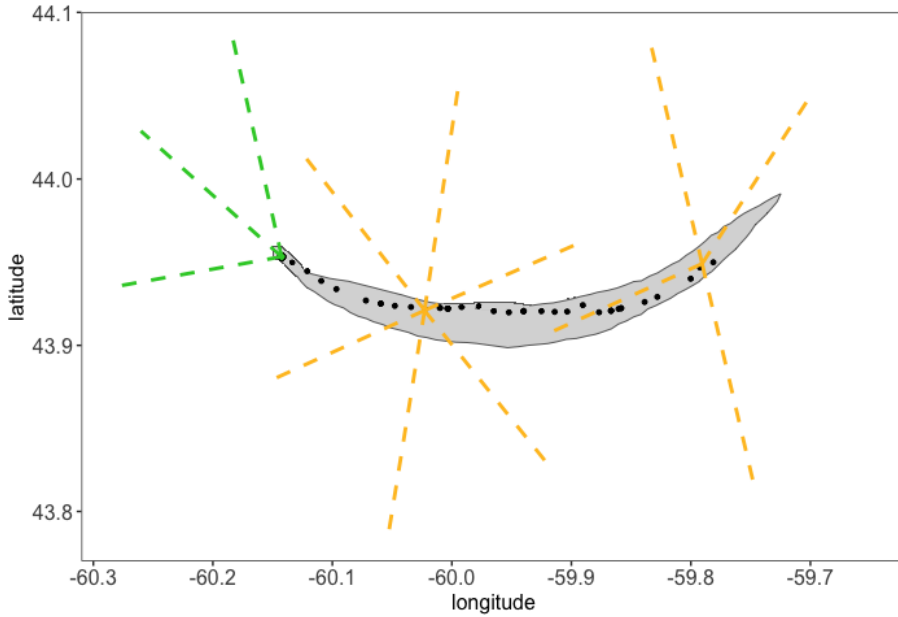
**Table 1.2** – Tag specifications and deployment details across study years. Location is USA states or Canadian provinces.

Year	Tag				Location	Deployment		n
	Model	Mass (g)	Burst rate (s)	Signal strength (dBm)		Time	Dates	
2013	NTQB-3-2	0.67	11.99	32	NS	migration	12–18 Apr	21
2018	ANTC-M2-1	0.65	30.68	27	DE, MD, VA	pre-migration	1–10 Mar	59
2019	NTQB-3-2	0.61	19.69	32	DE, MD, VA, NC	pre-migration	26 Feb–10 Mar	69
2019	NTQB-3-2	0.61	19.69	32	NS	migration	12–26 M	10
<b>TOTAL</b>								<b>159</b>

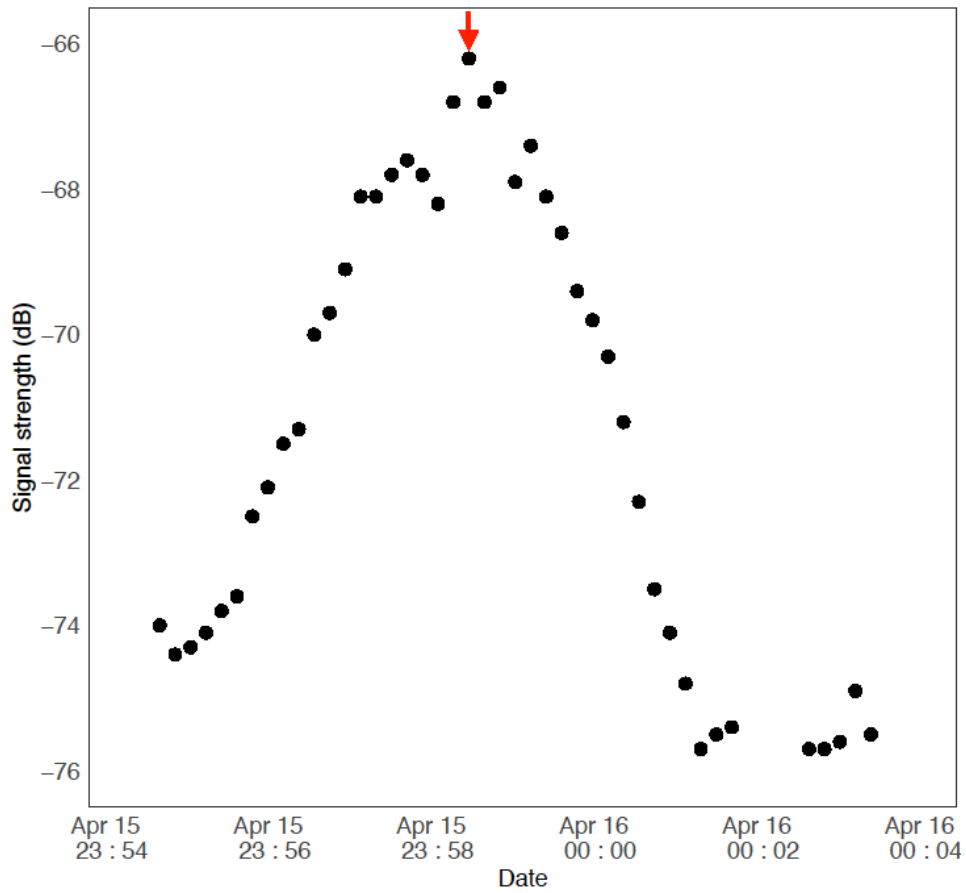
## 1.4 Figures



**Figure 1.1** – A) Range of Ipswich Sparrows from anecdotal reports (dark grey shading; Sullivan et al. 2014) with the location of receivers along the Atlantic Coast in all study years (2013, 2018, and 2019; open yellow dots), a receiver active in 2013 only (open blue dot), receivers active in 2018 only (open pink dots), and receivers active in 2019 only (open green dots). B) Location of Lotek receivers (orange dots) and SensorGnome receivers (blue dots) along the Atlantic Coast. C) Tag deployment sites on wintering grounds prior to migration in 2018 and 2019 (blue dots) and during migration in 2013 and 2019 (red dots).



**Figure 1.2** – Location of receivers on Sable Island. Dashed lines indicate antenna bearing and a detection range of ~10 km. Yellow receivers were active in all study years (2013, 2018, and 2019) and the green receiver was active in 2019 only. Black dots represent the scanning locations of grid surveys. Note that some scanning locations appear to be offshore Sable Island because this map does not show the exact extent of the island due to the changing dune system.



**Figure 1.3** – Example of detection pattern of a tagged bird on a receiver. Each black point represents a detection. This bird was detected over 8 mins between the night of 15 April and morning of 16 April. The time of maximum signal strength (red arrow) indicates the time the bird was closest to the receiver. Note signal strength values are measured in decibels (dB; log scale). Larger numbers indicate higher strength.



## **CHAPTER 2: OPTIMAL MIGRATION STRATEGIES IN IPSWICH SPARROWS (*PASSERCULUS SANDWICHENSIS PRINCEPS*) DURING SPRING MIGRATION**

### **2.1 Abstract**

Optimal migration theory predicts that birds should follow time- or energy-minimizing strategies during migration. I determined the spring strategy of a short-distance migratory songbird, the Ipswich Sparrow (*Passerculus sandwichensis princeps*), that winters in the eastern USA and breeds on Sable Island, Canada. I used VHF radio-tags and an automated radio-telemetry network to determine the timing of migratory initiation (departure from wintering grounds), duration, and completion (arrival on breeding grounds); flight speed; distance flown/night; and stopover location and duration. I also assessed whether strategy differed by age (adult or juvenile), sex, or year. Sparrows migrated between March and June, and males initiated and completed migration before females. Sparrows took 29 d to fly an average of 1558 km to breeding grounds. Flight speed was variable at  $7.1 \pm 9.3$  m/s (range = 0.03–44.9) and did not differ by age or sex. Sparrows flew distances of  $126 \pm 122$  km each night, spent ~85% of migration at stopover sites, and some made long stopovers > 7 d. The relatively long migratory duration, slow flight speeds, short nightly distances flown, and long stopovers compared to other songbirds are largely consistent with an energy-minimizing strategy, which is in contrast to most other songbirds that have a time-minimizing strategy in spring. Ipswich Sparrow may follow an energy-minimizing strategy to avoid predation pressure along the Atlantic Coast, or because they moult during spring migration, both of which increase daily energy costs. Abundant resources on Sable Island might also preclude the need to make a demanding time-minimizing migration for early arrival to acquire these resources.

### **2.2 Introduction**

Migration between breeding and wintering grounds is a common life-history trait among songbirds. Migration allows birds to take advantage of seasonally available resources in different locations while avoiding inclement weather and limiting predation

and competition (Alerstam et al. 2003). Migration is also costly, primarily in terms of time and energy (Alerstam and Hedenström 1998; Wikelski et al. 2003). Therefore, selection should favour migratory behaviours that reduce these costs in ways that maximize survival (Lindström and Alerstam 1992).

Optimal migration theory is a framework that can be used to assess and interpret migratory behaviours (Alerstam and Hedenström 1998). This theory predicts that birds follow strategies to optimize the competing costs of time and energy. Birds are thought to follow two main strategies: a time-minimizing strategy that minimizes the duration of migration so birds reach their destination as soon as possible but at the cost of high energy expenditure. This strategy appears to be used by species such as Barn Swallows (*Hirundo rustica*) where there is high competition for nest sites (Møller 1994) and early arrival confers a clear fitness advantage. The second is an energy-minimizing strategy that minimizes the amount of energy expended and allows birds to finish migration in good body condition (e.g., with excess fat), but at the cost of completing migration later. This strategy is used by species such as the Lesser Snow Goose (*Chen caerulescens caerulescens*) that relies on the fat reserves remaining after migration for clutch initiation (Ankney and MacInnes 1978). In reality these strategies fall on a continuum of time- or energy-minimization, meaning birds may use either strategy both within and across migrations (Warnock et al. 2004).

Each strategy is characterized by specific behaviours (Hedenström and Alerstam 1997; Farmer and Wiens 1999; Alerstam 2001; Nilsson et al. 2013). When following a time-minimizing strategy, birds reduce the duration of migration by flying at higher speeds. They also make fewer and longer stopovers to deposit larger fat reserves. These reserves allow birds to make long flights and thus move at a relatively faster pace, but at the energetic cost of carrying the reserves (Kokko 1999; Hedenström 2008). In contrast, when following an energy-minimizing strategy, birds decrease energetic costs of flight by stopping frequently for shorter periods, and acquiring smaller fat reserves during stopovers (Åkesson et al. 2002; Bayly 2012; Tøttrup et al. 2012). They may also avoid flying in weather conditions that increase energetic costs such as strong headwinds (e.g., Delingat et al. 2008; Åkesson 2016).

Optimal migration theory also predicts that these strategies can vary by season. Birds appear to be more time constrained in the spring and thus typically follow time-minimizing strategies during that season (Lindström and Alerstam 1992; Nilsson et al. 2013). This allows early arrival on breeding grounds to secure high-quality nest sites, initiate breeding earlier, with more time to fledge young (van Noordwijk 1995). Conversely, birds appear to be less time constrained in the fall and thus may follow energy-minimizing strategies. This allows arrival on wintering grounds in good body condition without the fitness penalty for later arrival (Hedenström and Alerstam 1997).

Strategies may also vary in relation to intrinsic factors such as sex and age. For instance, in the spring there may be stronger selection on males to follow a time-minimizing strategy to arrive early on breeding grounds to secure territories (Dierschke et al. 2005). In contrast, there may be stronger selection on females to follow an energy-minimizing strategy to arrive on breeding grounds later but in good body condition to permit breeding shortly after arrival (Schmaljohann and Dierschke 2005). Differences in age-related patterns are less clear, mostly because they have not been studied. Timing differences are common with adults migrating earlier than juveniles (Stewart et al. 2002), but this does not necessarily translate into different use of time- or energy-minimizing strategies by age (Jakubas et al. 2010).

Modern field studies have improved our understanding of how the costs of time and energy constrain individual migratory behaviours (e.g., timing and stopovers), and, in turn drive migratory strategies (e.g., Cohen et al. 2017; Kramer et al. 2017; Moore 2018). Despite these advances, studies on population-level differences in migratory strategy are few, especially for songbirds (Faaborg et al. 2010; McKinnon and Love 2018). Further, some studies report results that are inconsistent with optimal migration theory. For instance, Red-eyed Vireos (*Vireo olivaceus*) make lengthy stopovers of > 20 d during the spring migration, which runs counter to the expectation that they should be using a time-minimizing strategy during this season (Callo et al. 2013). Such results suggest that there are gaps in our understanding of how time and energy drive the migratory strategies of songbirds, and how the strategies they use affect survival and fitness (Alerstam and Hedenström 1998; Dänhardt and Lindström 2001; Schmaljohann and Dierschke 2005). Understanding how season, age, and sex affect these strategies may also have

conservation benefits because differences in these factors may result in various timing, distribution, or stopover needs for birds in different migrations. This information is a key but rarely incorporated feature of conservation planning (Bennett et al. 2019).

I used automated radio-telemetry to study the migratory strategy of a short-distance migrant, the Ipswich Sparrow (*Passerculus sandwichensis princeps*). My goal was to determine if the strategy used by sparrows was time- or energy-minimizing during its spring migration, and to determine if strategy differed by age and sex class. Specifically, I: 1) described spring migratory behaviour by determining timing (departure from wintering grounds, migratory duration, arrival on breeding grounds), diel timing, flight speed, distance flown/night, and stopover location and duration, and 2) determined if these factors varied by age or sex.

I expected that adults and juveniles would use the same strategy during spring as they should be under the same selection pressures to arrive either quickly or in good condition on breeding grounds to maximize breeding productivity. Thus, I expected birds of both ages to depart wintering grounds at similar times, fly at similar speeds, and have similar stopovers. In contrast, I expected males and females would differ by strategy. Males would use a time-minimizing strategy to arrive early on Sable Island and secure territories, while females would use an energy-minimizing strategy to arrive later on Sable Island but in good body condition for breeding. Thus, I expected males to depart wintering grounds earlier, fly faster, and have longer stopovers than females.

## **2.3 Methods**

### **Migratory timing**

I calculated three variables that relate to the timing of spring migration – migratory initiation, migratory completion, and migratory duration. I included sparrows tagged on wintering grounds for all calculations, and sparrows tagged in NS for migratory completion calculations only.

I considered migration to begin (i.e., migratory initiation) on the day of the final detection on the receiver nearest to the tagging site. In cases where sparrows were not

detected by the nearest receiver, I used the day of detection by the first receiver  $\leq 100$  km N of the tagging site, and excluded first detections  $> 100$  km N.

I considered migration to have ended (i.e., migratory completion) on the day a sparrow was first detected on Sable Island. I excluded detections from manual telemetry surveys because they were undertaken after sparrows had arrived on Sable Island and did not represent arrival timing.

Migratory duration (i.e., total number of days migrating, inclusive) was calculated as the number of days between the initiation and completion of migration.

I used generalized linear models (GLM) to determine if migratory initiation or completion (converted to Julian day) differed by age, sex, or year (Gaussian distribution). I could not do a similar analysis for duration because sample size was too small (Table 2.1). I also fit a model to determine if migratory duration was influenced by initiation date (i.e., if later initiating sparrows migrated faster or slower than earlier initiating sparrows; Gómez et al. 2017; González-Prieto 2018; Gaussian distribution), but could not assess age, sex, or year effects as sample size was too small (Table 2.1). Sample sizes were also too small to fit two-way or higher interactions in either model (Table 2.1). I did not expect this limitation to affect my interpretation of the data as there was no *a priori* reason to suspect these variables interacted to influence the response.

## **Migratory movements**

### *Diel timing*

I determined the diel timing of birds making direct flights (individuals moving  $\geq 5$  m/s; see below) between receivers. Flights were coded as “nocturnal” (departure and arrival occurred at night), “diurnal” (departure and arrival occurred during the day), “night-to-day” (departure occurred at night and arrival occurred during the day), or “day-to-night” (departure occurred during the day and arrival occurred at night; Table 2.1).

### *Flight speed and distance*

Flight speed (ground speed, m/s) from one receiver to the next was calculated by dividing the great-circle route distance (Vincenty 1975) by the difference in time between detections on each receiver. Ipswich Sparrows are nocturnal migrants (see Results), therefore only hours during the night were included in the time. When sparrows were

detected by receivers for two or more nights, I subtracted the length of the day at the latitude halfway between receivers from the total time to retain only hours during the night. I excluded flights between receivers  $\leq 25$  km apart that could simultaneously detect tags and therefore produce incorrect flight speeds. To assess if flight speed varied with age, sex, or year, I initially fit a generalized linear mixed model (GLMM; Gamma distribution + log link) with individual as a random effect to account for multiple observations of flights per bird. The random intercept accounted for no variance, so I instead fit a simpler GLM (Gamma distribution + log link) and only present results for the GLM. Sample size was too small to fit two-way or higher interactions (Table 2.1).

To determine migration distance per night, I selected sparrows detected on  $> 1$  receiver in a single night and summed the great-circle route distances between these receivers. These distances represent a minimum because an entire flight made in a night may not be captured by receivers. Sample size was too small to evaluate differences by age, sex, or year (Table 2.1).

To determine the total distance of migration (how far sparrows flew between wintering and breeding grounds), I summed the great-circle route distance between receivers for birds with complete migratory durations (i.e., sparrows detected throughout the entire migration). Sample size was too small to evaluate differences by age, sex, or year (Table 2.1).

### *Stopovers*

I identified two types of movement patterns on receivers: stopovers and flybys. I considered a behaviour to be a stopover when a sparrow was detected by a single receiver for  $\geq 1$  h on a given night, which indicated that a sparrow remained at a single site for the night instead of migrating. I considered a behaviour to be a flyby when a sparrow was detected by a single receiver for  $< 1$  h on a given night before subsequently being detected elsewhere, which indicated that a sparrow did not remain in the area near the receiver and migrated (Crewe et al. 2019b). I set the 1 h limit because most sparrows were detected by receivers for short periods during the night (median = 0.06 h) and there was a natural break in the data between movement patterns at this point. In cases where sparrows were detected by a single receiver for any duration on  $\geq 2$  nights without being

detected elsewhere in the interim, I classified as stopovers because sparrows remained at the site instead of migrating on the first night (Table 2.1).

Since many stopovers would also have occurred beyond the range of receivers, I also determined the overall stopover time during migration using flight speed. I did this by calculating stopover time for indirect flights (sparrows moving  $< 5$  m/s) between receivers. I calculated the time a direct flight would have taken at a flight speed of 5 m/s, and then subtracted this value from the duration of the indirect flight. The resulting time was assumed to be stopover time (*sensu* Smetzer and King 2018; Anderson et al. 2019). Using these methods, I was able to obtain an estimate of the total time sparrows spent stopping over but could not count or know the location of individual stopover events (Table 2.1).

To determine what proportion of migratory duration was spent at stopover sites, I divided stopover time by migratory duration. I excluded one bird from this analysis because it was only detected at its wintering site and on Sable Island, meaning there was too much uncertainty in its movement to determine stopover duration. Sample size was too small to assess if proportion differed by age, sex, or year (Table 2.1).

### **Statistical analyses**

Data manipulation was done in program R version 3.6.0 (version 3.6.0; R Core Team 2019) using the following packages: *motus* (Brzustowski and Lepage 2019), *tidyverse* (Wickham et al. 2019), and *geosphere* (Hijmans 2019). Maps were created using packages *maps* (Becker et al. 2018a), *mapdata* (Becker et al. 2018b), and *ggplot2* (Wickham 2016).

Model fitting was done in function *glm* in base R (GLM) and package *lme4* (GLMM; Bates et al. 2015). Model fit was assessed by examining the standard errors (SE) of parameter estimates and residual plots. Summary statistics are reported as mean  $\pm$  SD unless otherwise noted.

## 2.4 Results

One hundred and twenty-eight Ipswich Sparrows were tagged on wintering grounds in 2018 and 2019. Four tags deployed in 2019 detected the following year buried in the sand at the tagging location were presumably lost before migration, or, the tagged sparrows died before migration. This reduced total sample size to 124 sparrows, of which 93 (75.0%) were detected at least once by receivers. Eighty-two of the 93 (88.2%) sparrows were detected beyond the tagging site during migration (Table 2.2). Each sparrow was detected by  $4.2 \pm 2.8$  receivers (range = 1–13), and most detection patterns (289/359, 80.5%) were of short duration ( $4.36 \pm 4.79$  min, range = 0.32–30.53 min, median = 2.95 min), indicating the bird was flying past the receiver. The remaining 31 tagged sparrows were never detected, presumably because of tag loss, tag failure, or mortality. One sparrow spent the summer on mainland NS and so was never detected on Sable Island.

Thirty-one sparrows were tagged on mainland NS in 2013 and 2019. Two tags deployed in 2013 were undetected due to predation of sparrows shortly after tagging (Z Crysler, pers. comm.). This reduced the final sample size to 29 sparrows, of which 29 (100%) were detected at least once by receivers. Twenty-five of the 29 sparrows (86.2%) were detected beyond the tagging site at other receivers (Table 2.2). Each sparrow was detected by a mean of  $4.3 \pm 2.3$  receivers (range = 2–11), and most detections (121/228, 53.1%) were of short duration ( $8.5 \pm 6.6$  min, range = 0.8–40.1 min, median = 7.9 min), indicating the bird was flying past the receiver.

### Migratory timing

Migratory initiation occurred over a 34-d period between 26 March and 23 April (mean = 3 Apr  $\pm$  9.4 d; Table 2.3). Males initiated migration  $16.1 \pm 1.5$  d before females (GLM:  $\beta_{\text{male}} \pm \text{SE}$ ,  $P < 0.001$ ), but there was no evidence that initiation differed with age ( $\beta_{\text{juvenile}} = -0.9$ ,  $\text{SE} = 2.0$ ,  $P = 0.64$ ) or year ( $\beta_{2019} = -1.4$ ,  $\text{SE} = 1.7$ ,  $P = 0.39$ ; Table 2.4; Fig. 2.1).

Migratory completion occurred over a 43-d period between 16 April and 1 June (mean = 1 May  $\pm$  11.1 d; Table 2.3). Males completed migration  $15.0 \pm 3.7$  d before



females (GLM:  $\beta_{\text{male}} \pm \text{SE}$ ,  $P < 0.0001$ ) but there was no evidence that completion date differed by age ( $\beta_{\text{juvenile}} = 6.9$ ,  $\text{SE} = 4.6$ ,  $P = 0.15$ ) or year ( $\beta_{2018} = -13.3$ ,  $\text{SE} = 9.6$ ,  $P = 0.18$ ;  $\beta_{2019} = -3.4$ ,  $\text{SE} = 4.7$ ,  $P = 0.48$ ; Table 2.4; Fig. 2.1).

Migration occurred over a 67-d period between 26 March and 1 June. Migratory duration was  $29.1 \pm 7.83$  d (Table 2.3; Fig. 2.1). There was no evidence that duration differed by initiation date (GLM:  $\beta = 0.26$ ,  $\text{SE} = 0.33$ ,  $P = 0.47$ ).

## **Migratory movements**

### *Post-departure movements*

Sparrows tagged on wintering grounds moved along a coastal migratory route during spring migration (Fig. 2.2). Sparrows first traveled north along the coast of the Delmarva Peninsula. Subsequently, 76 (61.3%) were detected moving through Long Island Sound and Cape Cod. Only 23 (18.5%) sparrows were detected in the Gulf of Maine (GOM) possibly due to the small number of receivers along this coastline. Fifty-four sparrows (43.5%) were detected in NS and 22 (17.7%) were ultimately detected on Sable Island.

Sparrows tagged in NS remained in NS before crossing to Sable Island. Fifteen of the 31 (48.4%) sparrows were detected along the eastern shore of NS after tagging, while two (6.5%) were detected along the south shore of NS after tagging. Fourteen sparrows (45.2%) were ultimately detected on Sable Island.

### *Diel timing*

Ninety-five percent (133/140) of direct flights ( $\geq 5$  m/s) occurred at night. Seven (5.0%) flights were night-to-day; five of these occurred when sparrows crossed the GOM at night and arrived in southern NS early the following morning, or, crossed part of the Atlantic Ocean (AO) at night and arrived on Sable Island early the following morning. The remaining two night-to-day flights occurred when sparrows flew along large portions of the NS coastline at night (distance 188–215 km) and did not end flights until early the following morning.

### *Flight speed and distance*

Sparrows travelled at  $7.1 \pm 9.3$  m/s (Table 2.3). There was no evidence that flight speed differed by age (GLM;  $\beta_{\text{juvenile}} = -0.02$ ,  $\text{SE} = 0.22$ ,  $P = 0.93$ ) or sex ( $\beta_{\text{male}} = -0.10$ ,

SE = -0.16, P = 0.52), but did by year ( $\beta_{2019} = 0.38$ , SE = 0.18, P = 0.04; Fig. 2.3; Table 2.4), with speeds in 2019 higher than 2018.

Sparrows flew distances of  $126 \pm 122$  km (Table 2.3; Table 2.4; Fig. 2.4) in a single night. Distance flown during an entire migration was  $1558 \pm 200$  km (Table 2.3).

### *Stopovers*

Twenty-six of 359 (7.2%) movement patterns were stopovers within the range of receivers (mean duration =  $6.4 \pm 4.5$  d; Table 2.3, Table 2.4; Fig. 2.5). Most of these stopovers occurred before migratory barriers: one (3.8%) occurred in Long Island, NY, and four (15.4%) occurred in Cape Cod, MA before the GOM barrier, and three (11.5%) were along the GOM coastline. Eighteen (69.2%) occurred in NS before the AO barrier to Sable Island.

Sparrows spent  $24.8 \pm 7.1$  d stopping over during migration (indirect flights; Table 2.3, Table 2.4) which comprised most ( $85.2 \pm 4.9\%$ ) of spring migration.

## **2.5 Discussion**

Ipswich Sparrow spring migration occurred between March and June, and males initiated and finished migration before females. Sparrows migrated along the Atlantic Coast almost exclusively at night and there was no evidence that flight speed, nightly distance flown, or stopover duration differed by age or sex. Below, I discuss each migratory behaviour within the framework of optimal migration theory, and propose possible explanations for age-related, and lack of sex-related, differences.

### **Time- or energy-minimizing?**

My results suggest that Ipswich Sparrows follow an energy-minimizing strategy during spring migration. Sparrows took a mean of 29 d to travel the ~1558 km from wintering grounds to Sable Island. This is in contrast to the time-minimizing Wood Thrush (*Hylocichla mustelina*) that takes 13–15 d to travel ~4600 km during spring migration (Stutchbury et al. 2009; Stanley et al. 2012). Sparrows also had relatively slow flight speeds (7.1 m/s) compared to other songbirds (11.3–12.7 m/s; reviewed in Karlsson et al. 2012) during spring migration, consistent with an energy-minimizing strategy.

Further, sparrows flew a median distance of only 91 km/night, despite some being physiologically capable of flying ~400 km/night (see below). This is in contrast to other songbirds, many of which travel > 200 km/night during spring migration (reviewed in McKinnon et al. 2013). Though I was unable to count the distinct number of stopovers sparrows made, slow flight speeds and short nightly flight distances suggest sparrows made frequent, and presumably short, stops. Collectively, these behaviours are consistent with an energy-minimizing strategy. They suggest sparrows keep daily energy costs low by reducing travel speed (i.e., flying slowly for short distances), stopping frequently, and presumably saving energy by carrying small fuel loads so they arrive on Sable Island in good condition (Bolshakov et al. 2003; Åkesson et al. 2012; Tøttrup et al. 2012).

Ten sparrows made relatively long stopovers of 7–18 d, consistent with an energy-minimizing strategy. Stopovers > 7 d are considered “prolonged” (McKinnon et al. 2013) and theoretically exceed the time required for typical refuelling for a migratory flight (Alerstam 1991). Tracking studies have documented prolonged stopovers of, for instance, > 20 d in Red-eyed Vireos (Callo et al. 2013), > 25 d in Rusty Blackbirds (*Euphagus carolinus*; Wright et al. 2018), and ~19 d in Swainson’s Thrushes (*Catharus ustulatus*; Delmore et al. 2012). In my study, eight prolonged stopovers occurred before barriers and likely reflect fuelling needs associated with passing barriers (Bayly 2012; Fraser et al. 2013; Gómez et al. 2017; Smetzer and King 2018). One prolonged stopover occurred in NS after a sparrow crossed the GOM and may represent additional refuelling needs after a long flight. Another prolonged stopover occurred in the Bay of Fundy but was not adjacent to a barrier. This stopover was not followed by a long-distance flight and does not appear to be associated with an attempt to speed up migration (time-minimization; Gudmundsson et al. 1991; Piersma and Rogers 2005). Thus, the purpose of this prolonged stopover is unclear at this time.

Although most behaviours were consistent with an energy-minimizing strategy, nine sparrows flew ~400 km across the GOM ecological barrier in a single night (see Chapter 3), which is more consistent with a time-minimizing strategy. Crossing rather than circumventing a barrier allows birds to pass the barrier in as little time as possible at relatively high energetic cost (Gudmundsson et al. 1991; Alerstam 2001; Piersma and Rogers 2005). Though some sparrows also circumvented the GOM, this shows that some

followed a time-minimizing strategy during this specific part of spring migration. In these cases, it is possible that sparrows encountered supportive weather conditions (e.g., strong tailwinds) that reduced the energetic costs of crossing the barrier (Liechti and Bruderer 1998).

Contrary to my predictions, I found that Ipswich Sparrows followed an energy-minimizing rather than time-minimizing strategy in the spring, which is in contrast to most songbirds during this migration (Lindström and Alerstam 1992; Hedenström and Alerstam 1997; Nilsson et al. 2013). European Robins (*Erithacus rubecula*; Dänhardt and Lindström 2001) and Northern Wheatears (*Oenanthe oenanthe*; Schmaljohann et al. 2013) also follow an energy-minimizing strategy during spring.

There are several non-mutually exclusive explanations for why Ipswich Sparrows might follow an energy-minimizing strategy during spring migration. They are short-distance migrants, and thus may be more likely to follow an energy-minimizing strategy because they can afford to travel more slowly due to shorter travel distances. In contrast, long-distance migrants may be more likely to follow a time-minimizing strategy because they must travel quickly to cover long distances in a reasonable time (Nilsson et al. 2014; Anderson et al. 2019). Another possibility is that Ipswich Sparrows undergo moult during spring migration (Dale 2008) which would increase energetic demands during this period and necessitate frequent stopovers and slow travel speeds to recuperate energetic costs (Hedenström 2008). Similarly, if sparrows are exposed to increased predation in coastal areas where predators are concentrated (Ydenberg et al. 2007; Gangoso et al. 2013; Woodworth et al. 2015) they may keep fuel loads low to improve manoeuvrability and reduce predation risk (Kullberg et al. 1996). Thus, similar to other songbirds, high predation pressure along the coast may drive a need to keep daily energy costs low (Smetzer and King 2018). Finally, Ipswich Sparrows may be exposed to conditions on Sable Island that preclude the need to make a physiologically challenging time-minimizing migration. The island has abundant food resources during the breeding season and few predators (Stobo and McLaren 1975). Breeding productivity is high even in the poorest habitat, with sparrows laying up to four broods and fledging 74–84% of young (Stobo and McLaren 1975; Temple 2000) compared to 30–80% in other songbirds (Ricklefs 1973). Given these factors, it may be more advantageous to arrive on Sable

Island relatively later, but in good condition, so breeding can begin immediately. This would be in contrast to other songbirds, where late arrival on breeding grounds incurs significant fitness costs (Marra 1998; Smith and Moore 2005).

### **Intrinsic differences in behaviour**

Consistent with my prediction, there was no evidence of age-related differences in timing, flight speed, nightly flight distance, or stopover duration. This may be explained by individual experience. By spring migration, juveniles may have skills and abilities similar to adults and thus behave similarly (Berthold 1996, 2001; Thorup et al. 2007). Further, competition for resources on breeding grounds that drive timing differences between age classes in other songbirds (Morton 2002; Covino et al. 2020) may not be factor for Ipswich Sparrows given the surplus of resources on Sable Island (Stobo and McLaren 1975). Similarly, wing shape dimorphism that explains flight speed and flight distance differences between age classes in other songbirds (Lockwood et al. 1998) does not occur between adult and juvenile sparrows (Pyle 1997), thus may explain a lack of age-related differences. Lastly, if there is no difference in the condition or competitive ability of adults and juveniles by spring (Woodrey and Moore 1997), there are unlikely to be age-related differences in the stopover duration of sparrows.

Contrary to my prediction, I did not detect sex-related differences in migratory strategy. Evidence for sex-related differences in strategy in songbirds is mixed – some studies have reported differences (e.g., Farmer and Wiens 1999; Dierschke et al. 2005; Yosef and Wineman 2010) while others have found the opposite (e.g., Ellegren 1991). In general, there have been few studies on sex-related differences in strategy, making it difficult to understand overall sex-related patterns. For instance, many studies report faster migration in the spring by males than females (e.g., Coppack and Pulido 2009) but there is not enough information about other behaviours to know if this translates into a different overall migratory strategy between the sexes.

One explanation for the lack of sex-related differences in strategy in Ipswich Sparrows may be related to differences in the timing of migration. Males initiated and completed migration before females, suggesting the sexes were spatially and temporally segregated during migration. In species where sexes overlap, intraspecific competition at

stopover sites can result in female exclusion from high-quality sites by males (Moore et al. 2017), resulting in females in poorer condition. In turn, females may migrate more slowly and need to follow an energy-minimizing strategy to maintain good condition (Spina and Pilastro 1999; Moore et al. 2003). In Ipswich Sparrows, the segregation may minimize overlap and thus condition differences between the sexes. Thus, both sexes can employ an energy-minimizing strategy with males simply migrating earlier.

Flight speeds were slightly faster in 2019 compared to 2018.

### **Tag effects**

As in any tagging study, it is possible that tags affected the behaviour of Ipswich Sparrows. There was no way for me to quantitatively examine tag effects in my study as I lacked a control group. However, the ground-dwelling habits of these sparrows, attachment method (leg-loop harness), and tag mass (< 4% body mass) generally reduce the likelihood of tag effects (Barron et al. 2010; Costantini and Møller 2013). Further, a previous study on closely related Savannah Sparrows found no negative effects of tagging on pre-migratory condition (Rae et al. 2009). Therefore, I assume that tag effects in my study were negligible.

## **2.6 Conclusions**

Ipswich Sparrows follow an energy-minimizing strategy during spring migration. Energy-minimizing migrants rely on a network of high-quality stopover sites to support fuelling needs (Iverson et al. 1996; Poiani et al. 2000; Mehlman et al. 2005), particularly at ecological barriers where large fuel reserves may be required (Bayly 2012; Hewson et al. 2016). This has conservation implications for Ipswich Sparrows because habitat along the Atlantic Coast is increasingly degraded from rapid human population growth (Crossett et al. 2004; Nickerson et al. 2007; Longcore and Smith 2013). Conservation effort will be required to protect such a network of stopover sites along the Atlantic Coast.

## 2.7 Tables

**Table 2.1** – Sample size (n) of Ipswich Sparrows by age, sex, and year for each migratory event.

Event	Year	Age			Sex	
		Adult	Juvenile	Unknown	Male	Female
Initiation	2013	-	-	0	-	-
	2018	4	10	0	10	4
	2019	4	32	0	18	18
Completion	2013	8	1	0	7	2
	2018	0	1	0	0	1
	2019	3	11	0	8	6
Duration	2013	-	-	0	-	-
	2018	0	0	0	0	0
	2019	2	6	0	6	2
Diel timing	2013	-	-	-	-	-
	2018	5	21	0	15	11
	2019	11	101	2	56	58
Flight speed	2013	-	-	0	-	-
	2018	30	50	0	52	28
	2019	22	206	0	127	101
Single night distance	2013	-	-	0	-	-
	2018	3	11	0	8	6
	2019	5	54	2	31	30
Total distance	2013	-	-	0	-	-
	2018	0	0	0	0	0
	2019	2	6	0	6	2
Single stopover duration	2013	-	-	-	-	-
	2018	3	3	0	4	2
	2019	0	20	0	8	12
Total stopover duration	2013	-	-	0	-	-
	2018	-	-	0	-	-
	2019	1	6	1	6	2
Proportion stopping over	2013	-	-	0	-	-
	2018	-	-	0	-	-
	2019	1	6	1	6	2

**Table 2.2** – Number of Ipswich Sparrows tagged on both wintering grounds and in mainland NS across all study years, and detected at least once by the receiver network beyond the tagging site.

Tagging location	Adult male	Adult female	Juvenile male	Juvenile female	Unknown age male	Unknown age female
Wintering grounds	10	8	38	24	1	1
Mainland NS	15	3	5	2	0	0
TOTAL	25	11	43	26	1	1

**Table 2.3** – Summary statistics for Ipswich Sparrow migratory timing and movements.

Event	Mean ( $\pm$ SD)	Median	Minimum	Maximum	n
Initiation <sup>a</sup>	93.7 $\pm$ 9.4	88	79	113	51
Completion <sup>c</sup>	121 $\pm$ 11.2	121	106	149	25
Duration <sup>b</sup>	29.1 $\pm$ 7.83	28.3	20.5	42.7	9
Flight speed <sup>d</sup>	7.1 $\pm$ 9.3	2.2	0.03	45	314
Nightly distance <sup>e</sup>	126 $\pm$ 122	90.9	11.1	587	75
Total distance <sup>f</sup>	1558 $\pm$ 200	1523	1415	2075	9
Single stopovers <sup>g</sup>	6.4 $\pm$ 4.5	4.3	2.0	18.4	26
Total stopovers <sup>h</sup>	24.8 $\pm$ 7.1	22.6	17.2	34.9	8
Proportion stopovers <sup>i</sup>	85.2 $\pm$ 4.9	85.1	76.4	92.1	8

<sup>a</sup> day, <sup>b</sup> day, <sup>c</sup> day, <sup>d</sup> m/s, <sup>e</sup> km, <sup>f</sup> Total distance migrated (km), <sup>g</sup> Duration of single stopovers undertaken near receivers (d), <sup>h</sup> Duration of all stopovers, determined from indirect flight speeds < 5 m/s (d), <sup>i</sup> %



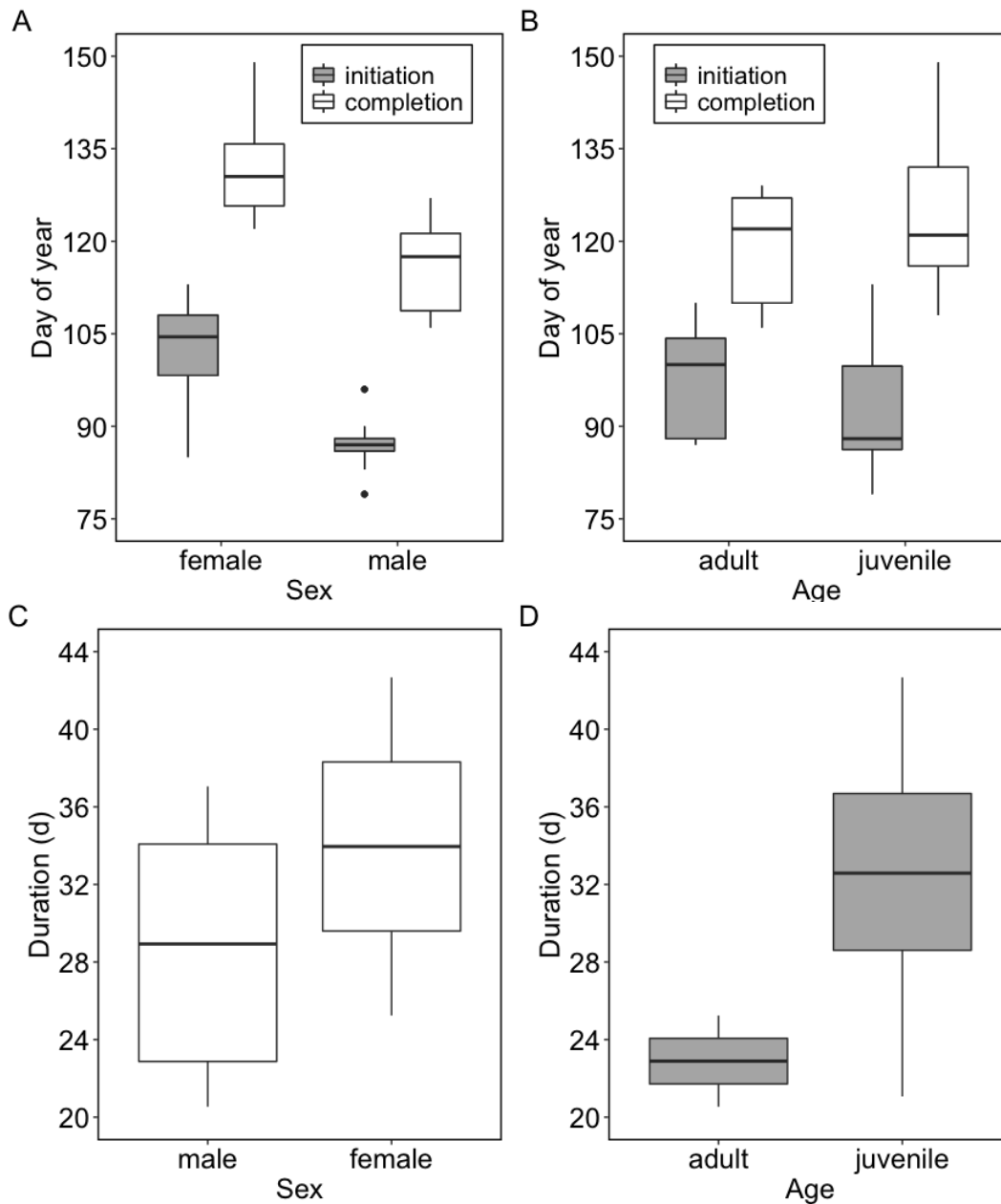
**Table 2.4** – Effect sizes (mean  $\pm$  SD) by sex, age, and year for Ipswich Sparrow migratory timing and movement.

Event	Sex		Age		Year			n
	Male	Female	Adult	Juvenile	2013	2018	2019	
Initiation <sup>a</sup>	86.9 $\pm$ 3.0	103.0 $\pm$ 6.72	98.0 $\pm$ 9.4	93.1 $\pm$ 9.3	-	92.6 $\pm$ 7.9	94.4 $\pm$ 10.0	51
Completion <sup>b</sup>	116.4 $\pm$ 7.5	132.3 $\pm$ 9.7	118.6 $\pm$ 9.0	124.2 $\pm$ 12.4	119.6 $\pm$ 0.1	109.0	123.9 $\pm$ 12.1	25
Duration <sup>c</sup>	28.7 $\pm$ 7.0	34.0 $\pm$ 12.3	22.9 $\pm$ 3.3	32.4 $\pm$ 7.62	-	-	30.0 $\pm$ 7.9	9
Flight speed <sup>d</sup>	6.8 $\pm$ 8.8	7.6 $\pm$ 9.9	6.9 $\pm$ 11.0	7.1 $\pm$ 8.9	-	5.3 $\pm$ 8.4	7.7 $\pm$ 9.5	308
Nightly distance <sup>e</sup>	118 $\pm$ 80	134 $\pm$ 156	157 $\pm$ 154	124 $\pm$ 119	-	128 $\pm$ 94	125 $\pm$ 128	75
Total distance <sup>f</sup>	1570 $\pm$ 228	1513 $\pm$ 39.6	1452 $\pm$ 46.7	1617 $\pm$ 225	-	-	1558 $\pm$ 200	9
Single stopovers <sup>g</sup>	6.6 $\pm$ 5.4	6.2 $\pm$ 3.6	7.0 $\pm$ 4.2	6.3 $\pm$ 4.6	-	5.9 $\pm$ 3.4	6.6 $\pm$ 4.8	26
Total stopovers <sup>h</sup>	24.9 $\pm$ 6.8	28.5 $\pm$ 9.2	22.0	27.5 $\pm$ 7.2	-	-	25.8 $\pm$ 6.9	8
Proportion stopovers <sup>i</sup>	85.4 $\pm$ 5.6	84.5 $\pm$ 3.7	87.2	84.8 $\pm$ 5.7	-	-	85.2 $\pm$ 4.9	8

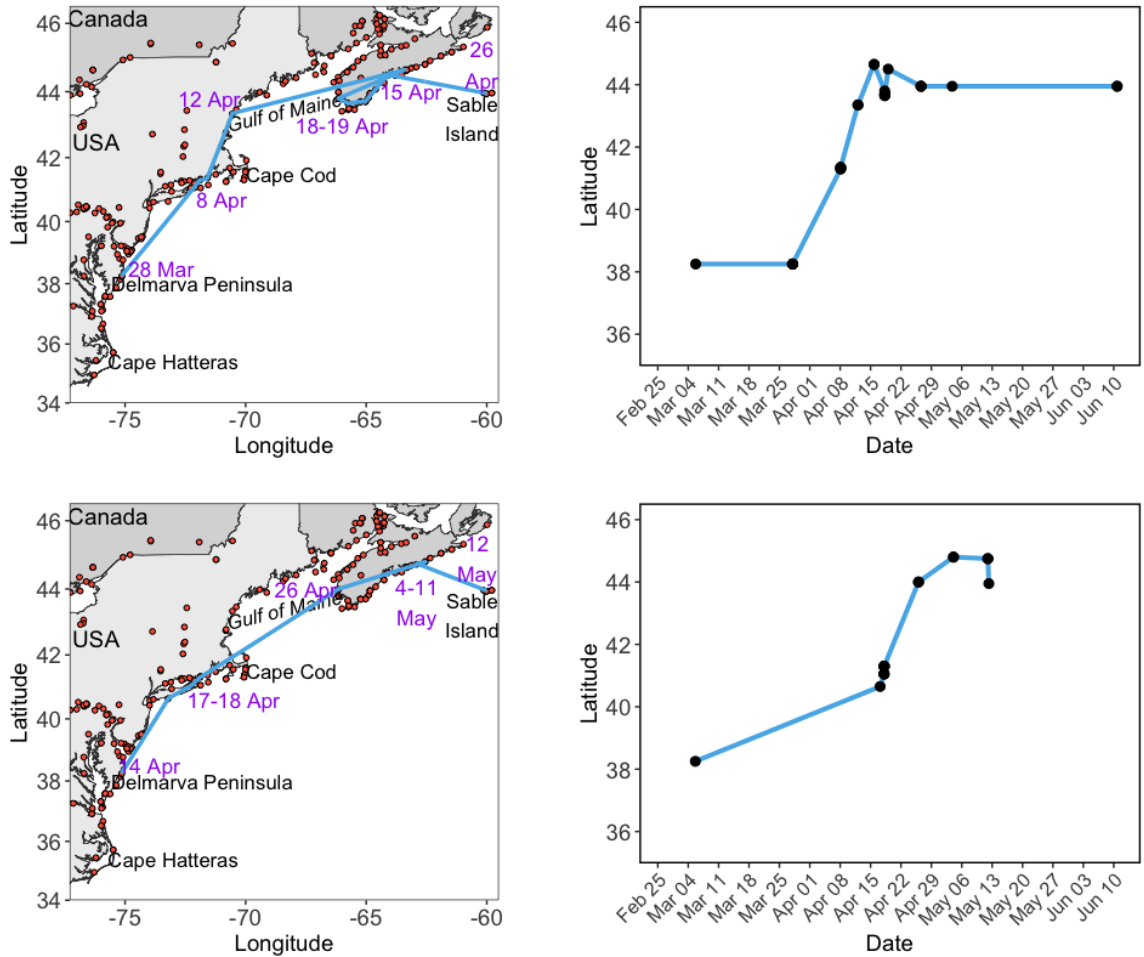
<sup>a</sup> day  $\pm$  d, <sup>b</sup> day  $\pm$  d, <sup>c</sup> d, <sup>d</sup> m/s, <sup>e</sup> km, <sup>f</sup> Total distance migrated (km), <sup>g</sup> Duration of single stopovers undertaken near receivers (d),

<sup>h</sup> Duration of all stopovers, determined from indirect flight speeds < 5 m/s (d),

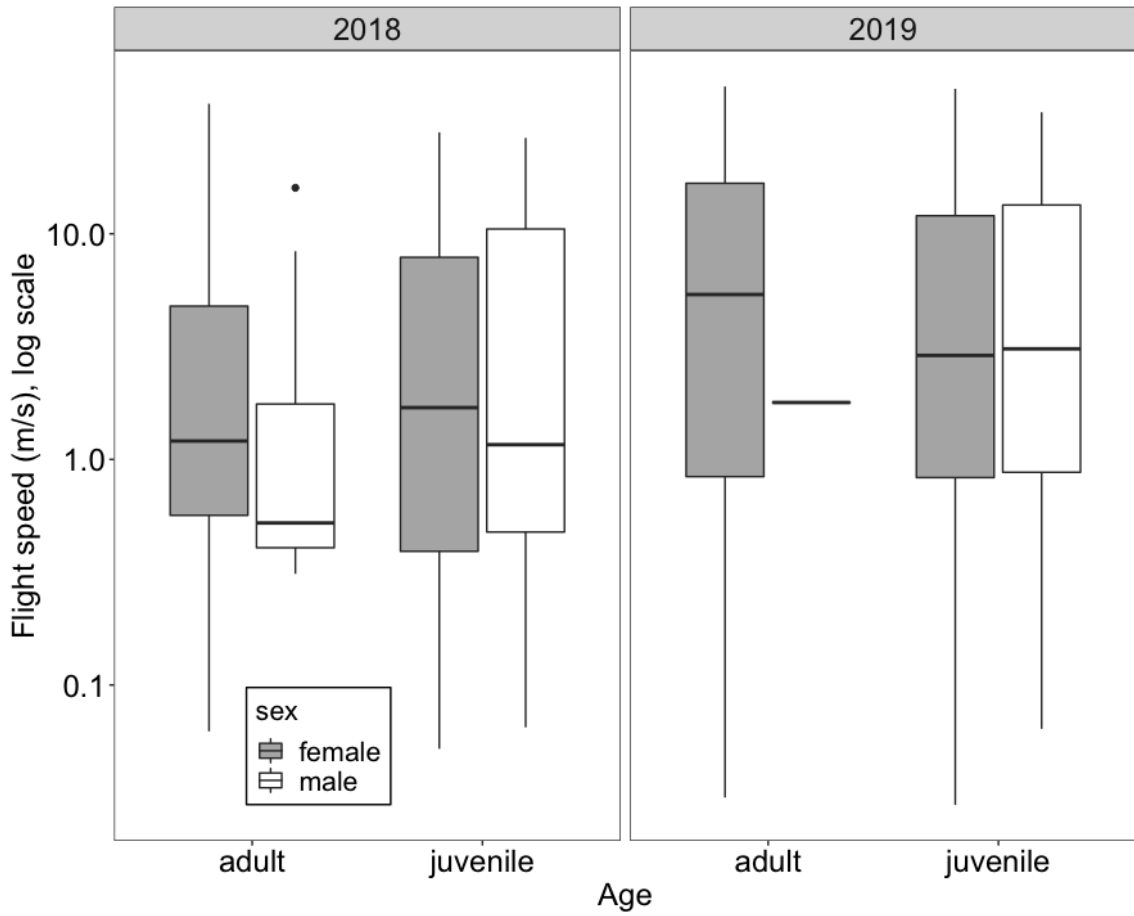
## 2.8 Figures



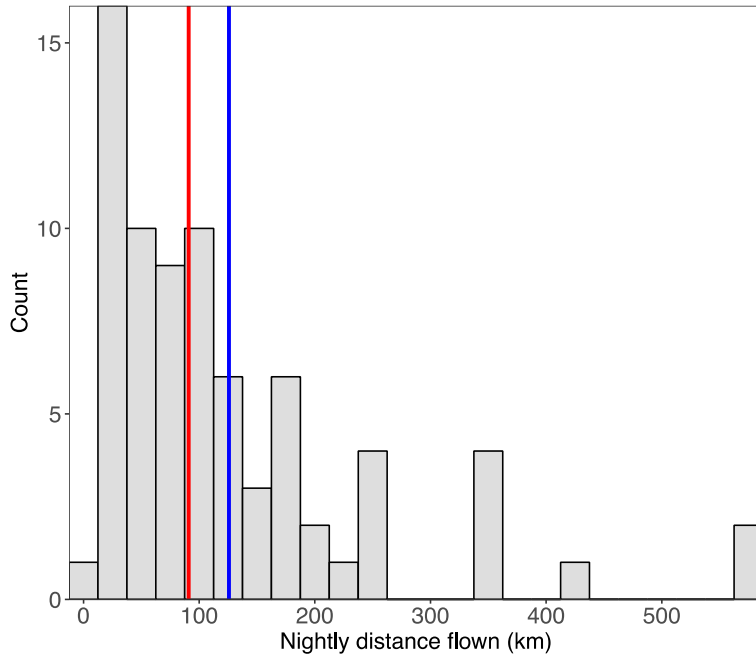
**Figure 2.1** – Boxplots of migratory timing: A) initiation and completion date by sex, B) initiation and completion date by age, C) duration by age, and D) duration by sex. Day of year 100 is 10 Apr 10, and day of year 140 is 20 May. Box hinges represent the first and third quartiles (25th and 75th percentiles), the mid-line represents the median, and the whiskers represent the inter-quartile range. Data beyond the whiskers outside the inter-quartile range are plotted as points.



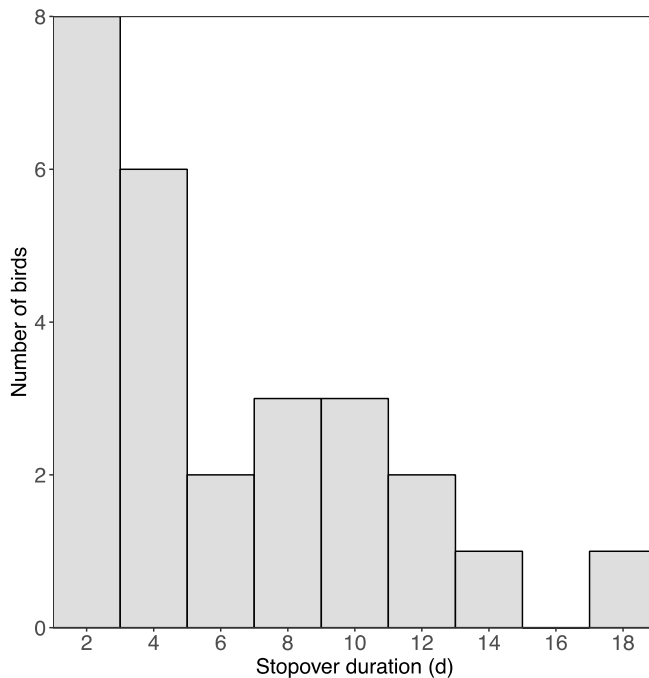
**Figure 2.2** – Examples of movement tracks of Ipswich Sparrows tagged on wintering grounds migrating to Sable Island in the spring. Each row represents a single sparrow. Blue tracks indicate movement between receivers but do not necessarily represent the exact flight path of each individual. Maps indicate the movement of birds along the Atlantic Coast by latitude and longitude, and plots show the same information by latitude and date.



**Figure 2.3** – Boxplots of flight speed of Ipswich Sparrows by age, sex, and year. Box hinges represent the first and third quartiles (25th and 75th percentiles), the mid-line represents the median, and the whiskers represent the inter-quartile range. Data beyond the whiskers outside the inter-quartile range are plotted as points.



**Figure 2.4** – Histogram of nightly flight distances of Ipswich Sparrows during spring migration. The red line represents the median distance (91 km) and the blue line represents the mean distance (126 km). Both flights of 500+ km occurred when sparrows flew from Long Island Sound area, across the GOM, to NS.



**Figure 2.5** – Histogram of Ipswich Sparrow stopover duration during spring migration. This only represents a subset of stopovers undertaken within the range of receivers.

## CHAPTER 3: BEHAVIOUR AND SURVIVAL OF A SONGBIRD AT TWO ECOLOGICAL BARRIERS DURING SPRING MIGRATION

### 3.1 Abstract

Ecological barriers influence the behaviour (e.g., pathway) and survival of birds during migration. Yet, there has been disproportionate focus on behaviour at larger barriers and consequently poor understanding of these factors at smaller barriers. Further, there is uncertainty about whether smaller barriers produce population-level differences in behaviour across age and sex cohorts. Behaviours that may vary by these factors include pathway, flight bearing, and propensity to make aberrant behaviours. Here, I assessed behaviour and survival of the Ipswich Sparrow (*Passerculus sandwichensis princeps*) which must pass the Gulf of Maine (GOM) and part of the Atlantic Ocean (AO) barriers to reach its breeding grounds on Sable Island, Canada during spring migration. I tracked 153 sparrows using automated radio-telemetry and assessed difference in behaviours mentioned above by age (adult or juvenile) and sex. I also estimated daily survival probability at barriers, as well as along other legs of the migratory pathway. Sparrows both crossed and circumvented the GOM but I could not assess whether pathway differed with age. Juveniles had less direct flight bearings than adults at the AO. Sparrows made aberrant behaviours before the AO crossing but not elsewhere along the migratory pathway, and, juveniles were more likely than adults to make aberrant behaviours. I did not detect sex-related differences in behaviour. Daily survival at the GOM (0.97) was among the highest across migratory legs, while survival was lowest at the AO (0.91). Results suggest that passing the smaller AO barrier (~350 km) may be more challenging than the larger GOM (~400 km). By spring migration, juveniles behave similarly to adults with regard to some behaviours but there remain differences in others.

### 3.2 Introduction

Songbirds make seasonal migrations between breeding and wintering areas. Migration allows birds to exploit temporary resources and avoid poor weather (Alerstam

et al. 2003) but it is costly in time and energy, and, exposes birds to challenges such as predation and intraspecific competition (Lindström and Alerstam 1992; Newton 2008). The presence of ecological barriers such as large bodies of water, mountains, and deserts, where birds are unable to stop, can amplify these challenges. For instance, predators are found at higher densities along barrier edges compared to other parts of the migratory pathway (Gangoso et al. 2013; Woodworth et al. 2014). Similarly, competition for resources may be increased because birds may pause before barriers and accumulate along the edges (Åkesson et al. 1996). Coastal water barriers such as the North Sea, Mediterranean Sea, and Gulf of Mexico may present additional challenges to migrants (Sandberg and Moore 1996; Bruderer and Liechti 1998; Cohen et al. 2017; Brust et al. 2019). These include navigating with limited visual cues over an open seascape, poor weather conditions (e.g., fog and strong winds; Newton 2008; Woodworth et al. 2015), and offshore structures (e.g., wind turbines; Hüppop et al. 2006). Consequently, birds must make behavioural decisions when they encounter barriers to contend with these challenges (Alerstam 2001; Deppe et al. 2015; Adamík et al. 2016; La Sorte et al. 2016).

Birds pass coastal water barriers using pathways that either cross or circumvent the barrier (Alerstam 2001; Smolinsky et al. 2013; Deppe et al. 2015). Each pathway confers different benefits, costs, and risks. Crossing barriers by flying overwater reduces the time and distance it takes to pass the barrier, but requires extensive fueling beforehand and exposes birds to the risks of starvation, exhaustion, navigation error, and poor weather during the crossing, all of which can be fatal (Alerstam 2001; Newton 2007). Circumventing barriers minimizes the risks associated with crossing (Newton 2007) but increases predation risk and the distance and time it takes to pass the barrier (Alerstam 2001; Buler and Moore 2011).

Behaviour at coastal water barriers differs from behaviour during other parts of migration. Birds may make prolonged stopovers before barriers to calibrate various external compasses (e.g., stellar and solar) used to set flight bearings (reviewed in Guilford and de Perera 2017), and to accumulate relatively large fat reserves (Delingat et al. 2008; Risely et al. 2015). Further, birds may exhibit aberrant behaviours that indicate difficulty passing a barrier. These include movements in non-migratory directions (temporarily moving inland away from a barrier; Åkesson et al. 1996; Smolinsky et al.

2013), abandoned flights, abrupt changes in orientation, and slow flight speeds (Bruderer and Liechti 1998; Strandberg et al. 2010).

Given the risks associated with passing ecological barriers, intrinsic differences between individuals such as age and sex, and extrinsic factors such as seasonal selection pressures, can produce population-level differences in behaviour (Spina and Pilastro 1999). For instance, age-related differences can occur because experienced adults who have previously passed barriers have information about geography and distance that juveniles lack (Guilford et al. 2011; Mueller et al. 2013). This can reduce variability in the flight bearings of adults, allowing them to take more direct pathways (Hake et al. 2003; Handel and Gill 2010; Crysler et al. 2016) and thus pass a barrier faster than juveniles (Smolinsky et al. 2013). Similarly, sex-related differences can occur because socially subordinate females may take longer to acquire fuel reserves than males (Moore et al. 2017). This can increase stopover length before barriers. Further, seasonal pressures to finish migration quickly or in good body condition (Alerstam and Hedenström 1998) can cause birds to cross a barrier in one season but circumvent in another (Deppe et al. 2015). The intrinsic and extrinsic factors that drive these population-level differences can clarify why some birds refrain from crossing barriers within their energetic capacity, or, cross despite the risks (Deutschlander and Muheim 2009; Schmaljohann and Naef-Daenzer 2011). However, study of these factors has been largely restricted to non-songbirds.

Survival along the migratory route may also be disproportionately low at ecological barriers (Strandberg et al. 2010; Cohen et al. 2017). At coastal water barriers, this is supported by anecdotal reports of dead songbirds on shorelines (Newton 2007), in stomachs of sharks eaten after dying overwater (Dodrill and Gilmore 1978), and on offshore oil and gas platforms, presumably where birds came to rest (Russell 2005). The few studies that have quantitatively examined survival at barriers for migratory songbirds report low survival rates, especially for juveniles (Owen and Black 1989; Strandberg et al. 2010; Lok et al. 2015; Ward et al. 2018) which suggests that passing barriers during migration can impact population dynamics (Newton 2008). Yet, robust estimates of survival when passing barriers are lacking for songbirds (Sillett and Holmes 2002;



Newton 2006), due to the difficulty of determining the fate of individuals across the large spatial and temporal scales of migration (Marra et al. 2015).

Although ecological barriers undoubtedly impact the behaviour of migrants, studies have primarily focused on larger barriers such as the Gulf of Mexico (~900 km across) meaning there is less information on how migrants pass smaller barriers such as the Gulf of Maine (~400 km across, reviewed in Lightfoot 2014; GOM). This creates uncertainty about what constitutes a true barrier to migrants (e.g., Snell and Thorup 2019) and whether smaller barriers produce population-level (i.e., age and sex) differences in behaviour and survival (Piersma and Rogers 2005), and, what any population-level differences may tell us about how some behaviours develop as ageing and sexual maturation occurs. These knowledge gaps about behaviour and survival at smaller barriers have conservation implications. Effective use of conservation resources requires knowing what landscape features shape the movement patterns of songbirds, which may include seemingly small barriers (Faaborg et al. 2010). Understanding spatially where mortality occurs during migration, including at barriers, is necessary to guide conservation efforts (Faaborg et al. 2010; Marra et al. 2015) because migration appears to be the period of lowest survival for songbirds (Sillert and Holmes 2002; Newton 2006; Rockwell et al. 2017).

To address these knowledge gaps, I studied the migratory behaviour and survival of the Ipswich Sparrow (*Passerculus sandwichensis princeps*) with a focus on overwater barriers. This songbird winters in the eastern USA and breeds exclusively on Sable Island, NS, a small (40 x 1 km), isolated island in the Atlantic Ocean (AO). During migration sparrows are restricted to coastal dune habitat along the northeast Atlantic Coast of North America and must pass two “small” coastal water barriers in the spring when migrating from wintering to breeding grounds. The first barrier, the GOM (~400 km across) has two options for passage. Birds can circumvent the barrier by taking a coastal pathway around the GOM (~580 km around), or, can take a shorter and more direct flight by crossing overwater between New England, USA and eastern Canada. Sparrows must then pass a second barrier, the AO, to reach their breeding grounds on Sable Island. Here, sparrows must cross the barrier by flying at least ~170 km across the open ocean. The Ipswich Sparrow is unique in that it must fly substantially farther

offshore than other island breeding migratory songbirds to reach its breeding location, and, Sable Island itself is small target to locate in the open ocean.

I used automated radio-telemetry to assess the migratory behaviour and survival of Ipswich Sparrows at the GOM and AO barriers during spring migration. My goals were twofold. First, to quantify behavior by determining pathway (cross or circumvent), flight bearing, and aberrant behaviours (e.g., non-migratory movements) at each barrier, and to determine if these behaviours varied by age or sex. Second, to quantify survival during spring migration and determine if survival differed when passing these water barriers compared to other legs of migration along the coastline.

I expected that behaviour would vary by age at both barriers because juveniles have not made northbound spring migrations, and therefore have more limited knowledge of the geography and distances along the Atlantic Coast compared to adults. I expected that juveniles would circumvent the GOM and would have less direct flight bearings, and, would take longer pathways to cross the AO than adults for the same reasons. I also expected that behaviour would vary by sex at both barriers because males are typically under selection in spring to arrive early on breeding grounds (Kokko et al. 2006; Morbey et al. 2012). I expected that males would be more likely than females to cross the GOM to reduce the duration of migration and permit earlier arrival on Sable Island. I did not have predictions for my goal of quantifying aberrant behaviours during spring migration because I did not know *a priori* if sparrows would make aberrant behaviours, or what these behaviours might entail. I expected that there would be no sex-related differences in bearing as males and females are not expected to have different navigational abilities (Mettke-Hofmann and Gwinner 2003). I expected survival to be lower at both barriers compared to other legs of migration given the challenges of increased predation risk along coastlines and risk of poor weather conditions overwater.

### **3.3 Methods**

#### **Behaviour at the Gulf of Maine barrier**

##### *Pathway to eastern Canada*

To describe movements of Ipswich Sparrows tagged on wintering grounds at the GOM barrier in spring migration, I split the GOM into N and S regions at 44°N (Crysler 2015) where S only included the USA (Fig. 3.1). I coded pathways as: 1) “circumvent,” if sparrows were detected moving from the S to N region past receivers along the GOM coastline, indicating primarily overland movements, and 2) “cross”, if sparrows detected in the S made direct flights ( $\geq 5$  m/s) to the N region, indicating an overwater pathway across the GOM in one flight. When sparrows made indirect flights the movements in the GOM were ambiguous and were not assigned pathways. Similarly, sparrows detected only in the S that did not arrive in eastern Canada were not assigned pathways.

To determine if pathway differed by sex or year, I used a GLM (binomial + logit link) with pathway (circumvent or cross) as the dependent variable. Sample size was too small to determine if pathway differed by age (Table 3.1), or, assess the bearings of flights at this barrier.

#### **Behaviour at the Atlantic Ocean barrier**

##### *Pathway to Sable Island*

To describe movements of Ipswich Sparrows tagged on wintering grounds and Nova Scotia (NS) at the AO barrier, I split NS into three regions of approximately equal coastline length (Fig. 3.1) and coded pathway based on the departure region of direct flights ( $\geq 5$  m/s) to Sable Island. Regions included the Bay of Fundy, South NS, and East NS and represented three distinct areas sparrows appeared to use in NS before migrating to Sable Island (Sullivan et al. 2014; see below). Sample size was too small to assess if pathway differed by age, sex, or year because almost all flights occurred from a single region.

##### *Departure flights*

To determine the departure region on mainland NS where flights to Sable Island occurred, I needed to isolate the specific receiver that captured the departure of the

sparrow from the mainland. I also used this receiver for bearing calculations (see below). This is a particular challenge at the AO barrier because there is a high density of receivers in NS, and so sparrows were often detected by multiple receivers. Further, birds increase their altitude when making migratory flights and thus increase the likelihood of detections on multiple nearby receivers (Mitchell et al. 2015; Fig. 3.2).

To isolate the receiver, I considered only sparrows that made direct flights ( $\geq 5$  m/s) to Sable Island, and, receivers that detected sparrows between sunset and one hour after sunset when sparrows initiate their migratory flights (S Bliss. unpubl. data; Chapter 2). I assumed that if sparrows were only detected by one receiver during this time period, then this receiver represented the departure receiver. If detected by multiple receivers, then the receiver that detected sparrows with the highest signal strength during this time period (indicating proximity to the receiver; Taylor et al. 2017) represented the departure receiver.

#### *Flight distance and bearing*

I calculated the distance of the crossing and departure bearing for flights from the mainland to Sable Island. I calculated departure bearing as the circular mean bearing on departure receiver antennas weighted by the signal strength of each detection (i.e., detections with higher strength were given more weight; Sjöberg and Nilsson 2015) using the last 10 minutes of detections at the receiver. I calculated the deviation of departure bearings from a straight-line path between the mainland departure site and Sable Island using the great-circle route distance (Vincenty 1975). I used a linear model (LM) to determine if this bearing difference varied by age or sex, but sample size was too small to assess by year (Table 3.1).

#### **Abandoned flights to Sable Island**

In each year, some sparrows made what appeared to be departure flights to Sable Island from beaches near Halifax, NS. Following the departure flight, there were no subsequent overnight detections of sparrows moving along the mainland coast or on Sable Island. Sparrows were next detected in the northern part of East NS or southern part of South NS several hours later or early the following morning (Fig. 3.3). I interpreted these patterns as abandoned flights to Sable Island because they occurred at

times of day and bearings consistent with known departures (direct flights, see above and Results). Further, a lack of detections along the coast overnight suggests sparrows arrived in the northern part of East NS or southern part of South NS after being out of range of receivers, likely overwater, as sparrows are not known to make inland movements (Stobo and McLaren 1975; Sullivan et al. 2014).

To assess if this behaviour differed by age, sex, or year, I used a generalized linear model (GLM; binomial distribution + logit link) using flight (yes or no) as the dependent variable. I included sparrows that were detected in the East NS or South NS regions, from all tagging sites, for this analysis. I excluded data from 2018 as it appeared that tag batteries were failing prematurely at this point in migration and receivers may not have accurately documented these movements (Table 3.1).

### **Non-migratory movements**

Some sparrows made non-migratory movements after arriving in the East NS or South NS regions (Table 3.1). These sparrows made movements in SW or NW non-migratory directions from either the East NS region to the South NS or Bay of Fundy, or, from the South NS to the Bay of Fundy. I interpreted these patterns as non-migratory movements because they increased the distance sparrows must travel to arrive at their final destination, Sable Island. Such movement did not occur in other areas along the Atlantic Coast.

To determine if non-migratory movements differed by sex, I used a GLM (binomial distribution + logit link) with movement (yes or no [sparrow in NS that did not make a non-migratory movement]) as the dependent variable. I did not use age as a predictor because all sparrows that made these movements were juveniles. Sample size was too small to assess if these movements differed by year (Table 3.1).

### **Migratory survival**

To estimate daily survival in different legs of spring migration, including migratory barriers, I treated the telemetry data as capture-recapture data where sparrows were deployed with tags at capture and tag detections on receivers were recapture events (White et al. 2006). I used data from sparrows tagged in 2018 and 2019 on the wintering

grounds and detected during the spring migratory period (Mar–June). I excluded one sparrow identified during manual tracking on Sable Island to have lost its tag to prevent confounding this tag loss with mortality.

#### *Statistical modelling approach*

I modelled these data using Cormack-Jolly-Seber (CJS) multi-state models with hidden Markov chains (Lebreton and Pradel 2002; Laake 2013; Santostasi et al. 2019). This model estimates two parameters: survival probability ( $S$ ) and detection probability ( $p$ ; probability that a tagged sparrow was detected). Using this approach, the model estimates  $S$  in each state (see below) while accounting for  $p$  (Lebreton et al. 1992). This improves  $S$  estimates because  $p$  will account for differences in the detection rates of tagged sparrows as a result of varying spatial configuration of receivers along the Atlantic Coast, circumstances when a sparrow does not fly sufficiently close to a receiver to be detected, and yearly differences in tag models (higher signal strength will lead to a higher probability of detection) and burst rate (higher burst rates will lead to a higher probability of detection).

To determine if survival probabilities differed spatially across legs of migration, including migratory barriers, I divided the range of Ipswich Sparrows into six spatial states of approximately equal coastline length that included both migratory barriers: Delmarva/NC (state A), Cape May to Cape Cod (state B), GOM (state C), South NS/Bay of Fundy (state D), East NS (state E), and Sable Island (state F; Fig. 3.4). The model also estimates a third parameter, transition probability ( $\Psi$ ; probability that a tagged sparrow will move from one state to another).

#### *Date preparation and capture histories*

I built a daily capture history for each sparrow using the tag detection data (Lebreton et al. 1992). For each day, I determined if a sparrow was detected or not, and if so, what spatial state it was detected in and whether it was detected in one or more state. Because each sparrow can only be assigned to a single state on a given day in the model, in cases where a bird was detected in more than one state on the same day, I either advanced or reduced the date on one receiver to preserve both states in the capture history. For instance, if a sparrow flew from East NS (state E) to Sable Island (state F) on the same day, I advanced the arrival day on Sable Island to the following day. This was

not expected to impact model estimates because the daily detection probability was unaffected by these changes. For each day, I only retained one detection (the first). For instance, if a bird was detected by a receiver 40 times on 1 May, only the first detection on that receiver for that date was retained. Days where sparrows were undetected were coded as 0.

I then assigned each daily detection to an alpha code corresponding to state. For instance, a sparrow tagged on Delmarva/NC (state A), undetected for four days, next detected in the Gulf of Maine (state C) on two days, then in South Nova Scotia/ Bay of Fundy (state D) on one day, would have the capture history: A0000CCD.

### *Statistical analyses*

I fit CJS multi-state models to estimate daily  $S$  in each state,  $p$  in each year, and  $\Psi$ . Estimates are probabilities in the interval from 0 to 1. A burn-in value of 500 and iteration value of 10,000 were used to compute estimates. It was not possible to estimate  $S$  by age, sex, or year due to poor model fit with these added covariates.

Ipswich Sparrows were expected to progress in N and NE directions along the Atlantic Coast during spring migration. Because sparrows were only detected moving in these directions, I fixed almost all  $\Psi$  to 0 for transitions in S or SW non-migratory directions to prevent the model from estimating such biologically improbable transitions (e.g., from state C [GOM] backwards to state A [Delmarva/NC]). The only exception was transitions was permitted between state E (East NS) and state D (East NS/Bay of Fundy) since sparrows were detected making such transitions (see Chapter 2).

The initial model coefficients were effectively 0 for some  $\Psi$ . To improve parameter estimates, these were also fixed to 0 and the model was re-run. To see the final combination of states for which  $\Psi$  was estimated, see Figure 3.5.

Survival estimates from capture-recapture studies typically estimate apparent  $S$ , where emigration from the study population cannot be distinguished from mortality. Accordingly, apparent  $S$  estimates typically underestimate true  $S$ , which is the true survival of study population. I considered  $S$  estimates in my study to be closer to true, rather than apparent because: 1) the entire range of Ipswich Sparrows is monitored by receivers and tagged sparrows should not make movements outside of this range (i.e., no emigration from the study area), and 2) tagged sparrows should return to a small island at

the end of migration where they will be documented (i.e., total surviving number of sparrows was documented).

### **Tag loss and failure**

Tag loss was assessed because CJS models assume marks (here, tags) are retained during the study. Otherwise, tag loss is confounded with mortality. It is typically difficult to validate this assumption due to the challenge of relocating birds over large areas after tagging. However, the restriction of Ipswich Sparrows to Sable Island during breeding allowed me to assess this by observing many tagged sparrows on the island. To assess tag loss, I used detection data from Sable Island receivers and assumed tags were retained by detected sparrows (i.e., tags were not lost after arrival on the island). I also used data from manual telemetry surveys (grid and opportunistic) where tagged sparrows were subsequently detected or observed on Sable Island and visually assessed for tag retention. I calculated tag loss as the proportion of tagged sparrows that had lost tags.

I also assessed tag failure, which can be confounded with tag loss or mortality. Though most tags are guaranteed by the manufacturer to function for a specific duration, this technology can suffer from unexpected failure. It is therefore prudent to assess if tags transmit as expected. I used detection data from Sable Island receivers and considered any detectable tags to be transmitting. I also used data from manual telemetry surveys (grid and opportunistic) where tagged sparrows that were detected or observed on Sable Island had tag transmission assessed using handheld telemetry equipment. I calculated tag failure as the proportion of tagged sparrows with failed tags. I calculated tag failure for all years, and, with 2018 excluded, as tags used in that year failed prematurely and were not representative of typical failure rates (see Tag data validation).

### **Statistical analyses**

Data manipulation was done in program R version 3.6.0 (R Core Team 2019) with packages *motus* (Brzustowski and Lepage 2019), *tidyverse* (Wickham et al. 2019), *geosphere* (Hijmans 2019), and *circular* (Agostinelli and Lund 2017). I did model fitting in base R (function *glm*; GLM). Maps were created using packages *maps* (Becker et al. 2018a), *mapdata* (Becker et al. 2018b), and *ggplot2* (Wickham 2016). Capture-recapture



models were developed in package marked (Laake et al. 2013). I assessed model fit by examining residual plots, and the standard errors (SE) and confidence limits of parameter estimates.

Summary statistics are reported as mean  $\pm$  SD unless otherwise noted.

### **3.4 Results**

Though 128 sparrows were tagged on wintering grounds in 2018 and 2019, and 31 on mainland NS in 2013 and 2019, tag loss and predation reduced the final sample size from 159 sparrows to 153 (see Chapter 2).

#### **Behaviour at the Gulf of Maine barrier**

##### *Pathway at the Gulf of Maine*

Of the sparrows tagged on wintering grounds, 54/124 (43.5%) were detected in eastern Canada (New Brunswick or Nova Scotia) after passing the GOM. Nine (16.7%) of those 54 sparrows used pathways that crossed the GOM, and two (3.7%) used pathways that circumvented the GOM (Fig. 3.6). The remaining 43 (79.6%) sparrows used pathways that were ambiguous or could not be assessed.

Pathway did not differ by sex (GLM:  $\beta_{\text{male}} = -2.3$ , SE = 1.3) or year ( $\beta_{2019} = -0.03$ , SE = 1.4). I could not statistically compare differences by age, but juveniles used both pathways (two circumvented and eight crossed), and, adults used one pathway (zero circumvented and one crossed; Table 3.2).

#### **Behaviour at the Atlantic Ocean barrier**

##### *Pathway to Sable Island*

All sparrows detected making departure flights from the mainland to Sable Island flew from NS (Table 3.1; Fig. 3.7). Flights occurred from East NS (n = 11) or South NS (n = 1). An additional 24 sparrows were detected on Sable Island but the departure from the mainland was not detected by receivers, therefore pathway could not be assigned.

##### *Departure flights*

Flights to Sable Island occurred from 15 April to 7 May in 2013, on 19 April in 2018, and from 28 April to 24 May in 2019. Mean distance flown overwater was  $375 \pm 42$  km (range = 326–482 km; Table 3.2). Flight bearing offset from a true bearing to Sable Island differed by age, with juveniles orienting  $46^\circ \pm 19^\circ$  offset compared to adults (LM;  $\beta_{\text{juvenile}} \pm \text{SE}$ ,  $P = 0.04$ ) but there was no significant effect of sex on flight bearing offset ( $\beta_{\text{male}} = 23.4$ ,  $\text{SE} = 22.0$ ,  $P = 0.32$ ;  $F_{(2,9)} = 2.9$ ,  $P = 0.12$ ,  $r^2 = 25.8\%$ ; Table 3.2; Fig. 3.7).

#### *Abandoned flights to Sable Island*

Eight of 54 sparrows detected in NS (14.8%) made abandoned flights. Of these sparrows, one made three abandoned flights, two made two flights each, and the rest made one flight each. There was no effect of age (GLM;  $\beta_{\text{juvenile}} = 1.34$ ,  $\text{SE} = 0.76$ ,  $P = 0.08$ ) or sex ( $\beta_{\text{male}} = -0.07$ ,  $\text{SE} = 0.72$ ,  $P = 0.92$ ) on this behaviour but there was an effect of year ( $\beta_{2019} = -2.83$ ,  $\text{SE} = 0.76$ ,  $P < 0.001$ ), where sparrows in 2013 were more likely to make abandoned flights than sparrows in 2019.

#### *Non-migratory movements in Nova Scotia*

Eight sparrows made non-migratory movements in directions opposite of what was expected for the season (Fig. 3.8). All such movements originated in East NS after arrival at suitable departure locations to cross the AO barrier, and none occurred elsewhere along the Atlantic Coast. All sparrows that made these movements were juveniles. There was no effect of sex on this behaviour (GLM;  $\beta_{\text{male}} = 0.75$ ,  $\text{SE} = 0.90$ ).

### **Migratory survival**

#### *Survival probability*

S was similar across most states of spring migration. S in Delmarva/NC (state A), Cape May to Cape Cod (state B), GOM (state C), South NS/Bay of Fundy (state D), and Sable Island (state F) ranged from 0.94–0.99. Survival in the remaining state, East NS (state E), was lower at 0.91 (Fig. 3.9).

Only four cases of mortality could be directly confirmed. All occurred in East NS (state E) prior to or during the overwater crossing to Sable Island. Three depredated carcasses were recovered on the mainland. A fourth sparrow was detected by an offshore supply vessel 110 km SW of Sable Island for 5.5 h (presumably resting on the vessel) and

was thereafter undetected, suggesting it died before arrival on Sable Island or it returned to the mainland.

#### *Detection probability*

The daily probability of detecting a sparrow ( $p$ ) was similar in both years in three of the states – Delmarva/NC (state A), GOM (state C), and South NS (state D). In the other three states - Cape May to Cape Cod (state B), East NS (state E), and Sable Island (state F) – estimates were higher in 2019 compared to 2018, which was likely partly driven by the tag manufacturing issue in 2018 (see Methods).

Estimates were lowest in Delmarva/NC (state A), GOM (state C), and South NS (state D), and ranged from 0.02–0.08. Estimates were highest in Cape May to Cape Cod (state B), East NS (state E), and Sable Island (state F), likely due to the high density of receivers in both states and manual tracking on Sable Island, and ranged from 0.24–0.47 (Fig. 3.9).

#### *Transition probability*

The coefficients were effectively 0 for some  $\Psi$  in the original model. This suggests that sparrows did not make movements in non-migratory S or SW directions during spring migration, except from East NS (state E) to South NS (state D). Similarly, sparrows moved along the Atlantic Coast without bypassing large portions of the coastline by flying overwater, except when crossing from Cape May to Cape Cod (state B) to South NS (state D), or, crossing from East NS (state E) to Sable Island (state F).

The  $\Psi$  of sparrows were similar along the Atlantic Coast and ranged from 0.04–0.23. The estimates were considerably higher transitions from East NS (state E) to South NS (state D), and South NS (state D) to East NS (state E) than other states (Fig. 3.9).

#### **Tag loss and failure**

Tag loss rate during migration was low. Of the sparrows assessed on Sable Island at the end of migration, 1/36 sparrows (2.8%, range = 1–88 d post-tagging) had lost their tag.

Tag failure rate was also low, with 4/36 tags (11.1%, range = 1–91 d post-tagging) having failed at the time of assessment. When 2018 tags were excluded, 0/30 tags (0%, range = 1–91 d post-tagging) had failed.

### **3.5 Discussion**

I found that Ipswich Sparrows both circumvented and crossed the first ecological barrier they encountered, the GOM, during spring migration. I was unable to statistically assess age-related differences and did not detect sex-related differences in pathway at this barrier. Sparrows crossed the AO almost exclusively from East NS, therefore I could not assess age- or sex-related differences in pathway at this second barrier. Juveniles had less direct bearings to Sable Island than adults. There were two examples of aberrant behaviours and both occurred in NS before the AO barrier and nowhere else along the migratory route. These behaviours were abandoned flights to Sable Island and non-migratory movements. I did not detect differences in abandoned flights by age or sex. Only juveniles made non-migratory movements, and there were no sex-related differences associated with these movements. I also estimated S along different legs of the Atlantic Coast, revealing relatively higher S at the GOM barrier and lower S at the AO barrier.

Below, I discuss possible explanations for the age-related differences and lack of sex-related differences in behaviour. I also discuss why S may differ along the Atlantic Coast and between barriers. Sample size for many analyses were small, likely due to a combination of a slow tag burst rate (30 s) and tag issues in 2018. Despite this, statistical models fit well and permit discussion about behaviour, but limit my ability to assess some intrinsic differences in behaviour.

#### **Age-related differences in behaviour**

I predicted pathway would differ by age at ecological barriers, with juveniles more likely than adults to circumvent the GOM. Though I was unable to statistically assess differences in pathway by age at the GOM, juveniles both crossed and circumvented this barrier. Similarly, I could not assess difference in pathway by age at the AO because almost all sparrows followed the same pathway and made the obligatory crossing to Sable Island from East NS, the region geographically closest to the island. As predicted, juveniles had less direct flight bearings than adults at the AO, though, I was unable to assess this at the GOM.

Pathway and bearing may differ by age due to endogenous genetic programs (Perdck 1967; Liedvogel et al. 2011) or individual experience (i.e., skills, abilities, and cues learned as birds age; Ralph 1981). In short-lived migrants (e.g., songbirds), juvenile behaviour during their first fall migration is largely under endogenous control (Helbig 1996). This is in contrast to the first spring migration, where individual experience (e.g., navigation skills and knowledge of regional geography) gained during the previous parts of the life cycle can have a strong role in determining behaviour (Berthold 1996, 2001; Thorup et al. 2007) and is thought to largely govern the behaviour of adults (Perdck 1967; Moore 1984; Thorup et al. 2007; Evens et al. 2017).

Individual experience likely explains the age-related behaviour in Ipswich Sparrow pathway at both barriers. In the fall, juveniles circumvent the GOM while adults cross, and they also take shorter pathways at the AO (Crysler et al. 2016). By spring, at least some juveniles cross the GOM and both juveniles and adults take the same pathway at the AO. This suggests that by spring, juveniles may have the appropriate experience to behave similarly to adults with regard to pathway. These results are consistent with studies on Blackpoll Warblers (*Setophaga striata*) where juveniles and adults have different spatial distributions at the GOM in the spring and fall, suggesting age-related pathway use at this barrier (Brown and Taylor 2015; DeLuca et al. 2015). My results add to a small but growing body of evidence in songbirds that pathway at ecological barriers may change with age (Sutherland 1998; Thorup et al. 2007; Brown and Taylor 2015; Crysler et al. 2016). This is similar to the greater variation in the migratory timing of juveniles compared to adults, implying that timing is refined with experience as birds age (Battley 2006).

However, other intrinsic factors can also contribute to pathway. For instance, birds in poorer condition may be less likely to cross barriers than those in better condition (Schmaljohann and Naef-Daenzer 2011; Covino et al. 2015). If juvenile sparrows are in similar condition to adults in the spring, they may be equally likely to take the same pathways at the GOM and AO. Although I did not test this directly, I did not find that the condition of juvenile and adult sparrows tagged in NS differed ( $n = 31$ ; S Bliss unpubl. data). Thus, it is unlikely that differences in condition explain the observed pattern.

Individual experience may also explain the age-related differences in flight bearing at the AO barrier. In the fall, juvenile sparrows have more variability in bearing than adults at the AO (Crysler 2015). My results suggest that by the end of spring migration, there still remains a difference in the navigation ability of juveniles and adults. Because adults have successfully flown to Sable Island at least once, it follows that they have more accurate bearings to this small target (40 km x 1 km) compared to juveniles that have never made flights in this direction. Similar differences have been observed between age classes of other songbirds, where juveniles are less accurate navigators than adults (Moore 1984; Thorup et al. 2003).

I did not detect age-related differences in abandoned flights to Sable Island. I therefore suggest these flights may be explained by alternative factors that likely affect both age cohorts equally. Sparrows may have difficulty locating Sable Island with no visual cues over an open seascape. Or, may be responding to poor weather conditions (e.g., strong head or cross winds) overwater that increase the energetic costs of flight. Or, may encounter fog conditions that limit the distance from which Sable Island can be seen. Though sparrows were more likely to make these flights in 2013 compared to 2019, the small sample size of this analysis ( $n = 8$ ) makes it difficult to interpret what such year differences may imply. However, despite the small sample size, the fact that at least 14.8% of sparrows in NS made these attempts signals this is not a rare behaviour.

Only juveniles were detected making non-migratory movements. Such movements are well-documented in other songbirds and may be an adaptive strategy to avoid intraspecific competition at barrier edges where birds may temporarily accumulate (Åkesson et al. 1996; Alerstam 2001; Smolinsky et al. 2013; Sjöberg 2015). Alternatively, juveniles may make non-migratory movements because they have poorer understanding of stopover site locations due to individual experience and must search for them (Woodrey and Moore 1997; Chernetsov 2006). This is consistent with other songbirds where juveniles are more likely to make such movements than adults (Bowlin et al. 2005). However, the small sample size for this analysis ( $n = 8$ ) makes it difficult to exclude the possibility that adults may also make such movements.

Collectively, these results for age-related behaviours are mixed. They suggest that by the first spring migration, juveniles behave similarly to adults in some ways, possibly

explained by learned experience during the previous parts of the life cycle. However, in other ways, juveniles still behave differently than adults likely due to remaining gaps in experience.

### **Sex-related differences in behaviour**

My ability to assess sex-related differences in behaviour was mixed. I predicted pathway would differ by sex at the GOM, with males more likely to cross the barrier than females. Contrary to my prediction, I did not detect sex-related differences in pathway at the GOM and was unable to assess differences at the AO. Consistent with my prediction, I did not detect sex-related differences in bearing at the AO but was unable to assess this at the GOM. I did not detect sex-related differences in non-migratory movements or abandoned flights.

There are several explanations for why I did not detect effects of sex on behaviour at barriers. Pathway and non-migratory movements may differ by sex if males and females are in different condition. If females are excluded from high-quality stopover sites by males (Rappole et al. 1976) they may be relatively leaner and lack reserves to support overwater flights across barriers and instead make a series of shorter flights (Dierschke et al. 2005). Or, they may be forced to make non-migratory movements to find alternative fuelling sites. My results suggest that females and males may be in similar condition. Alternatively, different seasonal pressures between sexes could, for instance, make males more likely to cross barriers to reduce migratory duration and allow early arrival on breeding grounds compared to females (Dierschke et al. 2005; Briedis et al. 2018). A lack of sex-related differences in my results suggests that seasonal pressures did not contribute to behaviour at barriers

In contrast, I found evidence for sex-related differences in the timing of migration (see Chapter 2) that may explain the lack of sex effects at barriers. Male Ipswich Sparrows migrated earlier than females, which presumably reduces temporal overlap and thus competition at stopover sites between the sexes. Thus, the sexes may be in similar condition during migration. Similarly, there may be weak selection for males to cross barriers to reduce the duration of migration compared to females (see Chapter 2).

It is unsurprising there was no effect of sex on bearing as males and females are not expected to have different navigational abilities (e.g., Smetzer et al. 2017).

### **Migratory survival**

To my knowledge, this is the first study to assess daily survival probabilities (S) along an entire migratory route, including at barriers. Therefore, it is difficult to compare my results to previous studies, which have estimated overall survival rates when passing barriers. For example, Swainson's Thrush (*Catharus ustulatus*) survival when passing the Gulf of Mexico ranges from 10–60% (Ward et al. 2018) and survival in other groups such as raptors can be as low as 30% (Strandberg et al. 2010).

There are many factors that drive survival at barriers, including the ability of a bird to acquire large fat reserves (Russell 2005; Ward et al. 2018), navigate correctly (Alerstam 2001), and avoid predators at stopover sites (Hope et al. 2020), weather conditions (Schmaljohann and Naef-Daenzer 2011; Deppe et al. 2015), and hazards (e.g., wind turbines; (Drewitt and Langston 2006).

Contrary to my prediction, S at the GOM ecological barrier was higher (0.97) compared to other legs of coastline. This may be because this barrier is relatively small (~400 km) and thus presents only a moderate energetic challenge to sparrows. It is also possible that if stopover habitat in this area is of high quality and weather conditions are fair when birds pass this barrier, survival may be high. In contrast, S in the Cape May to Cape Cod state was unexpectedly low (0.94). This could be due to factors such as poor-quality stopover habitat stemming from high anthropogenic pressure in this state compared to the GOM (Crossett et al. 2004), and/or higher predator pressure in this area. The reverse of these factors may explain higher S (0.98) in South NS.

Consistent with my prediction, S was lowest in East NS before the AO (0.91) compared to other states. Low survival in East NS could be caused by either mortality on the mainland or during overwater flights to Sable Island. There is no reason to suspect that sparrows have higher mortality in East NS compared to South NS where S was highest (0.98; e.g., different predator densities), which suggests lower S may be driven by unsuccessful flights across the AO to Sable Island.



There are several explanations why S at the AO barrier is lower than other states. The flight may be physically challenging, especially at the end of migration. But apparent survival of juveniles at this barrier in fall migration is ~85%, suggesting the flight is within the physical ability of the most inexperienced sparrows (Cryslar 2015). Alternatively, sparrows may have difficulty finding a small island when flying offshore with no cues. Heavy fog around Sable Island in the spring may further limit visual cues and navigational cues such as stars, which in other songbirds creates disorientation (Panuccio et al. 2019). Tailwinds may be less favourable in the spring compared to the fall. Or, interactions with the six oil and gas platforms < 100 km from Sable Island could create disorientation through light sources or cause mortality through collisions (Russell 2005). Indeed, there was direct evidence in 2013 that two tagged sparrows landed on these platforms, and there is anecdotal evidence of dead sparrows found on these platforms (Ronconi et al. 2015). Though I am unable to determine if sparrows are attracted to platforms or simply take advantage of these structures to rest, these events suggest sparrows could be susceptible to platform attraction.

Finally, sparrows may have been unable to cope with the energetic costs of carrying tags during the overwater flight to Sable Island. Tag effects might be especially important in this leg because there is no opportunity to circumvent this barrier and the flight occurs at the end of migration. However, I cautiously suggest this is an unlikely explanation. Most studies report no effects of radio-tags on songbird survival (e.g., Anders et al. 1998; Powell et al. 1998; Naef-Daenzer et al. 2001; Lang et al. 2002; Suedkamp Wells et al. 2003; Cardinal 2005; Anich et al. 2009; Townsend et al. 2012; Naef-Daenzer and Gruebler 2014). Three studies have reported reduced survival, but in each case it appears to be associated with defunct tag design or tagging young nestlings (Samuel and Fuller 1996; Dougill et al. 2000; Mattsson et al. 2006). Further, what is known about tag effects indicates that effect sizes are usually small (reviewed in Bodey et al. 2018; Geen et al. 2019). Accordingly, a tag effect driving reduced survival at the AO to the extent seen here would be unusual. However, I cannot exclude this possibility.

Survival can be underestimated due to erroneous right-censoring of data. In my study, this could occur by tag loss, tag failure, or failure to detect tagged sparrows. However, tag loss and failure rates were low, any premature tag failure in 2018 was

accounted for by the  $p$  (detection probability) parameter in the CJS model. Therefore, I have no reason to expect that my survival estimates are not robust.

### **Implications for Ipswich Sparrow ecology**

Ipswich Sparrows crossed to Sable Island exclusively from East NS, and within East NS, from beaches near Halifax (~375 km to Sable Island) despite the northernmost parts of the shore being closer to the island (~160 km). This is consistent with anecdotal observations of a build-up of Ipswich Sparrow numbers near Halifax but not elsewhere in NS in the spring (Stobo and McLaren 1975; Sullivan et al. 2014). This pattern, plus the tendency of sparrows to return to these same beaches after abandoned flights, indicate that beaches near Halifax are suitable to support flights to Sable Island. It is unclear what factors make this area suitable to support flights. Stopover sites near Halifax may be of higher quality than elsewhere along the East NS and allow sparrows to acquire the necessary fuel reserves to fly to Sable Island, and/or, weather conditions (e.g., wind direction) in this area may be more favourable to support flights to the island.

To my knowledge, there are no other direct examples of abandoned flight attempts at ecological barriers made by songbirds. Abandoned flights have been documented in raptors crossing the Sahara Desert (Strandberg et al. 2010) and Gulf of Mexico (McGrady et al. 2006) and have been attributed to poor weather. Because Ipswich Sparrows are unique in needing to locate a small island after a barrier crossing, the challenges associated with locating such a target may explain this behaviour.

The higher survival and lack of aberrant behaviours (non-migratory movements and abandoned flights) may suggest that the GOM is easier to pass than the AO and may not represent an appreciable barrier to the migration of Ipswich Sparrows. This is similar to other small overwater barriers such as Lake Erie (~200 km across) which also does not appear to be an appreciable barrier to songbirds (Sanders and Mennill 2014). However, the low density of receivers in the GOM in 2018 and 2019 meant that aberrant behaviours may not have been detected at this barrier if they occurred. This limits my ability to understand the difficulty of passing the GOM. The lower  $S$  at the AO, coupled with two aberrant behaviours before the barrier, suggest that crossing this barrier does present a meaningful challenge to sparrows and is possibly related to the unique challenges of

breeding on an offshore island. This presents an interesting ecological situation. Ipswich Sparrows have evolved to breed on a small offshore island presumably because this confers ecological advantages (e.g., absence of predators; Stobo and McLaren 1975). Assuming conditions have not drastically changed since this behaviour evolved, the advantages of breeding on Sable Island must continue to outweigh the lower survival incurred when flying to the island.

### **3.5 Conclusions**

The two ecological barriers that Ipswich Sparrows must pass during spring migration created some age-related differences, but no sex-related differences, in behaviour. These results suggest that although the distances across the GOM and AO are relatively small, both are significant enough to shape population-level differences in the behaviour of migrating songbirds. The age-related differences indicate that by spring, juvenile sparrows have developed skills and abilities similarly to adults, likely from learned experience. In contrast, the lack of sex-related differences indicates that males and females may have similar ability to contend with the challenge of passing these ecological barriers, which may be due to temporal segregation during migration.

It is somewhat unclear how challenging it is for sparrows to pass the GOM given my limited ability to assess aberrant behaviours at this barrier. Though, higher S at the GOM suggests that this barrier may be less challenging to pass than the AO and indeed other legs of the Atlantic Coast that do not include barriers. Lower S and aberrant behaviours suggest that the AO presents a true barrier to migrating sparrows. The factors that make this a true barrier to migration are likely associated with the difficulty of locating Sable Island rather than the size of the barrier itself.

### 3.6 Tables

**Table 3.1** – Sample size (n) of Ipswich Sparrows by age, sex, and year for each statistical analysis related to migratory behaviour at barriers.

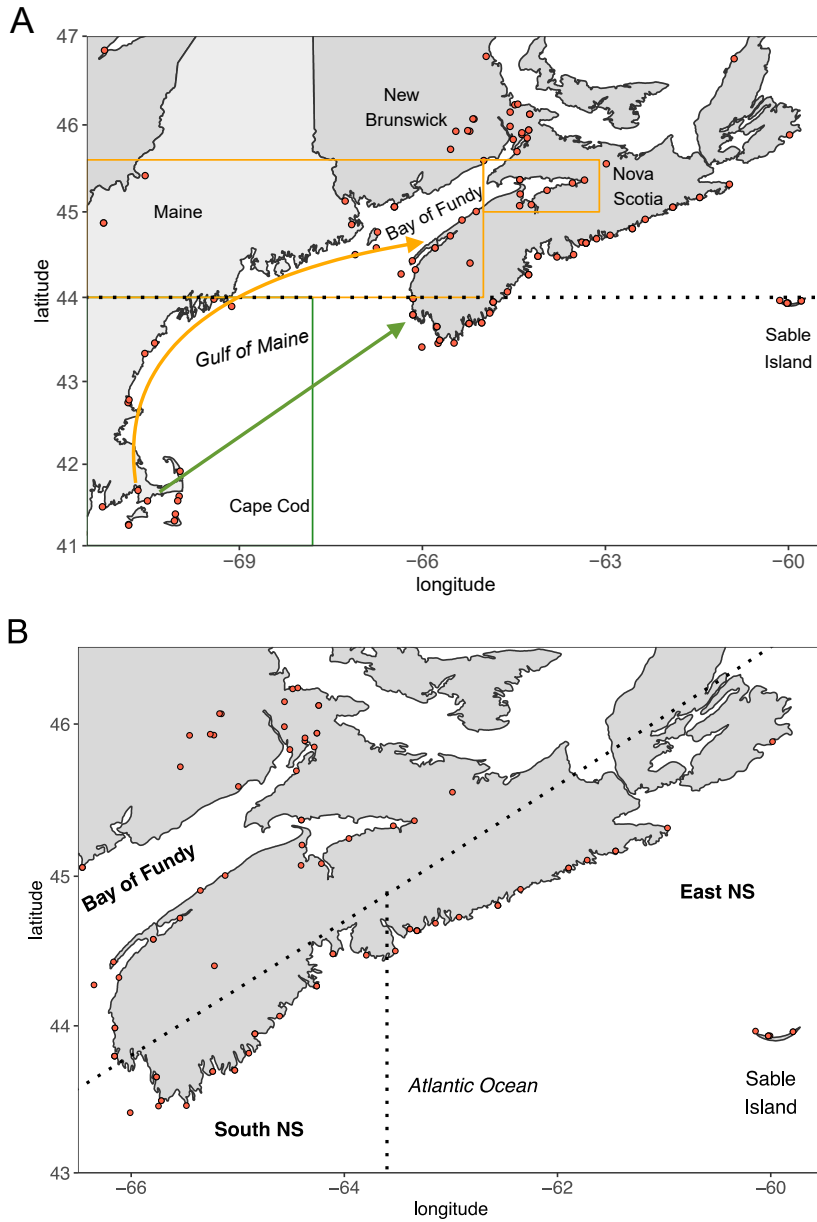
Event	Year	Age			Sex		Total
		Adult	Juvenile	Unknown	Male	Female	
Pathway to Canada (GOM)	2013	-	-	-	-	-	-
	2018	1	3	0	3	1	4
	2019	0	11	0	5	6	11
Pathway to Sable Island (AO)	2013	6	0	0	5	1	6
	2018	0	1	0	1	0	1
	2019	1	4	0	3	2	5
Departure bearing	2013	6	0	0	5	1	6
	2018	0	1	0	1	0	1
	2019	1	4	0	3	2	5
Abandoned flights	2013	4	2	0	6	0	6
	2018	-	-	-	-	-	-
	2019	0	2	0	1	1	2
Non-migratory movements	2013	-	-	-	-	-	-
	2018	-	-	-	-	-	-
	2019	0	8	0	6	2	8

**Table 3.2** – Effect sizes (mean  $\pm$  SD) by sex, age, and year for Ipswich Sparrow migratory behaviour at barriers.

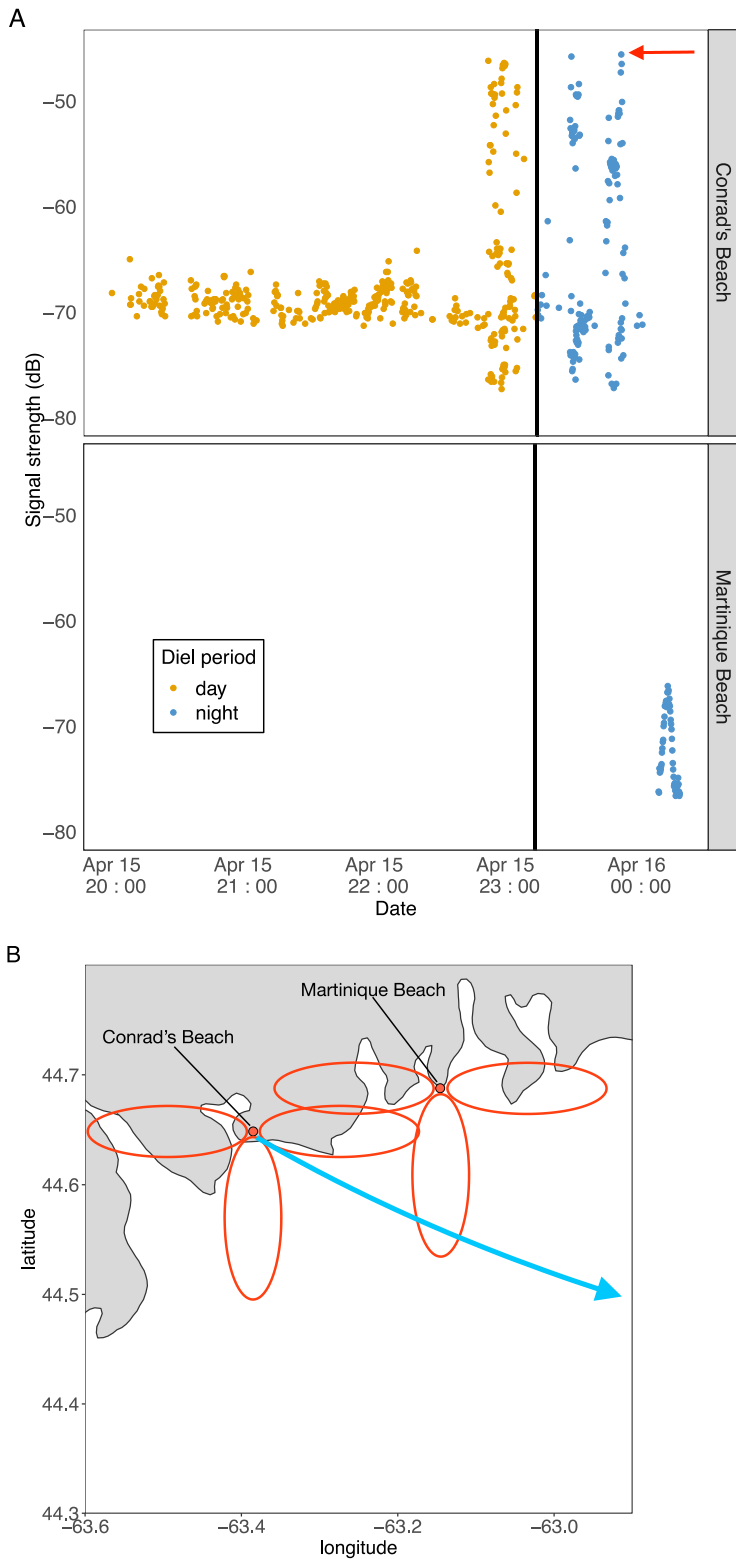
Event	Sex		Age		Year			n
	Male	Female	Adult	Juvenile	2013	2018	2019	
Distance at AO <sup>a</sup>	383 $\pm$ 41	352 $\pm$ 43	376 $\pm$ 21	373 $\pm$ 65	381 $\pm$ 20	482	346 $\pm$ 21	12
Duration at AO <sup>b</sup>	8.5 $\pm$ 3.8	8.2 $\pm$ 4.2	9.3 $\pm$ 3.8	7.2 $\pm$ 3.7	8.1 $\pm$ 2.3	6.2	9.2 $\pm$ 5.4	12
Bearing offset <sup>c</sup>	52 $\pm$ 42	44 $\pm$ 14	33 $\pm$ 33	73 $\pm$ 30	35 $\pm$ 36	108	57 $\pm$ 28	12

<sup>a</sup> km, <sup>b</sup> h, <sup>c</sup> o

### 3.7 Figures

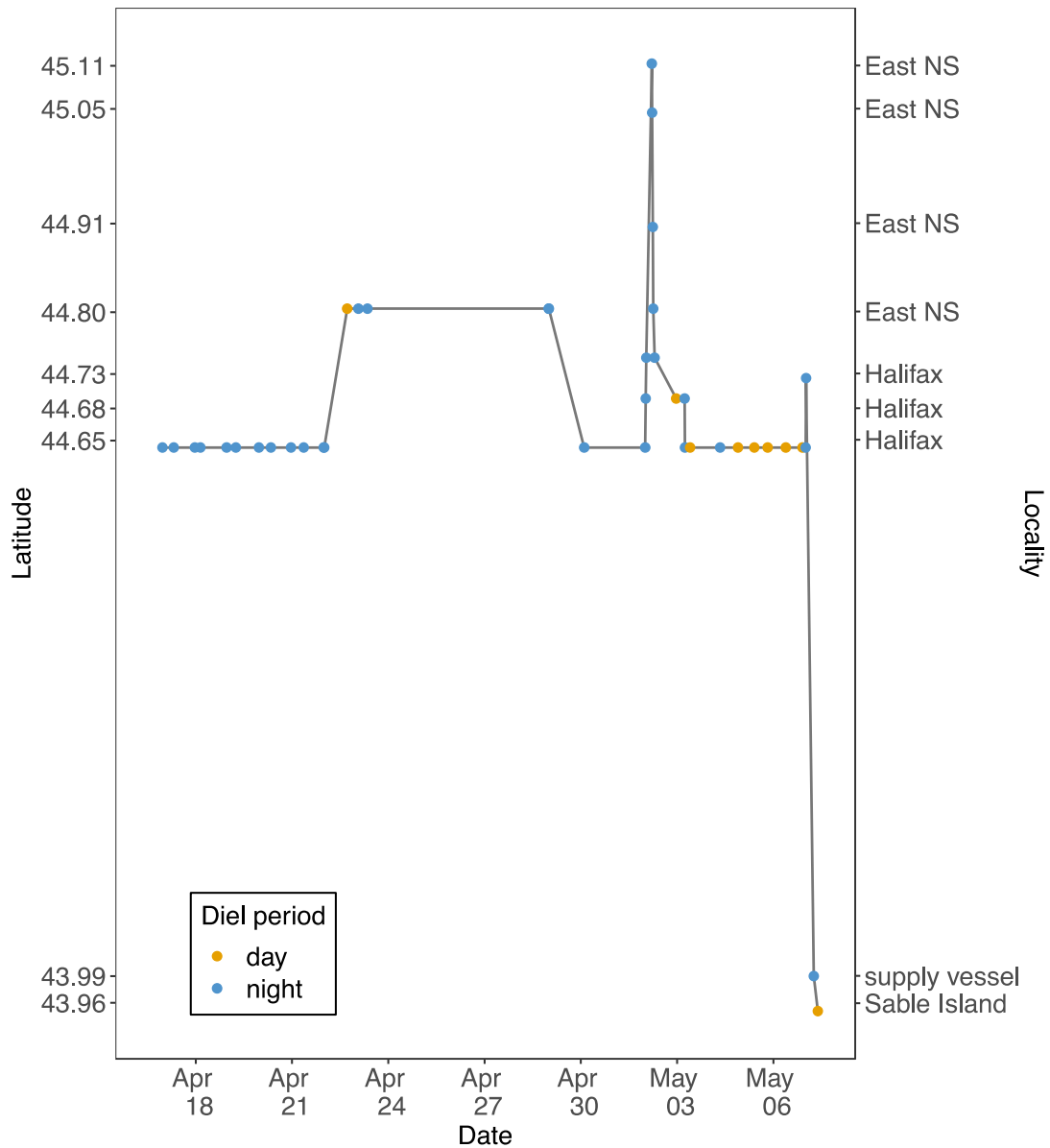


**Figure 3.1** – A) Two regions in the GOM delineated by dotted lines: S of 44°N (green rectangle) and N of 44°N (orange rectangle). The orange arrow indicates an example of a sparrow circumventing the GOM, while the green arrow is an example a sparrow crossing the GOM. Red dots indicate receivers. B) Three regions in NS delineated by dotted lines: Bay of Fundy, South NS, and East NS. Red dots indicate receivers.



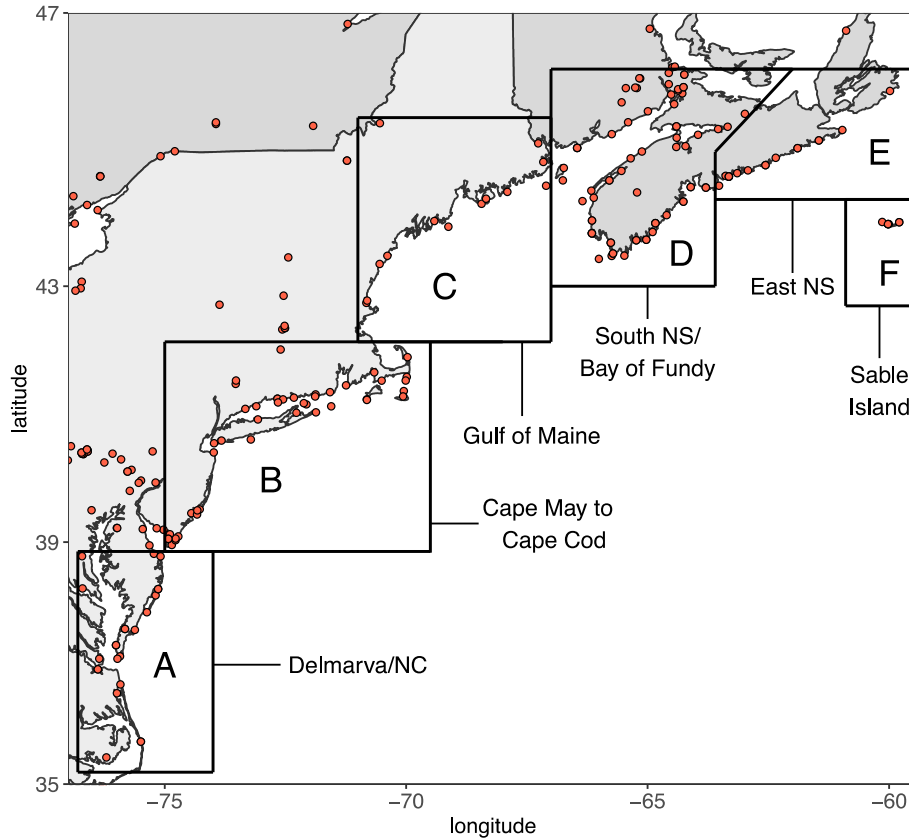
**Figure 3.2** – Example of a departure flight from the mainland to Sable Island. A) Each dot represents a detection on a receiver. This sparrow was detected throughout a day at Conrad's Beach, NS (top panel; 44.65°N, -63.39°W; last 3 h shown). The peaks in signal strength suggest it departed from Conrad's Beach shortly after sunset (black line) at

20:45:30 (red arrow) and was subsequently detected on a flyby of Martinique Beach, NS (bottom panel; 44.69°N, -63.15°W) 26.7 km away. Consequently, Conrad's Beach was coded as the departure site. This sparrow arrived on Sable Island 7.1 h later (not shown). Note signal strength values are measured in decibels (dB; log scale). Larger numbers indicate higher strength. B) The same departure flight shown on a map. Conrad's Beach and Martinique Beach receivers are indicated by closed red circles. Open red ovals indicate estimated antenna ranges of each receiver. The blue line shows a hypothetical flight path of the bird from the mainland to Sable Island. Based on the signal strength values and detection pattern, after leaving Conrad's Beach the bird flew through the beam of an antenna at the Martinique Beach receiver but was unlikely to have actually moved to Martinique Beach.



**Figure 3.3** – Example of an abandoned flight to Sable Island. This sparrow stopped over at two beaches near Halifax, NS for a combined 14.6 d before it departed 0.76 h after sunset at a bearing of 101° and arrived overnight in the north part of the East NS region of NS. It was then detected on a flyby of every receiver in East NS over the following 2.1 h overnight moving SW as it returned to the same site near Halifax and made another 3.8 d stopover. After that stopover, it was then briefly detected over the AO by a supply vessel before arriving on Sable Island.

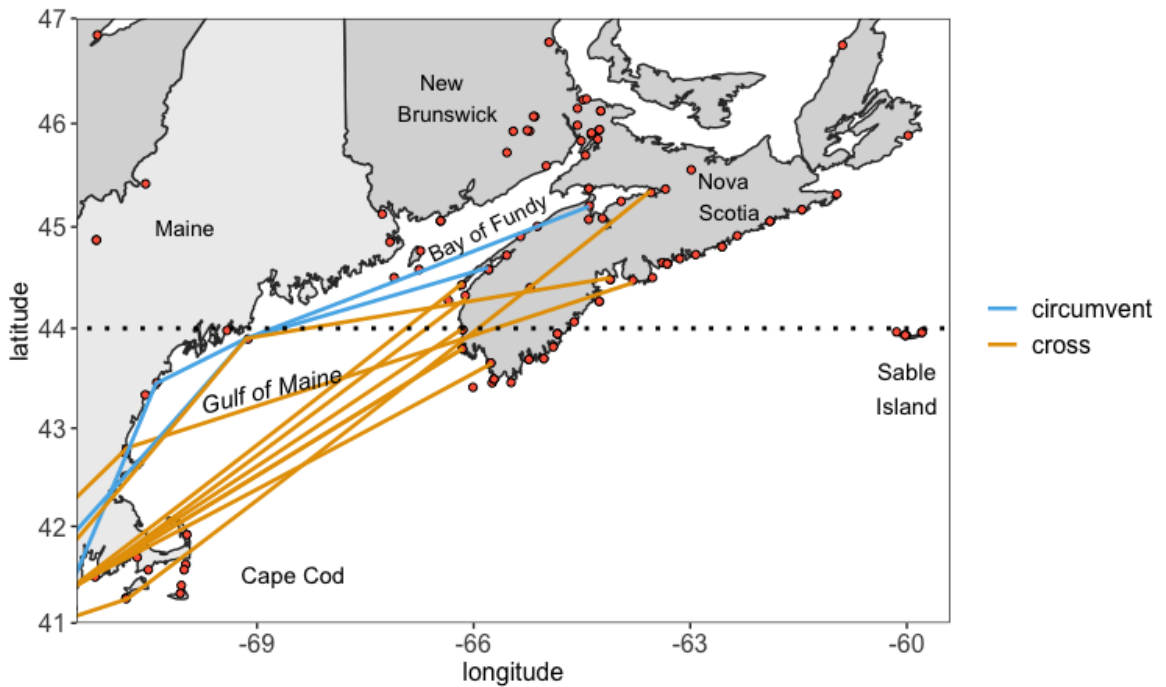




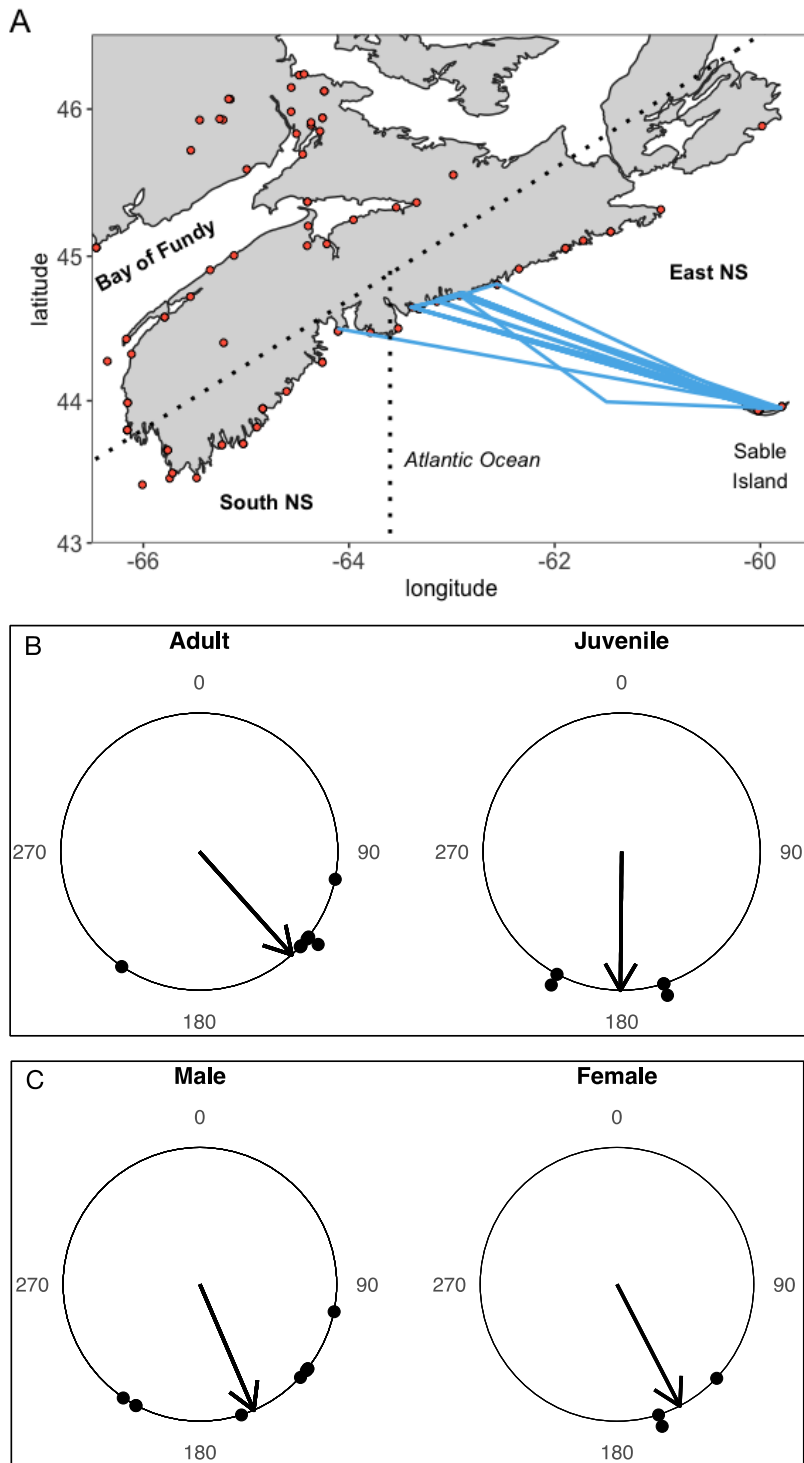
**Figure 3.4** – Six spatial states (geographic locations used by sparrows) used in CJS multi-state models of Ipswich Sparrow survival during spring migration. Each state is assigned an alpha code from A to F. Red dots indicate receivers active in 2018 and 2019.

$$\begin{bmatrix}
 & A & B & C & D & E & F \\
 A & 1 & 1 & 0 & 0 & 0 & 0 \\
 B & 0 & 1 & 1 & 1 & 0 & 0 \\
 C & 0 & 0 & 1 & 1 & 0 & 0 \\
 D & 0 & 0 & 0 & 1 & 1 & 0 \\
 E & 0 & 0 & 0 & 1 & 1 & 0 \\
 F & 0 & 0 & 0 & 0 & 0 & 1
 \end{bmatrix}$$

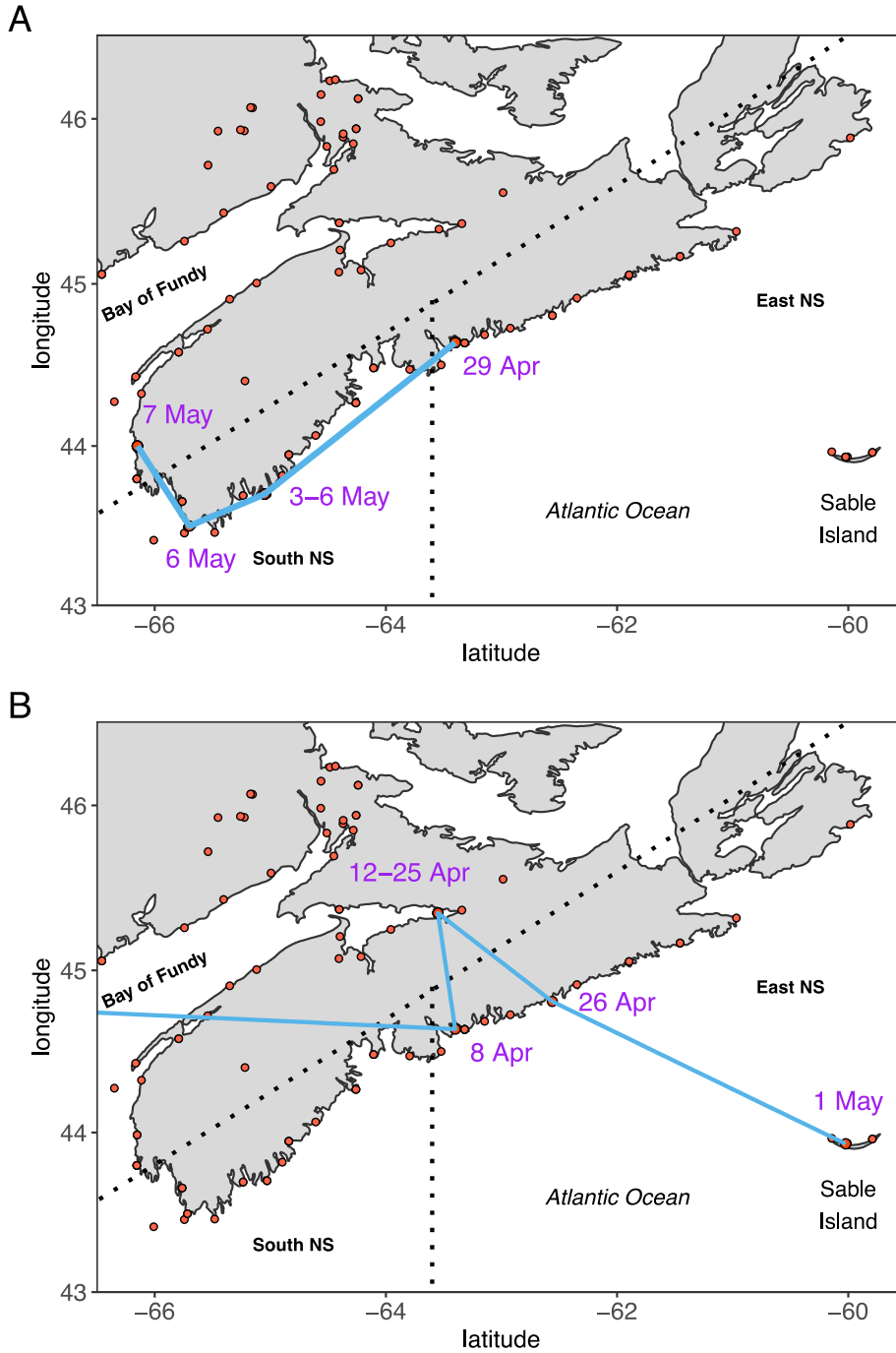
**Figure 3.5** – Matrix of  $\Psi$  between spatial states along the Atlantic Coast in the final CJS multi-state model. 1s indicate state combinations where  $\Psi$  was estimated, and 0s indicate combinations where  $\Psi$  was not estimated. The matrix is read as transitioning from a state in a row to the state in a column.



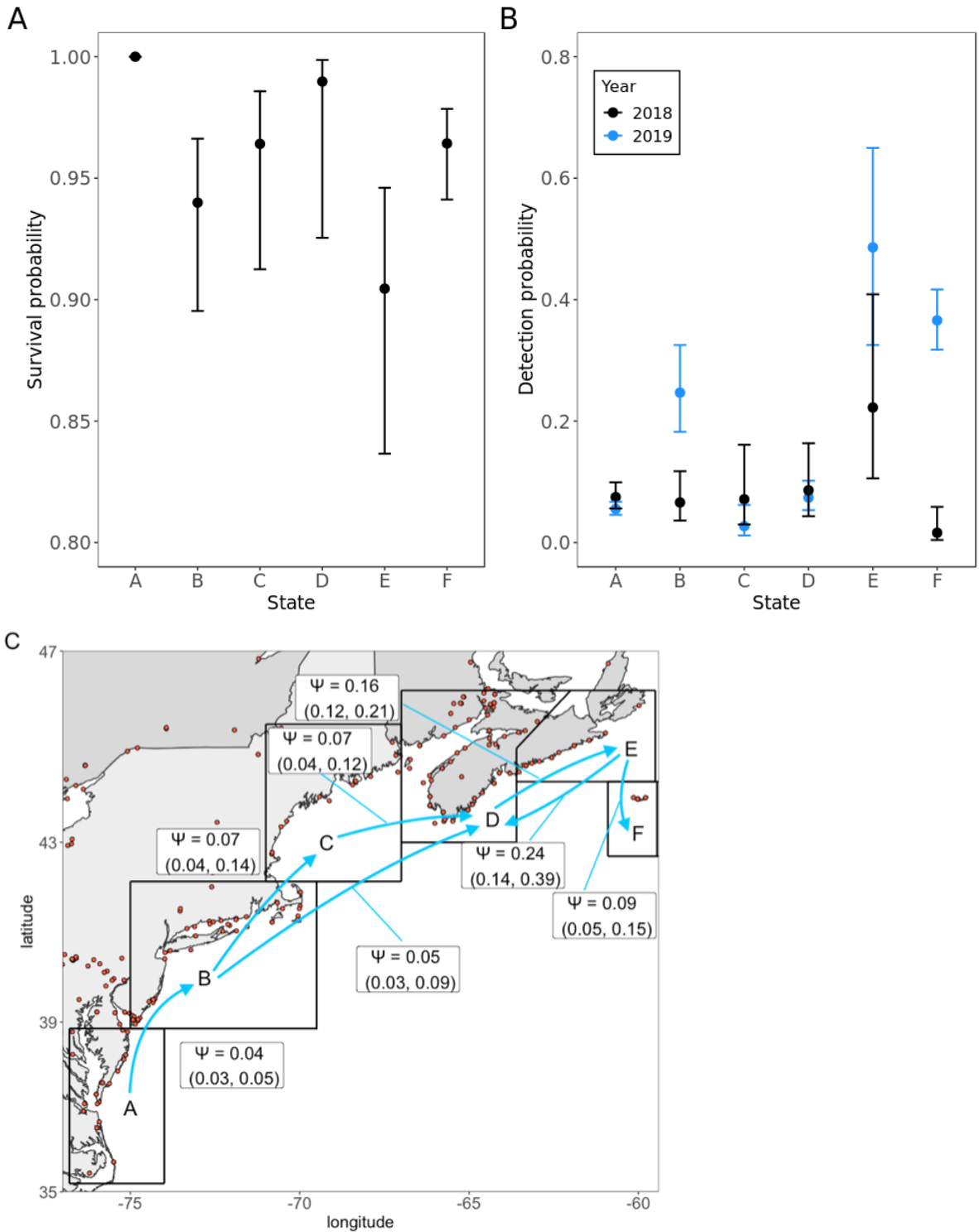
**Figure 3.6** – Ipswich Sparrow pathways in the GOM. Blue tracks show sparrows that circumvented the barrier while gold tracks show sparrows that crossed. The N and S regions are delineated by the dotted line at 44°N. Dark gray shading indicates Canada while light gray shading indicates the USA. Red dots indicate receivers. Only the first hour after arrival in Canada is shown. Ambiguous movements and sparrows that did not arrive in Canada are excluded.



**Figure 3.7** – A) Departure flights ( $\geq 5$  m/s) to Sable Island across the AO barrier, indicated by blue tracks. Only the last hour of detections on the mainland is shown. Sparrows that did not arrive on Sable Island are excluded. Regions are delineated by dotted lines. Receivers are indicated by red dots. B) Bearings of departure flights to Sable Island by age. Arrows represent the mean bearing. C) Bearing of departure flights to Sable Island by sex. Arrows represent the mean bearing.



**Figure 3.8** – Examples of non-migratory movements of sparrows in NS. Each map represents the movement of one sparrow. These sparrows arrived at appropriate departure locations for Sable Island in East NS before making movements in non-migratory directions to either South NS or the Bay of Fundy. Regions in NS are delineated by dotted lines. The sparrow in map A was tagged in NS partway through migration, and the sparrow in map B was tagged on wintering grounds in the eastern USA.



**Figure 3.9** – A) Scatterplot of  $S$  across spatial states, and B) Scatterplot of  $p$  across spatial states in both study years. State A includes Delmarva/NC, state B includes Cape May to Cape Cod, state C includes the GOM, state D includes South NS/Bay of Fundy, and state F includes Sable Island. C) Transition probability ( $\Psi$ ) across different spatial states during spring migration. Blue arrows indicate transitions between states. Values in brackets indicate the 95% lower and upper confidence limits of each  $\Psi$  estimate.

## CHAPTER 4: GENERAL DISCUSSION

### Summary of findings

This study focused on the behaviour and survival of a North American songbird, Ipswich Sparrow, during spring migration along the Atlantic Coast. I tagged 128 sparrows on wintering grounds and 31 sparrows partway through migration in NS and used automated radio-telemetry to track the tagged sparrows.

In Chapter 2, I showed that Ipswich Sparrows follow an energy-minimizing strategy. Sparrows migrated slowly and appeared to keep daily energetic costs low. This is likely related to the short distance of their migration (~1500 km), possibly coupled with high predation pressure along the coast, moult migration, or a relative lack of selection pressure to arrive early to Sable Island due to abundant resources on the island. I did not detect differences in strategy by age or sex.

In Chapter 3, I showed that sparrows both crossed and circumvented the GOM in the spring and only took one pathway across the AO from East NS to Sable Island. Sparrows made aberrant behaviours before the AO but nowhere elsewhere along the migratory pathway, and juveniles were more likely to make one of these behaviours. Age-related differences in behaviour are likely attributable to individual learning by juveniles in the first year of life. By spring their behaviour is largely, but not fully, comparable to adults. I did not detect sex-related differences in behaviour. S was higher at the GOM compared to other parts of the coastline, and lowest at the AO. Collectively, the behaviour and survival differences indicate that despite being geographically small, the AO barrier may present a significant challenge for sparrows to pass. This is possibly due the unique challenges associated with arriving on Sable Island related to navigation and overwater hazards.

I also identified several differences in the spring migration of sparrows compared to the fall. In the spring, juveniles both cross and circumvent the GOM and in fall appear to only circumvent the barrier (Crysler et al. 2016). Juvenile bearings when crossing the AO in both the spring and fall are more variable than adult bearings. Lastly, survival when crossing the AO in the spring appears to be lower than in the fall.

## **Conservation implications**

The results of my study have conservation implications for Ipswich Sparrow, a species of *Special Concern* in Canada and listed at a variety of levels in US states (COSEWIC 2009). Generally, the Atlantic Coast of the USA is under heavy development (Crossett et al. 2004; Bigelow and Borchers 2017) that threatens much of the migratory habitat used by sparrows (COSEWIC 2009). The energy-minimizing strategy used during spring highlights the need for broad-scale conservation of habitat that supports sparrows during this migration. Further, because the success of crossing a migratory barrier is related to the availability of food resources before the barrier, there is a particular need to protect habitat along the edges of the GOM and AO (Petit 2000; Sheehy et al. 2011).

Nocturnal migrants are also susceptible to hazards at ecological barriers such as oil and gas platforms (Loss et al. 2013), which appear to incur direct mortality at the AO (Ronconi et al. 2015).

## **Suggestions for future research**

A low density of receivers in the GOM limited my ability to assign pathway to sparrows at this barrier, and to detect aberrant behaviours. Together, this limited my ability to understand the relative challenge of passing the GOM for sparrows compared to the AO. Further research should assess these behaviours at the GOM, and if they differ by age or sex. This would require expansion of the existing receiver network throughout this area.

It would also be beneficial to conduct a longitudinal behaviour study where the same juveniles are tracked during fall and spring migration (i.e., over a single year). This would provide additional insight into how the behaviour of a single individual may change with age, and consistency in these changes across the population. This could be achieved by using more durable material for tag harnesses such as Teflon ribbon, which would ensure tags remain on birds for the necessary period of time.

Further, it would be helpful to understand overall spring migratory survival rates because there is poor understanding of such rates in general in songbirds. This would also allow assessment of where during the annual cycle the population of Ipswich Sparrows is the most limited (i.e., winter, spring migration, breeding, or fall migration) as there is

some information on winter and breeding survival rates (Stobo and McLaren 1975; Ross and McLaren 1981; McLaren and Horn 2006; Horn 2007). I did not do this because it was beyond the scope of my study. However, it could be calculated using a simulation with the daily survival probability ( $S$ ), detection probability ( $p$ ), and transition probability ( $\psi$ ) parameters estimated in my model.

Similarly, parameter estimates in the CJS survival model could be improved by collecting additional years of data. This could be done by deploying more radio-tags on wintering sparrows in future years. Or, by using techniques such as a colour bands to mark birds on wintering grounds and recapture them along the Atlantic Coast during spring migration, including on Sable Island.

### **Limitations**

This study took place over three years and had a relatively large size for a radio-telemetry study. However, the tag issues in experienced in 2018 resulted in fewer detections of tagged sparrows than expected and reduced sample size. Consequently, I could not fit two-way or higher interactions in my analyses. The combination of small sample size and lack of interactions makes it difficult to interpret some intrinsic differences in behaviour and make assumptions about the general patterns of behaviour of Ipswich Sparrows during spring.

A lack of information on seasonal survival throughout the life cycle of Ipswich Sparrows makes it difficult to understand how survival probability during spring migration may specifically affect population dynamics. The lower survival at the AO barrier might suggest that a demographic bottleneck exists at this location during spring migration, but, without additional contextual information on seasonal survival there is too much uncertainty to make this assertion.



## REFERENCES

- Able KP. 1969. Fall migration in coastal Louisiana and the evolution of migration patterns in the Gulf region. *The Wilson Bulletin*. 84:231–242.
- Adamík P, Emmenegger T, Briedis M, Gustafsson L, Henshaw I, Krist M, Laaksonen T, Liechti F, Procházka P, Salewski V, et al. 2016. Barrier crossing in small avian migrants: individual tracking reveals prolonged nocturnal flights into the day as a common migratory strategy. *Scientific Reports*. 6:21560.
- Agostinelli C, Lund U. 2017. R package 'circular': circular statistics. R package version 0.4-93.
- [AGRGR] Applied Geomatics Research Group. 2011. Sable Island, Nova Scotia 2009 Topography and Land Cover Atlas. Middleton (Canada). 122 pp.
- Åkesson S. 2016. Flying with the winds: differential migration strategies in relation to winds in moth and songbirds. *Journal of Animal Ecology*. 85(1):1–4.
- Åkesson S, Alerstam T, Hedenström A. 1996. Flight initiation of nocturnal passerine migrants in relation to celestial orientation conditions at twilight. *Journal of Avian Biology*. 27(2):95–102.
- Åkesson S, Karlsson L, Walinder G, Alerstam T. 1996. Bimodal orientation and the occurrence of temporary reverse bird migration during autumn in South Scandinavia. *Behavioral Ecology and Sociobiology*. 38(5):293–302.
- Åkesson S, Walinder G, Karlsson L, Ehnbohm S. 2002. Nocturnal migratory flight initiation in Reed Warblers *Acrocephalus scirpaceus*: effect of wind on orientation and timing of migration. *Journal of Avian Biology*. 33(4):349–357.
- Åkesson S, Klassen R, Holmgren J, Fox JW, Hedenström A. 2012. Migration routes and strategies in a highly aerial migrant, the Common Swift *Apus apus*, revealed by light-level geolocators. *PLoS ONE*. 7(7):1–9.
- Alerstam T. 1991. *Bird migration*. Cambridge (UK): Cambridge University Press.
- Alerstam T. 2001. Detours in bird migration. *Journal of Theoretical Biology*. 209(3):319–331.
- Alerstam T. 2009. Flight by night or day? Optimal daily timing of bird migration. *Journal of Theoretical Biology*. 258(4):530–536.
- Alerstam T, Hedenström A. 1998. The development of bird migration theory. *Journal of Avian Biology*. 29(4):343–369.

- Alerstam T, Hedenström A, Åkesson S. 2003. Long-distance migration: evolution and determinants. *Oikos*. 103(2):247–260.
- Anders AD, Faaborg J, Thompson FR. 1998. Postfledging dispersal, habitat use, and home-range size of juvenile Wood Thrushes. *The Auk*. 115(2):349–358.
- Anderson AM, Duijns S, Smith PA, Friis C, Nol E, Anderson AM. 2019. Migration distance and body condition influence shorebird migration strategies and stopover decisions during southbound migration. *Frontiers in Ecology and Evolution*. 7:251.
- Anich NM, Benson TJ, Bednarz JC. 2009. Effect of radio transmitters on return rates of Swainson's Warblers. *Journal of Field Ornithology*. 80(2):206–211.
- Ankney CD, MacInnes CD. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. *The Auk*. 95:459–471.
- Bairlein F, Norris DR, Nagel R, Bulte M, Voigt CC, Fox JW, Hussell DJT, Schmaljohann H. 2012. Cross-hemisphere migration of a 25 g songbird. *Biology Letters*. 8(4):505–507.
- Baker AJ, Gonzalez PM, Piersma T, Niles LJ, de Lima Serrano do Nascimento I, Atkinson PW, Clark NA, Minton CDT, Peck MK, Aarts G. 2004. Rapid population decline in red knots: fitness consequences of decreased refuelling rates and late arrival in Delaware Bay. *Proceedings of the Royal Society B: Biological Sciences*. 271(1541):875–882.
- Barron DG, Brawn JD, Weatherhead PJ. 2010. Meta-analysis of transmitter effects on avian behaviour and ecology. *Methods in Ecology and Evolution*. 1(2):180–187.
- Bates D, Maechler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*. 67(1):1–48.
- Battley PF. 2006. Consistent annual schedules in a migratory shorebird. *Biology Letters*. 2(4):517–520.
- Bayly NJ. 2012. Fall migration of the Veery (*Catharus fuscescens*) in northern Colombia: determining the energetic importance of a stopover site. *The Auk*. 129(3):449–459.
- Becker RA, Wilks AR, Brownrigg R, Minka TP, Deckmyn A. 2018a. maps: draw geographical maps. R package version 3.3.0.
- Becker RA, Wilks AR, Brownrigg R. 2018b. mapdata: extra map databases. R package version 2.3.0.

- Bennett RE, Rodewald AD, Rosenberg KV. 2019. Overlooked sexual segregation of habitats exposes female migratory landbirds to threats. *Biological Conservation*. 240:108266.
- Berthold P. 1996. *Control of bird migration*. London (UK): Chapman & Hall.
- Berthold P. 2001. *Bird migration: a general survey*. Oxford (UK): Oxford University Press.
- Bigelow DP, Borchers A. 2017. Major uses of land in the United States, 2012. United States Department of Agriculture. Washington (USA). 65 pp.
- Bodey TW, Cleasby IR, Bell F, Parr N, Schultz A, Votier SC, Bearhop S. 2018. A phylogenetically controlled meta-analysis of biologging device effects on birds: Deleterious effects and a call for more standardized reporting of study data. *Methods in Ecology and Evolution*. 9(4):946–955.
- Bolshakov CV, Bulyuk VN, Mukhin A, Chernetsov N. 2003. Body mass and fat reserves of Sedge Warblers during vernal nocturnal migration: departure versus arrival. *Journal of Field Ornithology*. 74(1):81–89.
- Bolus RT, Diehl RH, Moore FR, Deppe JL, Ward MP, Zenzal TJ. 2017. Swainson's Thrushes do not show strong wind selectivity prior to crossing the Gulf of Mexico. *Scientific Reports*. 7:14280.
- Bowlin M, Cochran W, Wikelski M. 2005. Biotelemetry of New World thrushes during migration: physiology, energetics and orientation in the wild. *Integrative and Comparative Biology*. 45:295–304.
- Bowlin MS, Bisson I, Shamoun-Baranes J, Reichard JD, Sapir N, Marra P, Kunz TH, Wilcove DS, Hedenström A, Guglielmo CG, et al. 2010. Grand challenges in migration biology. *Integrative and Comparative Biology*. 50(3):261–279.
- Briedis M, Hahn S, Krist M, Adamík P. 2018. Finish with a sprint: evidence for time-selected last leg of migration in a long-distance migratory songbird. *Ecology and Evolution*. 1–10.
- Brown JM, Taylor P. 2015. Adult and hatch-year blackpoll warblers exhibit radically different regional-scale movements during post-fledging dispersal. *Biology Letters*. 11:20150593.
- Bruderer B, Liechti F. 1998. Flight behaviour of nocturnally migrating birds in coastal areas: crossing or coasting. *Journal of Avian Biology*. 29(4):499–507.

- Brust V, Michalik B, Hüppop O. 2019. To cross or not to cross - thrushes at the German North Sea coast adapt flight and routing to wind conditions in autumn. *Movement Ecology*. 7:32.
- Brzustowski J, LePage D. 2019. motus: fetch and use data from the Motus Wildlife Tracking System. R package version 3.0.0.
- Buler JJ, Moore FR. 2011. Migrant-habitat relationships during stopover along an ecological barrier: extrinsic constraints and conservation implications. *Journal of Ornithology*. 152(Suppl 1):101–112.
- Cadahía L, Labra A, Knudsen E, Nilsson A, Lampe HM, Slagsvold T, Stenseth NC. 2017. Advancement of spring arrival in a long-term study of a passerine bird: sex, age and environmental effects. *Oecologia*. 184(4):917–929.
- Callo PA, Morton ES, Stutchbury BJM. 2013. Prolonged spring migration in the Red-eyed Vireo (*Vireo olivaceus*). *The Auk*. 130(2):240–246.
- Calvert AM, Walde SJ, Taylor P. 2009. Nonbreeding-season drivers of population dynamics in seasonal migrants: conservation parallels across taxa. *Avian Conservation and Ecology*. 4(2):5.
- Cardinal SN. 2005. Conservation of southwestern Willow Flycatchers: home range and habitat use by an endangered passerine. [M. Sc. thesis]. Flagstaff (USA): Northern Arizona University.
- Chambert T, Miller DAW, Nichols JD. 2015. Modeling false positive detections in species occurrence data under different study designs. *Ecology*. 96(2):332–339.
- Chernetsov N. 2006. Habitat selection by nocturnal passerine migrants en route: mechanisms and results. *Journal of Ornithology*. 147(2):185–191.
- Cohen EB, Barrow WC, Buler JJ, Deppe JL, Farnsworth A, Marra P, McWilliams SR, Mehlman DW, Wilson RR, Woodrey MS, et al. 2017. How do en route events around the Gulf of Mexico influence migratory landbird populations? *The Condor*. 119(2):327–343.
- Coppack T, Pulido F. 2009. Proximate control and adaptive potential of protandrous migration in birds. *Integrative and Comparative Biology*. 49(5):493–506.
- [COSEWIC] Committee on the Status of Endangered Wildlife in Canada. 2009. Assessment and status report on the Savannah Sparrow princeps subspecies *Passerculus sandwichensis* in Canada. Ottawa (Canada). vi + 21 pp.
- Costantini D, Møller AP. 2013. A meta-analysis of the effects of geolocator application on birds. *Current Zoology*. 59(6):697–706.

- Covino KM, Holberton RL, Morris SR. 2015. Factors influencing migratory decisions made by songbirds on spring stopover. *Journal of Avian Biology*. 46(1):73–80.
- Covino KM, Horton KG, Morris SR. 2020. Seasonally specific changes in migration phenology across 50 years in the Black-throated Blue Warbler. *The Auk*. 137:1–11.
- Crewe TL, Deakin JE, Beauchamp AT, Morbey YE. 2019a. Detection range of songbirds using a stopover site by automated radio-telemetry. 0(0):1–14.
- Crewe TL, Crysler ZJ, Taylor PD. 2019b. Motus R Book. Port Rowan (Canada). [[https://motus.org/MotusRBook/.](https://motus.org/MotusRBook/)]
- Crossett K, Culliton T, Wiley P, Goodspeed T. 2004. Population trends along the coastal United States: 1980–2008. Coastal Trends Report Series. National Oceanic and Atmospheric Administration. Washington (USA). 45 pp.
- Crossin GT, Phillips RA, Trathan PN, Fox DS, Dawson A, Wynne-Edwards KE, Williams TD. 2012. Migratory carryover effects and endocrinological correlates of reproductive decisions and reproductive success in female albatrosses. *General and Comparative Endocrinology*. 176(2):151–157.
- Crysler Z. 2015. Breeding ground dispersal and fall migratory movements of Ipswich Sparrows. [M. Sc. thesis]. Wolfville (Canada): Acadia University.
- Crysler Z, Ronconi R, Taylor P. 2016. Differential fall migratory routes of adult and juvenile Ipswich Sparrows (*Passerculus sandwichensis princeps*). *Movement Ecology*. 4(3):1–8.
- Dale C. 2008. Links between the winter and breeding seasons in a short-distance migrant, the Ipswich Sparrow. [M. Sc. thesis]. Halifax (Canada): Dalhousie University.
- Dänhardt J, Lindström Å. 2001. Optimal departure decisions of songbirds from an experimental stopover site and the significance of weather. *Animal Behaviour*. 62(2):235–243.
- Delingat J, Bairlein F, Hedenström A. 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.
- Delmore KE, Fox JW, Irwin DE. 2012. Dramatic intraspecific differences in migratory routes, stopover sites and wintering areas, revealed using light-level geolocators. *Proceedings of the Royal Society B: Biological Sciences*. 279(1747):4582–4589.

- DeLuca W, Woodworth B, Rimmer C, Marra P, Taylor P, McFarland K, Mackenzie S, Norris D. 2015. Transoceanic migration by a 12 g songbird. *Biology Letters*. 11:20141045.
- Deppe JL, Ward MP, Bolus RT, Diehl RH, Celis-Murillo A, Zenzal TJ, Moore FR, Benson TJ, Smolinsky JA, Schofield LN, et al. 2015. Fat, weather, and date affect migratory songbirds' departure decisions, routes, and time it takes to cross the Gulf of Mexico. *Proceedings of the National Academy of Sciences of the United States of America*. 112(46):E6331–E6338.
- Deutschlander ME, Muheim R. 2009. Fuel reserves affect migratory orientation of thrushes and sparrows both before and after crossing an ecological barrier near their breeding grounds. *Journal of Avian Biology*. 40(1):85–89.
- Dierschke V, Mendel B, Schmaljohann H. 2005. Differential timing of spring migration in northern wheatears *Oenanthe oenanthe*: hurried males or weak females? *Behavioral Ecology and Sociobiology*. 57(5):470–480.
- Dingle H, Drake VA. 2007. What is migration? *BioScience*. 57(2):113–121.
- Dodrill J, Gilmore R. 1978. Land birds in the stomachs of Tiger Sharks *Galeocerdo cuvieri* (Peron and Lesueur). *The Auk: Ornithological Advances*. 95(3):585–586.
- Dossman BC, Mitchell GW, Norris DR, Taylor P, Guglielmo CG, Matthews SN, Rodewald PG. 2016. The effects of wind and fuel stores on stopover departure behavior across a migratory barrier. *Behavioral Ecology*. 27(2):567–574.
- Dougill SJ, Johnson L, Banko PC, Goltz DM, Wiley MR, Semones JD. 2000. Consequences of antenna design in telemetry studies of small passerines. *Journal of Field Ornithology*. 71(3):385–388.
- Drake A, Rock CA, Quinlan SP, Martin M, Green DJ. 2014. Wind speed during migration influences the survival, timing of breeding, and productivity of a neotropical migrant, *Setophaga petechia*. *PLoS ONE*. 9(5):1–8.
- Drewitt A, Langston R. 2006. Assessing the impacts of wind farms on birds. *Ibis*. 148:29–42.
- Ellegren H. 1991. Stopover ecology of autumn migrating Bluethroats *Luscinia s. svecica* in relation to age and sex. *Ornis Scandinavica*. 22(4):240–348.
- Evans DR. 2018. The post-fledging survival and movements of juvenile Barn Swallows (*Hirundo rustica*): an automated telemetry approach. [Ph. D. thesis]. London (Canada): University of Western Ontario.

- Evens R, Beenaerts N, Witters N, Artois T. 2017. Repeated migration of a juvenile European Nightjar *Caprimulgus europaeus*. *Journal of Ornithology*. 158(3):881–886.
- Faaborg J, Holmes RT, Anders A, Bildstein KL, Dugger KM, Gauthreaux SA, Heglund P, Hobson KA, Jahn A, Johnson DH. 2010. Conserving migratory landbirds in the New World: do we know enough? *Ecological Applications*. 20(2):398–418.
- Faaborg J, Holmes RT, Anders D, Bildstein K. 2010. Recent advances in understanding migration systems of New World land birds. *Ecological Monographs*. 80(1):3–48.
- Fair J, Paul E, Jones J, Barrett Clark A, Davie C, Kaiser G. 2010. Guidelines to the use of wild birds in research. Ornithological Council. Washington (USA). 215 pp.
- Farmer AH, Wiens JA. 1999. Models and reality: time-energy trade-offs in Pectoral Sandpiper (*Calidris melanotos*) migration. *Ecology*. 80(8):2566–2580.
- Fraser KC, Stutchbury BJM, Kramer P, Silverio C, Barrow J, Newstead D, Mickle N, Shaheen T, Mammenga P, Applegate K, et al. 2013. Consistent range-wide pattern in fall migration strategy of Purple Martin (*Progne subis*), despite different migration routes at the Gulf of Mexico. *The Auk*. 130(2):291–296.
- Gangoso L, López-López P, Grande JM, Mellone U, Limiñana R, Urios V, Ferrer M. 2013. Ecological specialization to fluctuating resources prevents long-distance migratory raptors from becoming sedentary on islands. *PLoS ONE*. 8(4):8–11.
- Geen GR, Robinson RA, Baillie SR. 2019. Effects of tracking devices on individual birds - a review of the evidence. *Journal of Avian Biology*. e01823.
- Godfrey JD, Bryant DM, Williams MJ. 2003. Radio-telemetry increases free-living energy costs in the endangered Takahe *Porphyrio mantelli*. *Biological Conservation*. 114(1):35–38.
- Gómez C, Bayly NJ, Norris DR, Mackenzie SA, Rosenberg K V, Taylor P, Hobson KA, Cadena CD. 2017. Fuel loads acquired at a stopover site influence the pace of intercontinental migration in a boreal songbird. *Scientific Reports*. 7(1):1–11.
- González-Prieto AM. 2018. The relative importance of native forest and shade-growing coffee plantations for habitat use, individual fitness and migration strategies of overwintering neotropical migrant songbirds in Colombia. [Ph. D. thesis]. Saskatoon (Canada): University of Saskatchewan.
- Gow EA, Done TW, Stutchbury BJM. 2011. Radio-tags have no behavioral or physiological effects on a migratory songbird during breeding and molt. *Journal of Field Ornithology*. 82(2):193–201.

- Griffiths R, Double MC, Orr K, Dawson RJG. 1998. A DNA test to sex most birds. *Molecular Ecology*. 7(8):1071–1075.
- Gudmundsson GA, Lindström Å, Alerstam T. 1991 Optimal fat loads and long-distance flights by migrating knots *Calidris canutus*, sanderlings *C. alba* and turnstones *Arenaria interpres*. *Ibis*. 133:140–152.
- Guilford T, Freeman R, Boyle D, Dean B, Kirk H, Phillips R, Perrins C. 2011. A dispersive migration in the Atlantic Puffin and its implications for migratory navigation. *PLoS ONE*. 6(7).
- Guilford T, de Perera TB. 2017. An associative account of avian navigation. *Journal of Avian Biology*. 48(1):191–195.
- Gwinner E. 1996. Circadian and circannual programmes in avian migration. *Journal of Experimental Biology*. 199(1):39–48.
- Gwinner E. 2003. Circannual rhythms in birds. *Current Opinion in Neurobiology*. 13(6):770–778.
- Hake M, Kjellen N, Alerstam T. 2003. Age-dependent migration strategy in honey buzzards *Pernis apivorus* tracked by satellite. *Oikos*. 103(2):385–396.
- Handel CM, Gill RE. 2010. Wayward youth: trans-Beringian movement and differential southward migration by juvenile Sharp-tailed Sandpipers. *Arctic*. 63(3):273–288.
- Hedenström A. 2008. Adaptations to migration in birds: behavioural strategies, morphology and scaling effects. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 363(1490):287–299.
- Hedenström A, Alerstam T. 1997. Optimum fuel loads in migratory birds: distinguishing between time and energy minimization. *Journal of Theoretical Biology*. 189:227–234.
- Helbig AJ. 1996. Genetic basis, mode of inheritance and evolutionary changes of migratory directions in palearctic warblers (Aves: Sylviidae). *Journal of Experimental Biology*. 199(1):49–55.
- Hewson C, Thorup K, Pearce-Higgins JW, Atkinson PW. 2016. Population decline is linked to migration route in the Common Cuckoo. *Nature Communications*. 7:1–8.
- Hijmans RJ. 2019. geosphere: spherical trigonometry. R package version 1.5-10.



- Hope DD, Lank DB, Smith PA, Paquet J, Hope D. 2020. Migrant Semipalmated Sandpipers (*Calidris pusilla*) have over four decades steadily shifted towards safer stopover locations. *Frontiers in Ecology and Evolution*. 8(3).
- Horn AG. 2007. Preliminary report on the 2006 census of Ipswich Sparrows. Halifax (Canada). 11 pp.
- Horn AG, Dale C. 2007. Wintering location and breeding success of individual Ipswich sparrows: 2006 progress report. Unpublished report for the Sable Island Preservation Trust. Halifax (Canada). 2 pp.
- Horton KG, Van Doren BM, Stepanian PM, Farnsworth A, Kelly JF. 2016. Seasonal differences in landbird migration strategies. *The Auk*. 133(4):761–769.
- Hüppop O, Dierschke J, Exo KM, Fredrich E, Hill R. 2006. Bird migration studies and potential collision risk with offshore wind turbines. *Ibis*. 148:90–109.
- Irvine RJ, Leckie F, Redpath SM. 2007. Cost of carrying radio transmitters: a test with racing pigeons *Columba Livia*. *Wildlife Biology*. 13(3):238–243.
- Iverson GC, Warnock SE, Butler RW, Bishop MA, Warnock N. 1996. Spring migration of Western Sandpipers along the Pacific Coast of North America: a telemetry study. *The Condor*. 98(1):10–21.
- Jakubas D, Wojczulanis-Jakubas K. 2010. Sex- and age-related differences in the timing and body condition of migrating Reed Warblers *Acrocephalus scirpaceus* and Sedge Warblers *Acrocephalus schoenobaenus*. *Naturwissenschaften* 97:505–511.
- Jorge PE, Sowter D, Marques PAM. 2011. Differential annual movement patterns in a migratory species: effects of experience and sexual maturation. *PLoS ONE*. 6(7):e22433.
- Karlsson H, Nilsson C, Bäckman J, Alerstam T. 2012. Nocturnal passerine migrants fly faster in spring than in autumn: a test of the time minimization hypothesis. *Animal Behaviour*. 83(1):87–93.
- Kenward RE. 2001. A manual for wildlife radiotracking. London (UK): Academic Press.
- Kokko H. 1999. Competition for early arrival in migratory birds. *Journal of Animal Ecology*. 68:940–950.
- Kokko H, Gunnarsson TG, Morrell LJ, Gill JA. 2006. Why do female migratory birds arrive later than males? *Journal of Animal Ecology*. 75(6):1293–1303.

- Kramer GR, Streby HM, Peterson SM, Lehman JA, Buehler DA, Wood PB, McNeil DJ, Larkin JL, Andersen DE. 2017. Nonbreeding isolation and population-specific migration patterns among three populations of Golden-winged Warblers. *The Condor*. 119(1):108–121.
- Kullberg C, Fransson T, Jakobsson S. 1996. Impaired predator evasion in fat Blackcaps (*Sylvia atricapilla*). *Proceedings of the Royal Society B: Biological Sciences*. 263:1671–1675.
- La Sorte FA, Fink D. 2017. Migration distance, ecological barriers and en-route variation in the migratory behaviour of terrestrial bird populations. *Global Ecology and Biogeography*. 26(2):216–227.
- La Sorte FA, Fink D, Hochachka WM, DeLong JP, Kelling S. 2014. Spring phenology of ecological productivity contributes to the use of looped migration strategies by birds. *Proceedings of the Royal Society B: Biological Sciences*. 281:20140984.
- La Sorte FA, Fink D, Hochachka WM, Kelling S. 2016. Convergence of broad-scale migration strategies in terrestrial birds. *Proceedings of the Royal Society B: Biological Sciences*. 283: 20152588.
- Laake JL. 2013. Capture-recapture analysis with hidden Markov models. National Oceanic and Atmospheric Administration. Seattle (USA). v + 34 pp.
- Laake JL, Johnson DS, Conn PB. 2013. marked: an R package for maximum-likelihood and MCMC analysis of capture-recapture data. *Methods in Ecology and Evolution*. 4:885-890.
- Lack D. 1968. Bird migration and natural selection. *Oikos*. 19(1):1–9.
- Lang D, Powell LA, Krementz D, Conroy M. 2002. Wood Thrush movements and habitat use: effects of forest management for Red-cockaded Woodpeckers. *The Auk*. 119(1):109–124.
- Lebreton J-D, Burnham KP, Clobert J, Anderson DR. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs*. 62(1):67–118.
- Lebreton JD, Pradel R. 2002. Multistate recapture models: modelling incomplete individual histories. *Journal of Applied Statistics*. 29(1):67–118.
- Lemke HW, Tarka M, Klaassen RHG, Åkesson M, Bensch S, Hasselquist D, Hansson B. 2013. Annual cycle and migration strategies of a trans-Saharan migratory songbird: a geolocator study in the Great Reed Warbler. *PLoS ONE*. 8(10):1–10.

- Liechti F, Bruderer B. 1998. The relevance of wind for optimal migration theory. *Journal of Avian Biology*. 29(4):561–568.
- Liedvogel M, Åkesson S, Bensch S. 2011. The genetics of migration on the move. *Trends in Ecology and Evolution*. 26(11):561–569.
- Lightfoot H. 2014. Factors influencing decisions on birds during fall migration in the Gulf of Maine region. Acadia University. [M. Sc. thesis]. Wolfville (Canada): Acadia University.
- Lindström A, Hasselquist D, Bensch S, Grahn M. 1990. Asymmetric contests over resources for survival and migration: a field experiment with bluethroats. *Animal Behaviour* 40(3):453–461.
- Lindström Å, Alerstam T. 1992. Optimal fat loads in migrating birds: a test of the time-minimization hypothesis. *The American Naturalist*. 140(3):477–491.
- Lok T, Overdijk O, Piersma T. 2015. The cost of migration: spoonbills suffer higher mortality during trans-Saharan spring migrations only. *Biology Letters*. 11:20140944.
- Longcore T, Smith PA. 2013. On avian mortality associated with human activities. *Avian Conservation Ecology*. 8:8–11.
- Loss SR, Will T, Marra PP. 2013. Estimates of bird collision mortality at wind facilities in the contiguous United States. *Biological Conservation*. 168:201–209.
- Marra P. 1998. The causes and consequences of sexual habitat segregation in a migrant bird during the non-breeding season. [Ph. D. thesis]. Hanover (USA): Dartmouth College.
- Marra P, Cohen EB, Loss SR, Rutter JE, Tonra CM. 2015. A call for full annual cycle research in animal ecology. *Biology Letters*. 11:20150552.
- Mattsson BJ, Meyers JM, Cooper RJ. 2006. Detrimental impacts of radiotransmitters on juvenile Louisiana Waterthrushes. *Journal of Field Ornithology*. 77(2):173–177.
- McGrady MJ, Young GS, Seegar WS. 2006. Migration of a Peregrine *Falco Falco peregrinus* over water in the vicinity of a hurricane. *Ring and Migration*. 23(2):80–84.
- McKinnon E, Fraser KC, Stanley CQ, Stutchbury BJ. 2014. Tracking from the tropics reveals behaviour of juvenile songbirds on their first spring migration. *PLoS ONE*. 9(8).

- McKinnon E, Fraser KC, Stutchbury BJ. 2013. New discoveries in landbird migration using geolocators, and a flight plan for the future. *The Auk*. 130(2):211–222.
- McKinnon E, Love OP. 2018. Ten years tracking the migrations of small landbirds: lessons learned in the golden age of bio-logging. *The Auk*. 135(4):834–856.
- McLaren IA, Horn AG. 2006. The Ipswich Sparrow: past, present, and future. *Birding*. 38:52–59.
- Mehlman D, Mabey S, Ewert D, Duncan C, Abel B, Cimprich D, Sutter R, Woodrey M. 2005. Conserving stopover sites for forest-dwelling migratory landbirds. *The Auk*. 122(4):1281–1290.
- Mitchell GW, Woodworth B, Taylor P, Norris DR. 2015. Automated telemetry reveals age specific differences in flight duration and speed are driven by wind conditions in a migratory songbird. *Movement Ecology*. 3(1):19.
- Møller AP. 1994. Phenotype-dependent arrival time and its consequences in a migratory bird. *Behavioral Ecology and Sociobiology*. 35(2):115–122.
- Moore FR. 1984. Age-dependent variability in the migratory orientation of the Savannah Sparrow (*Passerculus sandwichensis*). *The Auk*. 101(4):875–880.
- Moore FR. 2018. Biology of landbird migrants: a stopover perspective. *The Wilson Journal of Ornithology*. 130(1):1–12.
- Moore FR, Mabey S, Woodrey M. 2003. Priority access to food in migratory birds: age, sex and motivational asymmetries. In: Berthold P, Gwinner E, Sonnenschein E, eds. *Avian Migration*. New York (USA): Springer.
- Moore FR, Covino KM, Lewis WB, Zenzal TJ, Benson TJ. 2017. Effect of fuel deposition rate on departure fuel load of migratory songbirds during spring stopover along the northern coast of the Gulf of Mexico. *Journal of Avian Biology*. 48:123–132.
- Morbe Y, Coppack T, Pulido F. 2012. Adaptive hypotheses for protandry in arrival to breeding areas: a review of models and empirical tests. *Journal of Ornithology*. 153(Suppl 1):207–215.
- Morton ML. 2002. The Mountain White-crowned Sparrow: migration and reproduction at high altitude. *Studies in Avian Biology*. 24:1–236.
- Mueller T, O’Hara RB, Converse SJ, Urbanek RP, Fagan WF. 2013. Social learning of migratory performance. *Science*. 341:999–1002.

- Murray DL. 2006. On improving telemetry-based survival estimation. *The Journal of Wildlife Management*. 70(6):1530–1543.
- Naef-Daenzer B, Gruebler MU. 2014. Effects of radio-tag characteristics and sample size on estimates of apparent survival. *Animal Biotelemetry*. 2(2):2–8.
- Naef-Daenzer B, Widmer F, Nuber M. 2001. A test for effects of radio-tagging on survival and movements of small birds. *Avian Science*. 1(1):15–23.
- Neudorf DL, Pitcher TE. 2016. Radio transmitters do not affect nestling feeding rates by female Hooded Warblers. *Journal of Field Ornithology*. 68(1):64–68.
- Newton I. 2004. Population limitation in migrants. *Ibis*. 146(2):197–226.
- Newton I. 2006. Can conditions experienced during migration limit the population levels of birds? *Journal of Ornithology*. 147(2):146–166.
- Newton I. 2007. Weather-related mass-mortality events in migrants. *Ibis*. 149(3):453–467.
- Newton I. 2008. *The migration ecology of birds*. London (UK): Academic Press.
- Nickerson C, Ebel R, Borchers S, Carriazo F. 2007. Major uses of land in the United States. United States Department of Agriculture Economic Research Service [cited 1 Jan 2020]. <https://www.ers.usda.gov/data-products/major-land-uses.aspx>.
- Nilsson C, Bäckman J, Alerstam T. 2014. Seasonal modulation of flight speed among nocturnal passerine migrants: differences between short- and long-distance migrants. *Behavioral Ecology and Sociobiology*. 68(11):1799–1807.
- Nilsson C, Klaassen RHG, Alerstam T. 2013. Differences in speed and duration of bird migration between spring and autumn. *American Naturalist*. 181(6):837–845.
- Nudds T, Sjöberg K. 1989. Effects of radio transmitters on the foraging behavior of Barn Swallows. *The Wilson Bulletin*. 101(3):505–506.
- Owen M, Black J. 1989. Factors affecting the survival of Barnacle Geese on migration from the breeding grounds. *Journal of Animal Ecology*. 58(2):603–617.
- Panuccio M, Dell’Omo G, Bogliani G, Catoni C, Sapir N. 2019. Migrating birds avoid flying through fog and low clouds. *International Journal of Biometeorology*. 63(2):231–239.
- Pennycuik CJ, Fast PLF, Ballerstädt N, Rattenborg N. 2012. The effect of an external transmitter on the drag coefficient of a bird’s body, and hence on migration range, and energy reserves after migration. *Journal of Ornithology*. 153(3):633–644.

- Perdeck A. 1967. Orientation of starlings after displacement to Spain. *Ardea*. 55:194–202.
- Petit D. 2000. Habitat use by landbirds along nearctic-neotropical migration routes : Implications for conservation of stopover habitats. *Studies in Avian Biology*. 20:15–33.
- Piersma T, Rogers D. 2005. In: Greenberg J, Marra PP, eds. *Birds of Two Worlds: the ecology and evolution of migration*. Baltimore (USA): Johns Hopkins University Press.
- Pigot AL, Owens IPF, Orme CDL. 2010. The environmental limits to geographic range expansion in birds. *Ecology Letters*. 13(6):705–715.
- Poiani K, Richter B, Anderson M, Richter H. 2000. Biodiversity conservation at multiple scales: functional sites, landscapes, and networks. *BioScience*. 50(2):133.
- Powell LA, Lang JD, Krementz DG, Conroy MJ. 1998. Effects of radio transmitters on migrating Wood Thrushes. *Journal of Field Ornithology*. 69(2):306–315.
- Pyle P. 1997. Savannah Sparrow. In: Howell SNG, DeSante DF, Yunick RP, Gustafson M, eds. *Identification guide to North American birds*. Bolinas (USA): Slate Creek Press.
- Rae LF, Mitchell GW, Mauck RA, Guglielmo CG, Norris DR. 2009. Radio transmitters do not affect the body condition of Savannah Sparrows during the fall premigratory period. *Journal of Field Ornithology*. 80(4):419–426.
- R Core Team. 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria (<http://www.R-project.org/>).
- Ralph C. 1981. Age ratios and their possible use in determining autumn routes of passerine migrants. *The Wilson Bulletin*. 93(2):164–188.
- Rappole JH, Tipton A. 1991. New harness design for attachment of radio transmitters to small passerines. *The Journal of Field Ornithology*. 62(3):335–337.
- Rappole JH, Warner DW, Url S. 1976. Relationships between behavior, physiology and weather in avian transients at a migration stopover site. *Oecologia*. 26(3):193–212.
- Reed TE, Harris MP, Wanless S. 2015. Skipped breeding in Common Guillemots in a changing climate: restraint or constraint? *Frontiers in Ecology and Evolution*. 3(1):1–13.

- Ricklefs RE. 1973. Fecundity, mortality, and avian demography. In: Farmer DS, ed. Breeding biology of birds. Washington (USA): National Academy of Science:
- Risely A, Blackburn E, Cresswell W. 2015. Patterns in departure phenology and mass gain on African non-breeding territories prior to the Sahara crossing in a long-distance migrant. *Ibis*. 157(4):808–822.
- Rockwell SM, Wunderle JM, Sillett TS, Bocetti CI, Ewert DN, Currie D, White JD, Marra P. 2017. Seasonal survival estimation for a long-distance migratory bird and the influence of winter precipitation. *Oecologia*. 183(3):715–726.
- Ronconi RA, Taylor P, Crysler Z, Pollett I, Stephens J, Woodworth B, Brzustowski J. 2015. Assessment of bird interactions with offshore infrastructure associated with the oil and gas industry of Nova Scotia, Canada. Wolfville, NS. Unpublished final report for Encana-NSERC CRD. Wolfville (Canada). 120 pp.
- Ross HA, McLaren IA. 1981. Lack of differential survival among young Ipswich Sparrows. *The Auk*. 98(3):495–502.
- Russell R. 2005. Interactions between migrating birds and offshore oil and gas platforms in the northern Gulf of Mexico. U.S Department of the Interior. Baton Rouge (USA). 348 pp.
- Samuel MD, Fuller MR. 1996. Wildlife radio telemetry. In: Bookout TA, ed. Research and Management Techniques for Wildlife and Habitats. Bethesda (USA): The Wildlife Society.
- Sandberg R, Moore FR. 1996. Fat stores and arrival on the breeding grounds: reproductive consequences for passerine migrants. *Oikos*. 77(3):577–581.
- Sanders CE, Mennill DJ. 2014. Acoustic monitoring of migratory birds over western Lake Erie: avian responses to barriers and the importance of islands. *Canadian Field-Naturalist*. 128(2):135–144.
- Santostasi NL, Ciucci P, Caniglia R, Fabbri E, Molinari L, Reggioni W, Gimenez O. 2019. Use of hidden Markov capture–recapture models to estimate abundance in the presence of uncertainty: application to the estimation of prevalence of hybrids in animal populations. *Ecology and Evolution*. 9(2):744–755.
- Schmaljohann H, Dierschke V. 2005. Optimal bird migration and predation risk: a field experiment with Northern Wheatears *Oenanthe oenanthe*. *Journal of Animal Ecology*. 74(1):131–138.

- Schmaljohann H, Korner-Nievergelt F, Naef-Daenzer B, Nagel R, Maggini I, Bulte M, Bairlein F. 2013. Stopover optimization in a long-distance migrant: the role of fuel load and nocturnal take-off time in Alaskan Northern Wheatears (*Oenanthe oenanthe*). *Frontiers in Zoology*. 10(1). 2–12.
- Schmaljohann H, Naef-Daenzer B. 2011. Body condition and wind support initiate the shift of migratory direction and timing of nocturnal departure in a songbird. *Journal of Animal Ecology*. 80:1115–1122.
- Senner NR, Verhoeven MA, Abad-Gómez JM, Gutiérrez JS, Hooijmeijer JCEW, Kentie R, Masero JA, Tibbitts TL, Piersma T. 2015. When Siberia came to the Netherlands: the response of continental black-tailed godwits to a rare spring weather event. *Journal of Animal Ecology*. 84(5):1164–1176.
- Sheehy J, Taylor CM, Norris DR. 2011. The importance of stopover habitat for developing effective conservation strategies for migratory animals. *Journal of Ornithology*. 152(1 SUPPL).
- Sillett S, Holmes RT. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology*. 71(2):296–308.
- Simpfendorfer CA, Huveneers C, Steckenreuter A, Tattersall K, Hoenner X, Harcourt R, Heupel, MR. 2015. Ghosts in the data: false detections in VEMCO pulse position modulation acoustic telemetry monitoring equipment. *Animal Biotelemetry*. 3:55.
- Sjöberg S. 2015. Stopover behaviour in migratory songbirds: timing, orientation and departures. [Ph. D. thesis]. Lund (Sweden): Lund University.
- Sjöberg S, Nilsson C. 2015. Nocturnal migratory songbirds adjust their travelling direction aloft: evidence from a radiotelemetry and radar study. *Biology Letters*. 11:20150337.
- Slowinski SP, Fudickar AM, Hughes AM, Mettler RD, Gorbatenko O V., Spellman GM, Ketterson ED, Atwell JW. 2018. Sedentary songbirds maintain higher prevalence of haemosporidian parasite infections than migratory conspecifics during seasonal sympatry. *PLoS ONE*. 13(8):1–18.
- Smetzer JR, King DI. 2018. Prolonged stopover and consequences of migratory strategy on local-scale movements within a regional songbird staging area. *The Auk*. 135(3):547–560.
- Smetzer JR, King DI, Taylor P. 2017. Fall migratory departure decisions and routes of Blackpoll Warblers and Red-eyed Vireos at a coastal barrier in the Gulf of Maine. *Journal of Avian Biology*. 48:1–11.



- Smith LM, Burgoyne LA. 2004. Collecting, archiving and processing DNA from wildlife samples using FTA® databasing paper. *BMC Ecology*. 4:1–11.
- Smith RJ, Moore FR. 2005. Arrival timing and seasonal reproductive performance in a long-distance migratory landbird. *Behavioral Ecology and Sociobiology*. 57(3):231–239.
- Smolinsky JA, Diehl RH, Radzio TA, Delaney D, Moore FR. 2013. Factors influencing the movement biology of migrant songbirds confronted with an ecological barrier. *Behavioral Ecology and Sociobiology*. 67:2041–2051.
- Snell KRS, Thorup K. 2019. Experience and survival in migratory European Robins *Erithacus rubecula* and Song Thrushes *Turdus philomelos* negotiating the Baltic Sea. *Bird Study*. 66(1):83–91.
- Somveille M, Manica A, Rodrigues ASL. 2019. Where the wild birds go: explaining the differences in migratory destinations across terrestrial bird species. *Ecography*. 42(2):225–236.
- Spina F, Pilastro A. 1999. Strategy of sea and desert crossing in spring passerine migrants as suggested by the analysis of intra- and inter-specific variation of residual fat levels. In: Adam N, Slotow R, eds. *Proceedings XXII International Ornithology Congress*. Durban (South Africa): BirdLife South Africa.
- Stanley CQ, MacPherson M, Fraser KC, McKinnon EC, Stutchbury BJM. 2012. Repeat tracking of individual songbirds reveals consistent migration timing but flexibility in route. *PLoS ONE*. 7(7):e40688.
- Stobo WT, McLaren IA. 1971. Late-winter distribution of the Ipswich sparrow. *American Birds*. 25:941–944.
- Stobo WT, McLaren IA. 1975. *The Ipswich Sparrow*. Halifax (Canada): Nova Scotia Institute of Science.
- Strandberg R, Klaassen RHG, Hake M, Alerstam T. 2010. How hazardous is the Sahara Desert crossing for migratory birds? Indications from satellite tracking of raptors. *Biology Letters*. 6:297–300.
- Streby HM, McAllister TL, Peterson SM, Kramer GR, Lehman JA, Andersen DE. 2015. Minimizing marker mass and handling time when attaching radio-transmitters and geolocators to small songbirds. *The Condor*. 117(2):249–255.
- Stutchbury BJM, Tarof SA, Done T, Gow E, Kramer PM, Tautin J, Fox JW, Afanasyev V. 2009. Tracking long-distance songbird migration by using geolocators. *Science*. 323:896.

- Suedkamp Wells K, Washburn B, Millspaugh J, Ryan M, Hubbard M. 2003. Effects of radio-transmitters on fecal glucocorticoid levels in captive Dickcissels. *The Condor*. 105:805–810.
- Sullivan BL, Aycrigg JL, Barry JH, Bonney RE, Bruns N, Cooper CB, Damoulas T, Dhondt AA, Dietterich T, Farnsworth A, et al. 2014. The eBird enterprise: an integrated approach to development and application of citizen science. *Biological Conservation*. 169:31–40.
- Sutherland WJ. 1998. Evidence for flexibility and constraint in migration systems. *Journal of Avian Biology*. 29(4):441–446.
- Sykes PJ, Carpenter J, Holzman S, Geissler P. 1990. Evaluation of three miniature radio transmitter attachment methods for small passerines. *Wilson Society Bulletin*. 18(1):41–48.
- Taylor P, Crewe T, Mackenzie S, Lepage D, Aubry Y, Crysler Z, Finney G, Charles M. 2017. The Motus Wildlife Tracking System: a collaborative research network to enhance the understanding of wildlife movement. *Avian Conservation and Ecology*. 12(1):8.
- Temple M. 2000. Microsatellite analysis of extra-pair fertilizations in the Ipswich Sparrow. Dalhousie University. [M. Sc. thesis]. Halifax (Canada): Dalhousie University.
- Thorup K, Alerstam T, Hake M, Kjellén N. 2003. Bird orientation: compensation for wind drift in migrating raptors is age dependent. *Proceedings of the Royal Society B: Biological Sciences*. 270(Suppl. 1):8–11.
- Thorup K, Bisson I-A, Bowlin MS, Holland RA, Wingfield JC, Ramenofsky M, Wikelski M. 2007. Evidence for a navigational map stretching across the continental U.S. in a migratory songbird. *Proceedings of the National Academy of Sciences*. 104(46):18115–18119.
- Thorup K, Holland RA, Tøttrup AP, Wikelski M. 2010. Understanding the migratory orientation program of birds: extending laboratory studies to study free-flying migrants in a natural setting. *Integrative and Comparative Biology*. 50(3):315–322.
- Tøttrup AP, Klaassen RHG, Strandberg R, Thorup K, Kristensen MW, Jorgensen PS, Fox J, Afanasyev V, Rahbek C, Alerstam T. 2012. The annual cycle of a trans-equatorial Eurasian-African passerine migrant: different spatio-temporal strategies for autumn and spring migration. *Proceedings of the Royal Society B: Biological Sciences*. 279:1008–1016.

- Townsend JM, Rimmer C, McFarland K. 2012. Radio-transmitters do not affect seasonal mass change or annual survival of wintering Bicknell's Thrushes. *Journal of Field Ornithology*. 83(3):295–301.
- van Noordwijk AJ. 1995. On bias due to observer distribution in the analysis of data on natal dispersal in birds. *Journal of Applied Statistics*. 22(5–6):683–694.
- Verhoeven MA, Loonstra AHJ, Hooijmeijer JCEW, Masero JA, Piersma T, Senner NR. 2018. Generational shift in spring staging site use by a long-distance migratory bird. *Biology Letters*. 14(2):2009–2012.
- Vincenty T. 1975. Direct and inverse solutions of geodesics on the ellipsoid with application of nested equations. *Survey Review*. 23(176):88–93.
- Walker KA, Trites AW, Haulena M, Weary DM. 2012. A review of the effects of different marking and tagging techniques on marine mammals. *Wildlife Research*. 39(1):15–30.
- Ward MP, Benson TJ, Deppe J, Zenzal TJJ, Diehl RH, Celis-Murillo A, Bolus R, Moore FR. 2018. Estimating apparent survival of songbirds crossing the Gulf of Mexico during autumn migration. *Proceedings of the Royal Society B: Biological Sciences*. 285:20181747.
- Warnock N, Takekawa JY, Bishop MA. 2004. Migration and stopover strategies of individual Dunlin along the Pacific coast of North America. *Canadian Journal of Zoology*. 82(11):1687–1697.
- White GC, Garrott RA. 1990. *Analysis of Wildlife Radio-Tracking Data*. San Diego (USA): Academic Press.
- White GC, Kendall WL, Barker RJ. 2006. Multistate survival models and their extensions in program MARK. *The Journal of Wildlife Management*. 70(6):1521–1529.
- Wickham H. 2016. *ggplot2: elegant graphics for data analysis*. New York (USA): Springer-Verlag.
- Wickham H, Averick M, Bryan J, Chang W, D'Agostino McGowan L, François R, Grolemund G, Hayes A, Henry L et al. 2019. Welcome to the tidyverse. *Journal of Open Source Software*. 4(43): 1686.
- Wikelski M, Tarlow EM, Raim A, Diehl RH, Larkin RP, Visser GH. 2003. Costs of migration in free-flying songbirds. *Nature*. 423(6941):704.
- Wilmers C, Nickel B, Bryce C, Smith J, Wheat R, Yovovich V. 2015. The golden age of bio-logging: how animal-borne sensors are advancing the frontiers of ecology. *Ecology*. 96(7):1741–1753.

- Woodrey MS, Moore FR. 1997. Age-related differences in the stopover of fall landbird migrants on the coast of Alabama. *The Auk*. 114(4):695–707.
- Woodworth B, Francis CM, Taylor P. 2014. Inland flights of young Red-eyed Vireos *Vireo olivaceus* in relation to survival and habitat in a coastal stopover landscape. *Journal of Avian Biology*. 45(4):387–395.
- Woodworth B, Mitchell GW, Norris DR, Francis CM, Taylor P. 2015. Patterns and correlates of songbird movements at an ecological barrier during autumn migration assessed using landscape- and regional-scale automated radiotelemetry. *Ibis*. 157:326–339.
- Wright JR, Powell LL, Tonra CM. 2018. Automated telemetry reveals staging behavior in a declining migratory passerine. *The Auk*. 135(3):461–476.
- Ydenberg R, Butler R, Lank D. 2007. Effects of predator landscapes on the evolutionary ecology of routing, timing and molt by long-distance migrants. *Journal of Avian Biology*. 38(5):523–529.
- Yosef R, Wineman A. 2010. Differential stopover of blackcap (*Sylvia atricapilla*) by sex and age at Eilat, Israel. *Journal of Arid Environments*. 74:360–367.

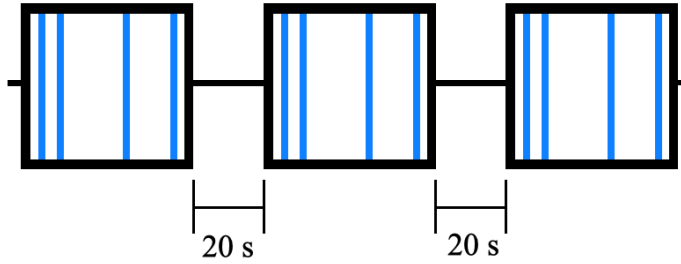
## **APPENDIX A: FILTERING FALSE DETECTIONS IN RADIO-TELEMETRY DATA**

In radio-telemetry, tags emit bursts of radio signal and each burst is comprised of a series of pulses. Bursts occur at a specific burst rate and on a specific radio frequency. They travel through the air and are detected by a receiver, identified as a tag, and recorded. Random radio noise can be falsely identified as a tag (Simpfendorfer et al. 2015). These false detections must be systematically filtered out of the dataset to avoid errors in the interpretation of the data, which can lead to incorrect biological conclusions about animal movement and behaviour (Chambert 2015).

There are two primary methods to filter out false detections from radio telemetry data collected with Motus. The first method examines the radio frequency of the pulses in bursts of a run (series of consecutive tag bursts; Fig. 4.1) for detections recorded on receivers. The standard deviation (SD) of each pulse from the Motus frequency (166.380 MHz) is calculated. A mean standard deviation of  $> 0.08$  kHz suggests that the run of detections are false positives (Crewe et al. 2019b).

The second method compares the recorded detections on receivers to recordings made of tags pre-deployment. The time difference between bursts in a run is calculated for both the recorded detections on receivers and the pre-deployment recordings. The difference between these times is calculated in seconds, and this value is called the burst slop. A burst slop  $> 0.20$  s (i.e., there is at least a 0.20 s difference between the recorded detections on the receiver and the pre-deployment recording) suggests that the run of detections are false positives (Crewe et al. 2019b).

Although this method of filtering out false positives is imperfect and may remove a small number of valid detections, it ensures that only valid detections are retained in the final dataset.



**Figure A1** – Example of a run. This run is comprised of three consecutive tag bursts (black squares) where the time difference in bursts is 20 s. Each burst is comprised of four pulses (blue lines). The timing of the pulses is unique to each tag and permits identification of a tag.