MIGRATION AND CARRY-OVER EFFECTS IN TREE SWALLOWS (*TACHYCINETA BICOLOR*)

by

Lauren J. Burke

Submitted in partial fulfilment of the requirements
for the degree of Master of Science

at

Dalhousie University
Halifax, Nova Scotia
March 2014

TABLE OF CONTENTS

List of Tables……………………………………………………………………...v

List of Figures…………………………………………………………………………vi

Abstract……………………………………………………………………………..vii

List of Abbreviations and Symbols Used………………………………………….viii

Acknowledgements……………………………………………………………………ix

Chapter 1: Introduction…………………………………………………………………1

1.1 Carry-Over Effects…………………………………………………............2

1.2 Purpose of Study...3

1.3 Geolocators………………………………………………………………4

1.4 Study Site………………………………………………………………...6

1.5 Study Species……………………………………………………………6

1.6 Chapter Outlines…………………………………………………………8

Chapter 2: Migration Routes of Tree Swallows………………………………………..9

2.1 Introduction…………………………………………………………………9

2.2 Methods……………………………………………………………………13

2.2.1 Study Species……………………………………………………13

2.2.2 Study Site…………………………………………………………..13

2.2.3 Geolocators…………………………………………………...14

2.2.4 Statistical Analysis…………………………………………………18

2.3 Results………………………………………………………………………..19

2.4 Discussion……………………………………………………………………36

Chapter 3: Carry-Over Effects in Tree Swallows……..40
3.1 Introduction……..40
3.2 Methods……43
3.2.1 Study Site……..43
3.2.2 Breeding Parameters……43
3.2.3 Female Condition……..44
3.2.4 Geolocators……...44
3.2.5 Migration Parameters……45
3.2.6 Statistical Analysis……46
3.3 Results……..47
3.4 Discussion……55
Chapter 4: The Effects of Geolocators on Tree Swallows……59
4.1 Introduction……..59
4.2 Methods……63
4.2.1 Study Site……..63
4.2.2 Breeding Parameters and Female Condition……63
4.2.3 Geolocators……...64
4.2.4 Statistical Analysis……65
4.3 Results……..67
4.3.1 Return Rate……...67
4.3.2 Breeding Parameters and Female Condition……67
Across female comparison……67
Within female comparison……74

4.4 Discussion…………………………………………………………………78

Chapter 5: General Discussion…………………………………………………...82

5.1 Summary………………………………………………………………..82

5.2 Limitations……………………………………………………………...83

5.3 Future Work…………………………………………………………….84

References………………………………………………………………………..86

LIST OF TABLES

Table 2.1 Timeline of migration events for geolocator tagged tree swallows in 2011/12 and 2012/13……………………………………………………………21

Table 2.2 Approximate locations of stopover and wintering sites of geolocator tagged tree swallows in 2011/12 and 2012/13………………………………..22

Table 2.3 Autumn migration duration, distance, rate, and speed of geolocator tagged tree swallows in 2011 and 2012……………………………………….23

Table 3.1 Spearman correlations between breeding parameters and migration parameters………………………………………………………………………..48

Table 4.1 Mann-Whitney U tests of egg initiation date, clutch size, fledging success, and average nestling weight on day 6/7 and day 13 for untagged and tagged females (all tagged), as well as untagged females and females that returned with their geolocators (return with tag), in 2013………………..68

Table 4.2 Repeated measures ANOVA for egg initiation date, clutch size and condition of tagged and untagged females in 2012 and 2013………………....75

LIST OF FIGURES

Figure 2.1 Migration route of bird 436……………………………………………………..25

Figure 2.2 Migration route of bird 766……………………………………………………..26

Figure 2.3 Migration route of bird 765…………………………………………..................27

Figure 2.4 Migration route of bird 441………………………………………………......28

Figure 2.5 Migration route of bird 439…………………………………….....................29

Figure 2.6 Migration route of bird 006……………………………………………………..30

Figure 2.7 Migration route of bird 007……………………………………………………..31

Figure 2.8 Migration route of bird 043……………………………………………………..32

Figure 2.9 Migration route of bird 164……………………………………………………..33

Figure 2.10 Autumn migration routes of all geolocator-tagged birds…………………...34

Figure 2.11 Spring migration routes of all geolocator-tagged birds……………………..35

Figure 3.1 The relationships between brood size and migration parameters…………….49

Figure 3.2 The relationships between fledging date and migration parameters…………51

Figure 3.3 The relationships between condition at deployment and migration parameters………………………………………………………………….53

Figure 4.1 Egg initiation date in 2013 for female tree swallows………………………...69

Figure 4.2 Clutch size in 2013 of female tree swallows…………………………………70

Figure 4.3 Fledging success in 2013 of female tree swallows…………………………...71

Figure 4.4 Average weight per nestling in 2013 from nests of female tree swallows…...72

Figure 4.5 Condition after migration of female tree swallows…………………………..73

Figure 4.6 Egg initiation dates of tagged and untagged females in 2012 and 2013……..76

Figure 4.7 Clutch size of tagged and untagged females in 2012 and 2013……………...76

Figure 4.8 Condition of tagged and untagged females in 2012 and 2013………………77

ABSTRACT

Migratory birds spend much of the year away from the breeding grounds, yet little is known about their movements during migration and on the wintering grounds. The development of light level geolocators allows for the tracking of small passerines throughout the annual cycle and provides the opportunity to determine if events in one season carry-over to affect events in subsequent seasons. Understanding the connections between each season is important for species in decline, especially aerial insectivores, which are rapidly declining across northeastern North America. Although geolocators can provide important information about the annual cycle, they may also negatively affect the bearers.

My first goal was to deploy geolocators on tree swallows in order to map the migration routes and wintering grounds. Geolocators revealed that tree swallows began migration in July and immediately had an extended stopover in the northeastern United States (Maine, Pennsylvania, New Hampshire, New York, and Massachusetts) for 1.5 – 3.5 months. After this stopover, they continued to migrate down the eastern coast of the US until they reached their wintering grounds in Florida or Cuba in late October – early November. Tree swallows remained on their wintering grounds until March or April, when they migrated north, arriving at the breeding grounds in late April – early May.

My second goal was to determine if breeding events have carry-over effects on migration strategy. I found that swallows with later fledging dates began migration later than swallows with early fledging dates but arrived on the wintering grounds around the same time as early fledging birds, possibly due to shorter stopovers. This suggests tree swallows may adjust their migration strategy to compensate for shifts in the timing of breeding.

My third goal was to examine the effects of geolocators on female tree swallows. I found that tagged and untagged birds did not differ in return rate or reproductive success. The condition of tagged birds was poorer than untagged birds following migration; however, this was because both tagged and untagged birds showed declines in condition following migration, and the subset of tagged birds that returned were also in poorer condition in the deployment year than the subset of untagged birds in the deployment year. Overall, I found no short term effects of tags on female tree swallows; however, these results should be viewed with caution due to the small sample sizes.

Overall, this study revealed new information about the annual cycle of tree swallows breeding in Nova Scotia and revealed that this population has important stopover sites in the northeastern US and wintering sites in Florida and Cuba. Also, I show for the first time that carry-over effects from the breeding season can affect tree swallow migration strategy.

LIST OF ABBREVIATIONS AND SYMBOLS USED

df	Degrees of freedom
F	F-test statistic
g	Grams
mm	Millimeters
n	Sample size
P	Statistical probability
km	Kilometers
r	Pearson correlation coefficient
r_s	Spearman correlation coefficient
SD	Standard deviation
SE	Standard error
t	t-test statistic
t_{paired}	Paired t-test statistic
U	Mann-Whitney U test statistic
χ^2	Chi-squared test statistic

ACKNOWLEDGEMENTS

This thesis would not have been possible without the support of many people in many different capacities. I would first like to thank Ryan Norris for allowing me to be a part of this Canada-wide study. I am grateful to the landowners around Wolfville who have generously allowed the use of their land over numerous years. I am also thankful for the assistance of Emma, Liam, and Krista, who made field work easier and more interesting. Their reliability, flexibility, and good humour made the summers a pleasure.

David Bradley cannot be thanked enough for his willingness to answer every question I had about processing geolocators. Also, thanks to Dave Shutler who was heavily involved in deploying and recovering geolocators around Wolfville and answered all my questions with his own quirky humour. Special thanks to my supervisor, Marty Leonard, for her support and commitment to helping me produce a stellar thesis. I would also like to thank Andy Horn and Hal Whitehead for statistics suggestions.

I would like to thank the family of grad students that made the LSC a little more beautiful, especially Zabrina, Jantina, Joana, Isabelle, and Zoe for countless games of Fluxx over lunch, with a side of commiseration and encouragement. Last but not least, my heartfelt thanks to my husband, TJ, and my parents for their unwavering faith in me.

CHAPTER 1: INTRODUCTION

Migration, the persistent, undistracted, large scale movement that results in a round trip between two or more home ranges (Fryxell et al. 2011), is a strategy that has been adopted by a variety of species to exploit seasonal food supplies and avoid unfavourable weather conditions (Newton 2008). In North America, millions of birds from approximately 350 species undergo annual migrations (Kelly and Finch 1998) between their breeding grounds in the north and their wintering grounds in the south. Prior to migration, birds increase their energy reserves to facilitate often long flights (Bauer et al. 2011). Even so, migrating birds often use stopover sites to replenish energy reserves (Alerstam et al. 2003). Factors such as weather and food abundance determine the amount of time spent at stopover sites before continuing migration (Schneider and Harrington 1981; Calvert et al. 2009). Spatial changes in resources throughout the winter may also result in some birds using more than one wintering site, a practice that was unknown until recently (Jahn et al. 2013).

Although important stopover sites have been identified and the winter ranges of many species have been mapped, little is known about the movements of migratory birds once they leave the breeding grounds. This is because historically it has been very difficult to follow birds once they begin migration. The recent development of technology such as light-level geolocators has, however, made it possible to track the movements of individual birds (e.g. Stutchbury et al. 2009; Callo et al. 2013; Fraser et al. 2013). In turn, this has allowed researchers to study a bird’s complete annual cycle, including the complex interactions between events, such as reproduction and migration.

1.1 Carry-Over Effects

The annual cycle of a migratory species is necessarily influenced by conditions and events on the wintering grounds, during migration, and on the breeding grounds. Carry-over effects may explain how fitness in subsequent seasons is affected by conditions and events in a previous season. For example, poor quality wintering habitat may negatively affect body condition and the timing of departure for spring migration (Marra et al. 1998; Rockwell et al. 2012). Poor body condition and late departure from the wintering grounds may, in turn, affect arrival on the breeding grounds (Marra et al. 1998). Birds arriving late begin breeding later and are less likely to have high reproductive output (Marra et al. 1998; Norris et al. 2004a; Sorensen et al. 2009).

Carry-over effects have most often been studied by examining the effects of winter habitat on spring migration and reproductive success the following summer (e.g. Marra et al. 1998). However, the timing of breeding and conditions on the breeding grounds can affect the timing of molt and autumn migration. For example, late breeding can result in an overlap of molt with reproduction (Morton 1992; Norris et al. 2004b), a faster molt (Conklin and Battley 2012), or changes in the location of the molt (Norris et al. 2004b). Late breeding may delay migration (Stutchbury et al. 2011; Mitchell et al. 2012), which may influence migration strategy such as the length of stopovers or speed of migration. Poor reproductive success may also influence migration strategy, as unsuccessful breeders that invest less energy in reproduction may be able to overwinter farther north and arrive back on the breeding grounds earlier, or migrate farther to exploit high quality wintering sites than successfully reproducing birds (Bogdanova et al. 2011; Catry et al. 2013).

Carry-over effects can result in constraints on individual survival and reproductive success. This in turn gives information about the drivers of change in population size from year to year (Harrison et al. 2011). Many migratory bird species are currently in decline, but the specific causes are often unknown (Sanderson et al. 2006; Nebel et al. 2010). Identifying how carry-over effects result in population changes is complicated by the fact that individuals from the same breeding area may use different wintering sites (Ketterson and Nolan 1983), which may result in different carry-over effects. A population that uses a number of wintering sites and experiences different conditions may show different patterns of population change than a population that uses the same wintering site and experiences the same conditions. Models that incorporate carry-over effects and connectivity can help predict how populations will change with ecological changes such as habitat loss, habitat degradation, and climate change on the breeding and wintering grounds (Norris 2005; Norris and Taylor 2006), and thus inform decisions on what habitats should be protected.

1.2 Purpose of Study

Tree swallows (*Tachycineta bicolor*) are currently in decline; however, they are disproportionately declining east of Ontario (Nebel et al. 2010; Shutler et al. 2012). Although the causes of these declines are unknown, different breeding populations are known to use different stopover and wintering sites (Laughlin et al. 2013). If these sites differ in condition, they may differentially affect populations. In order to understand the factors driving tree swallow declines, especially those affecting populations in the northeast compared to the rest of North America, it is important to know the migratory routes and wintering sites of tree swallows breeding in the northeast, and how conditions at each site affect fitness in subsequent seasons.

The broad goal of my study, therefore, was to map the annual movements of adult tree swallows breeding in Nova Scotia that were tagged with geolocators. Specifically, I wanted to identify stopover and wintering sites and determine if events occurring in the breeding season influence migration events. I also took the opportunity to examine what effects, if any, geolocators had on tagged birds. Below, I will describe how geolocators are used to track migrating birds, my study site, and what is currently known about tree swallow movements in the migratory and wintering seasons.

1.3 Geolocators

Geolocators are small, inexpensive, non-transmitting light-level loggers that can be attached to birds via a leg ring or backpack harness. They are especially useful for tracking small birds that cannot carry larger tags like satellite tags. Geolocators sample light levels every minute and record the maximum light level during the previous five minutes. Using these data, graphs of light intensity are made and sunrise and sunset times can be estimated from the light curves. Sunrise and sunset provide four reference points: local midday and local midnight (with respect to Greenwich Mean Time), and day length and night length. Two location estimates are generated, one at noon and one at midnight. Latitude is determined by day or night length and longitude is determined by local midday or midnight (Afanasyev 2004). The location estimates can be plotted daily and this provides information about migration routes, distance, duration, rate, speed, stopovers, and wintering grounds.

Geolocators use light to estimate location, which results in some limitations. Due to light interference from factors such as vegetation, clouds, and varying topography, geolocators are not as accurate as transmitting tags like radio transmitters and satellite tags (Lisovski et al. 2012). Various studies have found errors of 400 ± 298 km (Shaffer et al. 2005), 186 ± 114 km (Phillips et al. 2004), and 143 ± 62 km in latitude and 50 ± 34 km in longitude (Fudickar et al. 2011) from the true location. In addition, during the equinoxes, day and night length is the same everywhere, so latitude cannot be determined for approximately 15 days on either side of the equinox.

Geolocators, like other tags, may have negative effects on the birds carrying the tags. For example, a recent review on the effects of geolocators on passerines and seabirds found a negative effect on return rates of tagged birds in 27 of 42 studies (Constantini and Moller 2013). Decreased hatching and fledging success have also been associated with geolocators (Rodriguez et al. 2009; Nisbet et al. 2011; but see Schmaljohann et al. 2012). However, other measurements such as nestling weight and nestling survival appear not to be affected by parents wearing tags, at least for common terns (*Sterna hirundo*, Nisbet et al. 2011) and northern wheatears (*Oenanthe oenanthe*, Tottrup et al. 2012). The weight of evidence from the recent reviews also suggests that geolocators may particularly affect aerial foragers, short distance migrants and small species (Bridge et al. 2013; Constantini and Moller 2013).

The negative effects documented in geolocator tagged birds appear to be the result of increased energy requirements and decreased agility associated with the weight and shape of the tags and harnesses (Barron et al. 2010). Additional weight may affect lift and increase energy expenditure in flight (Caccamise and Hedin 1985) which is why researchers aim to use tags that ≤ 5% of a bird's body weight (e.g. Bachler et al. 2010; Nisbet et al. 2011; Callo et al. 2013). Even a small amount of extra weight could, however, increase energy requirements, which ultimately can affect reproductive success (Sibly and McCleery 1980), survival (Warner and Etter 1983), and behaviour (Hooge 1991). As well, the shape of the tag may increase drag (Bowlin et al. 2010; Pennycuick et al. 2012), thereby increasing the energy needed for flight and decreasing agility. The addition of a harness increased drag as much as a harness with a transmitter, and tags with antennas increased drag to almost twice the level of an untagged bird (Pennycuick et al. 2012). Increases in drag decreased the predicted migration range of migrating common swifts (*Apus apus*) and Barnacle geese (*Branta leucopsis*) (Bowlin et al. 2010).

1.4 Study Site

Work was conducted at four well-established field sites in the Gaspereau Valley near Wolfville, Nova Scotia, Canada (45.07, -64.34; 45.07, -64.33; 45.07, -64.33; and 45.09, -64.29). Sites consisted of open fields along the Gaspereau River or old apple orchards. All sites were set up with nest boxes measuring 30 x 15 x 15 cm. Data were collected from May to July in 2011, 2012 and 2013.

1.5 Study Species

Tree swallows are small aerial insectivores (birds that eat flying insects while in flight) that breed in cavities throughout northern and central North America. Although they naturally nest in cavities in trees, tree swallows will readily breed in nest boxes (Chapman 1966), making them an ideal study species. They arrive on the breeding grounds in Nova Scotia in April-May and begin breeding in May. Tree swallows have one clutch per season of 2 to 8 eggs and incubation lasts about 12 days (Winkler et al. 2011). Both parents provision their young, and nestlings fledge when they are 18 – 22 days old (Winkler et al. 2011). Tree swallows begin autumn migration in July and August and form large roosts at night while migrating and on the wintering grounds (Burney 2002). Their winter range, from December to February, includes Florida, Mexico, northern Central America, Cuba, and other states along the Gulf coast (Winkler et al. 2011).

There is currently very little information about the non-breeding locations of specific individuals and populations. Based on re-sightings of a small number of banded birds outside of the breeding season, tree swallows are thought to use three different migration routes, depending on their breeding locations (Butler 1988). Eastern populations are thought to migrate down the Atlantic coast to Florida, Cuba, and Honduras, while central populations migrate along the Mississippi River to the southern United States and Central America, and western populations migrate down the Rocky Mountains or Pacific coast (Butler 1988). Recent geolocator work has revealed that some tree swallows breeding in Saskatchewan, Wisconsin, and Ontario use stopover sites in Louisiana before continuing to wintering sites in Mexico, southeastern United States, and the Bahamas (Laughlin et al. 2013).

Only one study has been done on the effects of geolocators on tree swallows, which included birds breeding in British Columbia, Saskatchewan, and Ontario. Geolocator-tagged swallows in Saskatchewan showed no difference in provisioning rates (number of times per hour the adults feed the nestlings), nestling weight, or nestling growth rate compared to untagged swallows (Gomez et al. 2014). Tagged swallows at all three sites also showed no difference in breeding success compared to untagged swallows (Gomez et al. 2014). However, tagged swallows breeding in British Columbia and Saskatchewan had significantly lower return rates than untagged swallows (Gomez et al. 2014).

1.6 Chapter Outlines

The purpose of this study was to track adult tree swallows with light level geolocators over one year as they migrate to and from their wintering grounds. In chapter two, I map the migration routes of tagged tree swallows, including the location of stopovers and wintering grounds, and look for temporal patterns in their migration strategy. In chapter three, I examine if events that occur in the breeding season result in carry-over effects on migration decisions. In chapter four, I examine the effects of geolocators on return rate, reproductive success, and body condition. Finally, in chapter five I summarize my results, discuss the limitations of my study, and end with suggestions for future work.

CHAPTER 2: MIGRATION ROUTES OF TREE SWALLOWS

2.1 Introduction

In the last few decades, aerial insectivore populations across North America have been in decline (Nebel et al. 2010). In Canada, many populations have decreased by over 70% since the late 1980s (McCracken 2008). Four aerial insectivores are listed as Threatened or Endangered under the *Species at Risk Act (SARA)* (chimney swifts *Chaetura pelagica*, olive-sided flycatchers *Contopus cooperi*, common nighthawks *Chordeiles minor*, Acadian flycatchers *Empidonax virescens*), while the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) has recommended another two be listed as Threatened (barn swallows *Hirundo rustica*, bank swallows *Riparia riparia*).

Interestingly, despite the variety of species included under aerial insectivores, there seem to be broad overall patterns associated with the magnitude of decline across North America. Populations that were more likely to be in decline were long-distance migrants rather than short-distance migrants, wintered in South America rather than Central America, or bred in the northeast rather than elsewhere in North America (Nebel et al. 2010). Although the declines have been drastic, the causes of these declines are currently unclear. Many reasons have been proposed, including habitat loss, atmospheric pollutants, increased predation on the breeding grounds, deforestation on wintering grounds in the tropics, or changes in insect populations in both locations (Bohning-Gaese et al. 1993; Newton 2008; Nebel et al. 2010).

In order to understand the threats facing different aerial insectivores and where these threats are occurring, it is necessary to explore their complete annual cycle. For example, researchers concerned that purple martin (*Progne subis*) populations in eastern North America are being affected by factors on the wintering grounds found that most purple martins wintered in mostly pristine rainforest, suggesting that stressors other than habitat degradation on the wintering grounds are causing the declines (Fraser et al. 2012). It also suggests that the rainforest is vital habitat for the eastern population of purple martins and should be kept free of development. Having a clear picture of the annual cycle can help identify important habitats required at each stage in the life cycle and aid in conservation decisions (Croxall et al. 2005). It can also reveal the degree of migratory connectivity (how many individuals from one breeding site use the same wintering site and vice versa) (Ryder et al. 2011), which can shed light on which populations are being affected by the threats in specific locations. All this information can be used to inform policy makers where resources should be allocated to best protect vulnerable species (Norris et al. 2006). Also, information about the different stressors and available resources associated with habitats that birds use annually can be incorporated into population models. Such models can be used to predict population changes that may result from habitat degradation or climate change, for example, allowing for the development of effective management plans (Norris and Taylor 2006). In order to make effective conservation decisions, the whole annual cycle must be revealed, from breeding sites in the north to wintering sites in the south and back again, including stopover sites and important migratory corridors.

The first attempt to determine where individual migratory birds overwintered was by banding birds in the breeding season and recapturing them outside of the breeding season (Bairlein 2001). Although this method was valuable for revealing migratory routes for waterfowl (Lincoln 1935), it was far less effective for passerines. For example, of over one million pied flycatchers (*Ficedula hypoleuca*) banded on the breeding grounds in Europe, a mere six were re-sighted on the wintering grounds in Africa (Webster et al. 2002). With the advent of modern technology, satellite tags, which transmit real time locations, were used to track individual birds throughout the year (e.g. Gschweng et al. 2008). Satellite tags have been useful for exploring the movements of large birds, but because of their size are unsuitable for birds <100g. Increasingly, light level geolocators, which use day length to estimate longitude and latitude, are being used to understand migration strategies and locate the wintering grounds of migratory birds (e.g. Stutchbury et al. 2009; Heckscher et al. 2011; Jahn et al. 2013). Although not as accurate as satellite tags, geolocators are currently the only option to track the movements of small birds that are unable to carry heavier tags.

Geolocators have already begun to fill in the gaps in the annual cycles and migratory strategies of several aerial insectivores. For example, purple martins from seven colonies tagged with geolocators used several different routes to fly around or across the Gulf of Mexico en route to their wintering grounds in South America (Fraser et al. 2013). Despite following different routes, all individuals had an initial rapid journey to a stopover site, followed by a slower migration rate to the wintering grounds. As well, late departing birds arrived later on the wintering grounds and had a faster rate of migration overall (Fraser et al. 2013). Similarly, work with geolocators showed that individual fork-tailed flycatchers (*Tyrannus savana*) used two different wintering sites, a pattern that seems to be more common across species than previously thought (Jahn et al.

2013). These studies have provided insights into the migratory movements of individuals from different populations, important habitats, and the temporal patterns of migration.

Another species for which there has been some effort to identify migratory routes and wintering sites is the tree swallow. Some tree swallows from Saskatchewan, Ontario and Wisconsin had a stopover in Louisiana before continuing on to their wintering grounds in Florida, the Bahamas, or the Yucatan Peninsula (Laughlin et al. 2013); however, not all individuals followed this route, and it is likely that stopover and wintering sites vary across North America. Therefore it is important to study populations across the breeding range to have a holistic view. It is especially important that information on stopovers and wintering grounds is collected for swallows in northeastern North America, as declines in this area are higher than anywhere else (Nebel et al. 2010). Based on the Breeding Bird Survey, the average annual percent change in population from 2002-2012 for tree swallows in Canada was 0.289 (95% CI = -1.81, 3.84), but in Nova Scotia and Prince Edward Island it was -3.01 (95% CI = -6.4, -0.301) (Environment Canada 2013).

The goal of my study was to describe the migration routes and examine the migration strategy of a population of tree swallows (*Tachycineta bicolor*) breeding in Nova Scotia, Canada. Specifically, I determined important stopover sites and wintering sites and calculated migration distance, duration, rate and speed. I also determined if tree swallows show any temporal patterns in their migration strategy by examining the timing of and relationships between different migratory events, such as the beginning and end of autumn migration.

2.2 Methods

2.2.1 Study Species

Tree swallows are small (~22 g) aerial insectivores that nest in tree cavities. They breed throughout northern and central North America, and begin autumn migration in July and August (Winkler et al. 2011), traveling to large roosts near the breeding grounds (Burney 2002) before continuing on to their wintering sites.

Currently, researchers have only a general picture of where tree swallows go in the non-breeding season. Swallows have been observed in the Gulf Coast states, Mexico, northern Central America, and Cuba from December to February (Winkler et al. 2011). Recent geolocator work has revealed that some tree swallows breeding in Saskatchewan, Wisconsin, and Ontario use stopover sites in Louisiana before continuing on to wintering sites in Mexico, Florida, and the Bahamas (Laughlin et al. 2013). However, there is little information on where specific individuals from other populations overwinter. The current information on migratory routes is also only a broad sketch. Based on band recovery data from 41 birds (21 in the winter, 20 during the migratory period), Butler (1988) hypothesized that tree swallows use three migratory routes: 1) along the Atlantic coast to Florida, Cuba, and Honduras; 2) along the Mississippi River to the southern United States and Central America; and 3) down the Rocky Mountains or Pacific coast.

2.2.2 Study Site

I conducted this study from May to July, 2011, 2012, and 2013, on a population of box-nesting tree swallows at four study sites near Wolfville, Nova Scotia, Canada (45.07, -64.34; 45.07, -64.33; 45.07, -64.33; and 45.09, -64.29). Sites consisted of open fields along the Gaspereau River or old apple orchards (see Leonard and Horn 1996 for more detail). I checked nest boxes every second day to determine when the first egg was laid and when incubation began. Nest boxes were not checked again until two days before the expected hatch date, when I checked them daily until hatch. When all eggs had hatched, nests were checked every second day, until day 18 (hatch day = day 1), when I again checked them daily to determine fledging day.

2.2.3 Geolocators

There were differences in the timing, attachment, and model of geolocators between years, so the procedure for each year is described separately. In 2011, 16 adult males and 14 adult females were caught with nest box traps when nestlings were ~4 days old and geolocators (Lotek Wireless model MK12-S) were attached using a leg loop harness made of 1 mm ethylenepropylene-diene rubber O-rings. The geolocators weighed 0.96 g with the harness, which is ≤5% of tree swallow body weight (~22 g). This weight is considered acceptable based on regulations set by the Canadian Council on Animal Care (CCAC 2003, Fair et al. 2010). Swallows were weighed to the nearest 0.5 g and banded with a Canadian Wildlife Service (CWS) band.

In 2012, 24 females (different females than the previous year) were removed from the nest box by hand two days before their expected hatch date. They were banded with a CWS band and an individual colour band to allow for the identification of the female later in the season, when geolocators were deployed. Females were weighed with a spring scale to the nearest 0.5 g and the tarsus was measured with digital calipers to the nearest

0.01 mm. All females were re-caught with nest box traps when their nestlings were 12-17 days old, weighed again, and tagged with geolocators (Lotek Wireless model MK6740).

The techniques I used to attach the geolocators in 2012 were identical to those used in 2011, with the following exceptions: 1) the geolocator plus harness varied in weight, but all were ≤1 g; and 2) a drop of cyanoacrylate adhesive (Krazy glue) was used to attach the main body of the geolocator to the female's down, and then the surrounding feathers were arranged to cover the geolocator and reduce drag.

I retrieved the geolocators in May and June of 2012 and 2013. I checked all females for geolocators by removing females from nest boxes during late incubation. I checked males for geolocators by trapping males during the nestling period using nest box traps. A total of 43 males were caught. Once I found a tagged bird, I removed the geolocator (if the swallow still carried it), weighed the swallow, and measured the tarsus.

Data from the geolocators was downloaded and processed using BASTrack software (British Antarctic Survey [BAS], Cambridge, United Kingdom). The clock in the geolocator may become asynchronous with the actual time, which is known as clock drift, so I first corrected for this using Decompressor (BAS). Light transitions were displayed with TransEdit2 (BAS) using a light threshold value of 5 on the arbitrary scale of 0 to 64 to define sunrise and sunset times. I removed false sunrises and sunsets that resulted from crossing this threshold during the day due to shading. Each geolocator was calibrated with an on-bird calibration using LocatorAid (BAS), using the sunrise and sunset light transition curves from the 6-10 days after fledging when the adult was still at or near the breeding site (following Laughlin et al. 2013). Calibrating each geolocator in this way accounts for differences in the sensitivity of the light sensor and shading that might be caused by the bird's behaviour, and gives a measure of the sun elevation angle that matches with the chosen light threshold value used in TransEdit2. Tree swallows most likely use the same kind of habitat throughout migration, so the sun elevation angle calculated on the breeding ground is acceptable for the duration of deployment (Laughlin et al. 2013). The calibration resulted in specific sun elevation angles for each geolocator, ranging from -3.23° to -4.71°. Using these individual sun elevation angles, deviation from the true breeding location was an average of 21.33 ± 21.17 km (mean ± SD; range 6-68 km) in latitude and 28.89 ± 20.82 km (range 2-71 km) in longitude. Average location estimates during this period deviated from the breeding grounds by 40.22 ± 22.01 km. The light transitions were then loaded into BirdTracker (BAS) with the individual sun elevation angles calculated previously, which provides two locations per day, one at noon and one at midnight. For the noon position, longitude is estimated using the time of local noon and latitude is estimated using day length. For the midnight position, longitude is estimated using the time of local midnight and latitude is estimated using night length. I only used midnight positions to plot the migratory path as swallows migrate during the day but are stationary at night (Winkler et al. 2011). I plotted these positions using ArcMap 10 (ESRI).

Around the autumn and spring equinox, day and night length are the same everywhere and latitude cannot be estimated. Therefore, I removed transitions 15 to 20 days on either side of the equinoxes (the equinox periods). I chose the length of this period based on previous studies (e.g. Heckscher et al. 2011; Ryder et al. 2011; Callo et al. 2013; Laughlin et al. 2013) coupled with visual inspection of the data. Longitude is still accurate at this time, so I examined the longitude values during the equinox periods, looking for any obvious directional changes that may indicate the beginning of spring migration. I also used the longitude values to look for periods where longitude stays constant, indicating a stopover. I was unable to identify the beginning of spring migration because the swallows tended to travel north up the Florida peninsula, following roughly the same longitude, and only began moving east after the spring equinox period was over (~15 days after the spring equinox). Therefore I could not see any east/west movements during the spring equinox period (end of February-beginning of April).

I needed to define the beginning and end of migration and when stopovers occurred to describe the migration of each individual. Migration is defined as persistent, undistracted movement on a larger than daily scale resulting in a round trip between two or more home ranges (Fryxell et al. 2011). For each individual, the beginning of autumn and spring migration is defined as when the bird moves 1 degree or more in longitude or latitude south/southwest (away from the breeding location) or north/northeast (away from the wintering location) and does not return to that location for at least six months (Jahn et al. 2013). Stopovers are defined as occurring when the location remains consistent for at least two days before the individual continues migrating (Stutchbury et al. 2011). Arrival on the wintering grounds is defined as when latitude and longitude cease to shift south or southwest and longitude fluctuates no more than 4 degrees until the beginning of spring migration (Stutchbury et al. 2011). Arrival on the breeding grounds is defined as when latitude and longitude cease to shift north or northwest and longitude is less than or equal to 65 degrees (the longitude of the western end of Nova Scotia) until July.

To estimate the location of each bird’s stopover and wintering sites, I calculated an average longitude and latitude using all midnight positions during the stopover or wintering period (Stutchbury et al. 2011). If this coordinate was over water, I moved it latitudinally to the nearest land location (see Delmore et al. 2012; Heckscher et al. 2011; Laughlin et al. 2013), as tree swallows may migrate over bodies of water but not stopover or winter on the ocean. One average wintering location was moved longitudinally, however, as that geolocator had severe clock drift, which affects longitude. Migration information is presented as mean ± SD.

To determine the migratory patterns followed by each individual, I considered: i) migration distance to be the straight line distance between the breeding site, any stopover sites, and the wintering site (Johnson et al. 2012); ii) duration of migration to be the number of days between the initiation of migration and arrival on the wintering ground (for autumn migration) or breeding ground (for spring migration) (Tottrup et al. 2012); iii) migration rate to be the distance divided by the duration, including stopover days (Fraser et al. 2013); iv) flying days to be the duration of migration minus the number of stopover days; and v) migration speed to be the migration distance divided by the number of flying days (Schmaljohann et al. 2012).

2.2.4 Statistical Analysis

I created kernel density distribution maps (ArcMap 10.0, ESRI) for each bird to determine the core area during their time on the wintering grounds using a search radius of 200 km and a cell size for the output raster dataset of 50 km (Phillips et al. 2004; Landers et al. 2011). This means a smooth surface is fitted over each point extending for 200 km, with the highest surface value at the peak and no value at the edges. Density is calculated by summing the surface values that overlap the center of the raster cell. My maps show 50%, 75%, and 90% kernel density.

I performed all statistical analyses using GraphPad Prism 5 (San Diego, California, GraphPad Software). Data were tested for normality using the D'Agostino and Pearson omnibus normality test. To look for patterns in the migration strategies of this population, I used Pearson (or Spearman for non-parametric data) correlations. Specifically, I determined if a later autumn departure resulted in a later arrival on the wintering grounds or a later arrival at the breeding site the following year. I also determined if a later departure in autumn resulted in a faster migration rate, and if birds that migrated farther had a faster migration rate. Results were considered significant when $P \leq 0.05$.

2.3 Results

In 2012, eight of the 30 (26.7%) swallows that had been fitted with geolocators in 2011 returned to the study sites (5 females, 3 males), although two swallows returned without their geolocators. Of the six geolocators recovered, one did not have recoverable data. Of the five remaining geolocators, four were carried by females and one was carried by a male. In 2013, nine of 24 (37.5%) tagged female swallows returned to the study sites; however, four returned without geolocators. Of the five geolocators recovered, one did not have useable data due to very severe clock drift. Therefore, in total 17 of 54 (31.5%) tagged birds returned to the study sites, with nine usable geolocators (16.7%).

The initiation of autumn migration ranged from 9 – 18 July in 2011 and 1 – 12 July in 2012 (Table 2.1). All birds had an extended stopover in the northeastern United

States lasting an average of 68.2 ± 22.1 days (range: 39-101 days). Following this, six of the nine swallows had a stopover in North Carolina until late October to early November (Tables 2.1 and 2.2). The other three swallows used different stopover sites or did not have a second stopover (Table 2.2). The geolocator carried by bird 164 had severe clock drift, so even with the correction its movements must be interpreted with caution. All birds then proceeded to their wintering grounds. Four swallows wintered in southern Florida and five swallows wintered in Cuba (Table 2.2). In 2011, the swallows arrived at their wintering grounds between 27 October and 19 November. In 2012, they arrived at their wintering grounds between 12 October and 9 November (Figures 2.1-2.10).

Spring migration began in March or April, and occurred during the equinox period so I could not determine the start of migration. The tree swallows flew north into the southern United States before moving northeast (Figures 2.1-2.9, Figure 2.11). They all had two or three short stopovers after the equinox period ended, except bird 436 (male) that only stopped over once (Table 2.1). The stopover sites followed no consistent geographical pattern, with stopover sites falling in Georgia, Virginia, North Carolina, South Carolina, Delaware, Massachusetts, Pennsylvania, New York, and Maine (Table 2.2). The swallows arrived in Nova Scotia between 17 April and 8 May in 2012 and between 21 April and 30 April in 2013 (Table 2.1).

Autumn migration duration was 117.8 ± 12.9 days (range: 93-133 days), but on average, swallows spent only 12 days flying (range: 8-15 days). The average migration distance between the breeding grounds and wintering grounds was 2978.08 ± 188.13 km, resulting in an autumn migration rate of 25.62 ± 3.84 km/day (including stopovers). Autumn migration speed, using only flying days, was 256.87 ± 55.23 km/day (Table 2.3).

Table 2.1: Timeline of migration events for geolocator tagged tree swallows in 2011/12 and 2012/13. Question marks denote unknown dates and dates estimated from longitude data only. The geolocator of Bird 164 had severe clock drift so its movements must be interpreted with caution.

Bird (Sex, Year)	Departure	Autumn Stopover 1	Autumn Stopover 2	Autumn Stopover 3	Arrival - Wintering	Spring Stopover 1	Spring Stopover 2	Spring Stopover 3	Arrival - Breeding
436 (M, 2011/12)	18 July	21 Jul - 30 Oct			10 Nov	26 Mar? - 14 Apr			17 Apr
766 (F, 2011/12)	14 July	15 Jul - 6 Oct?	9? - 30 Oct		6 Nov	25 Mar? - 15 Apr	18 - 20 Apr		26 Apr
765 (F, 2011/12)	14 July	17 Jul - 19 Sept?	? - 24 Oct		27 Oct	? - 14 Apr	17 Apr - 3 May		8 May
441 (F, 2011/12)	9 July	9 Jul - 6 Sept?	10 Sept? - 31 Oct	4 - 18 Nov	19 Nov	? - 25 Apr	28 Apr - 1 May		7 May
439 (F, 2011/12)	13 July	16 Jul - 2 Sept	6 Sept - 2 Nov		8 Nov	? - 15 Apr	16 - 20 Apr	23 - 29 Apr	2 May
006 (F, 2012/13)	2 July	7 Jul - 23 Aug	25 Aug - 3 Nov		7 Nov	17? - 31 Mar?	1? - 16 Apr	18 - 19 Apr	21 Apr
007 (F, 2012/13)	8 July	9 - 13 Jul	14 Jul - 16 Oct	19 Oct - 3 Nov	7 Nov	8? - 16 Apr	20 - 24 Apr		30 Apr
043 (F, 2012/13)	1 July	2 Jul - 20 Sept?	21 Sept? - 8 Oct?	10 Oct - 4 Nov	9 Nov	8 - 11 Apr	13 - 17 Apr	19 - 20 Apr	21 Apr
164 (F, 2012/13)	12 July	14 Jul - 22 Aug	25 Aug - 18 Sept?	21 Sept? - 6 Oct?	12 Oct?	11 - 15 Apr	18 - 21 Apr		22 Apr

Table 2.2: Approximate locations of stopover and wintering sites of geolocator tagged tree swallows in 2011/12 and 2012/13. The geolocator of Bird 164 had severe clock drift so its movements must be interpreted with caution.

Bird (Sex, Year)	**Autumn Stopover 1**	**Autumn Stopover 2**	**Autumn Stopover 3**	**Wintering**	**Spring Stopover 1**	**Spring Stopover 2**	**Spring Stopover 3**
436 (M, 2011/12)	New Jersey/ Pennsylvania			Cuba	New York		
766 (F, 2011/12)	Maine/ New Hampshire	North Carolina		Florida	North Carolina	Virginia	
765 (F, 2011/12)	Pennsylvania/ New York	North Carolina		Cuba	South Carolina	New Jersey/ Pennsylvania	
441 (F, 2011/12)	Maine/ New Hampshire	North Carolina	Florida	Cuba	Virginia	Maryland/ Delaware	
439 (F, 2011/12)	New Hampshire	North Carolina		Cuba	Pennsylvania	Pennsylvania	Maine
006 (F, 2012/13)	New York/ Vermont / Massachusetts	North Carolina		Florida	North Carolina	Maryland/ Delaware	Rhode Island/ Massachusetts
007 (F, 2012/13)	Maine/ New Hampshire	Connecticut/ New York	North Carolina	Florida	Georgia	North Carolina	
043 (F, 2012/13)	Maine	Connecticut/ New York	New Jersey/ Delaware	Cuba	Virginia	New York	Maine
164 (F, 2012/13)	Connecticut/ Massachusetts	New York	Georgia	Florida	Virginia	Maine	

Table 2.3: Autumn migration duration, distance, rate, and speed of geolocator tagged tree swallows in 2011 (birds 436 to 439) and 2012 (birds 006 to 164). Mean and standard deviation (SD) are also presented.

Bird (Sex)	Duration (days)	Distance (km)	Rate (km/day)	Speed (km/day)
436 (M)	115	3054.98	26.57	203.67
766 (F)	115	2696.33	23.45	224.69
765 (F)	105	3037.62	28.93	379.70
441 (F)	133	3132.00	23.55	284.73
439 (F)	118	3127.46	26.50	223.39
006 (F)	128	2809.48	21.95	234.12
007 (F)	122	2700.08	22.13	270.01
043 (F)	131	3100.94	23.67	281.90
164 (F)	93	3143.88	33.81	209.59
Average	117.78	2978.08	25.62	256.87
S.D.	12.85	188.13	3.84	55.23

The obscuring of data around the spring equinox made it difficult to estimate spring migration duration, rate, and speed. Despite this difficulty, the minimum and maximum duration can still be determined. If each bird began migration one day into the equinox period, the average maximum duration of spring migration is 53 days (range: 43 – 64 days). If each bird began migration one day before the end of the equinox period, the average minimum duration is 23 days (range: 13 – 34 days). Spring migration duration, therefore, must be between 13 and 64 days for each bird. The maximum and minimum average duration are both much shorter than autumn migration duration, and therefore spring migration is shorter than autumn migration. Spring migration distance was 3014.91 ± 277.82 km, and individuals did not migrate significantly farther during spring migration than autumn migration ($t_{paired} = 0.53$, df = 8, $P = 0.61$). Given that the distances do not differ significantly, and that the duration of migration in spring is much shorter than in the autumn, spring migration rate must be faster than the autumn migration rate.

There was no significant relationship between when a bird began autumn migration and when it arrived on the wintering grounds ($r_s = -0.28$, $n = 9$, $P = 0.46$), nor between when it departed from the first stopover site in the northeastern US and arrived on the wintering grounds ($r_s = 0.37$, $n = 9$, $P = 0.31$). Similarly, there was no significant correlation between the timing of autumn departure from the breeding grounds and spring return to the breeding grounds the following year ($r = 0.15$, $n = 9$, $P = 0.69$). It might be expected that birds starting migration later or traveling farther would travel faster, but autumn migration rate was not significantly correlated with autumn migration initiation ($r = 0.52$, $n = 9$, $P = 0.14$) or autumn migration distance ($r = 0.59$, $n = 9$, $P = 0.10$).

Figure 2.1: Migration route of bird 436 (male) from July 2011-April 2012. Red dots indicate locations of stopovers and wintering site. Density contours reflect 50%, 75% and 90% kernel density. Dates with "?" indicate estimates made from longitude data only (during equinox).

Figure 2.2: Migration route of bird 766 (female) from July 2011-April 2012. Red dots indicate locations of stopovers and wintering site. Density contours reflect 50%, 75% and 90% kernel density. Dates with "?" indicate estimates made from longitude data only (during equinox).

Figure 2.3: Migration route of bird 765 (female) from July 2011-May 2012. Red dots indicate locations of stopovers and wintering site. Density contours reflect 50%, 75% and 90% kernel density. Dates with "?" indicate estimates made from longitude data only (during equinox).

Figure 2.4: Migration route of bird 441 (female) from July 2011-May 2012. Red dots indicate locations of stopovers and wintering site. Density contours reflect 50%, 75% and 90% kernel density. Dates with "?" indicate estimates made from longitude data only (during equinox).

Figure 2.5: Migration route of bird 439 (female) from July 2011-May 2012. Red dots indicate locations of stopovers and wintering site. Density contours reflect 50%, 75% and 90% kernel density. Dates with “?” indicate estimates made from longitude data only (during equinox).

Figure 2.6: Migration route of bird 006 (female) from July 2012-April 2013. Red dots indicate locations of stopovers and wintering site. Density contours reflect 50%, 75% and 90% kernel density. Dates with "?" indicate estimates made from longitude data only (during equinox).

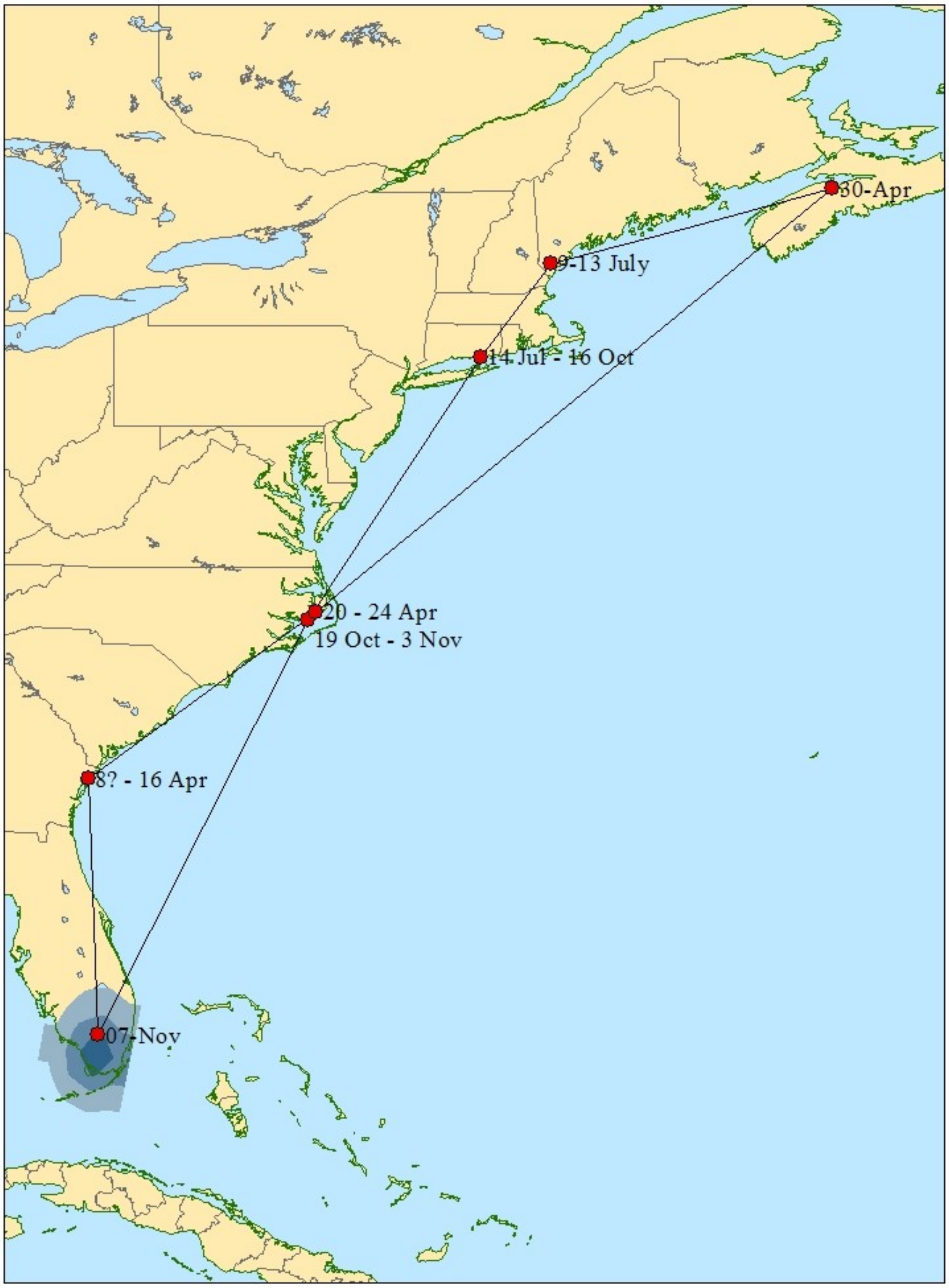

Figure 2.7: Migration route of bird 007 (female) from July 2012-April 2013. Red dots indicate locations of stopovers and wintering site. Density contours reflect 50%, 75% and 90% kernel density. Dates with "?" indicate estimates made from longitude data only (during equinox).

Figure 2.8: Migration route of bird 043 (female) from July 2012-April 2013. Red dots indicate locations of stopovers and wintering site. Density contours reflect 50%, 75% and 90% kernel density. Dates with "?" indicate estimates made from longitude data only (during equinox).

Figure 2.9: Migration route of bird 164 (female) from July 2012-April 2013. Red dots indicate locations of stopovers and wintering site. Density contours reflect 50%, 75% and 90% kernel density. Dates with "?" indicate estimates made from longitude data only (during equinox). This bird had severe clock drift so movements must be interpreted with caution.

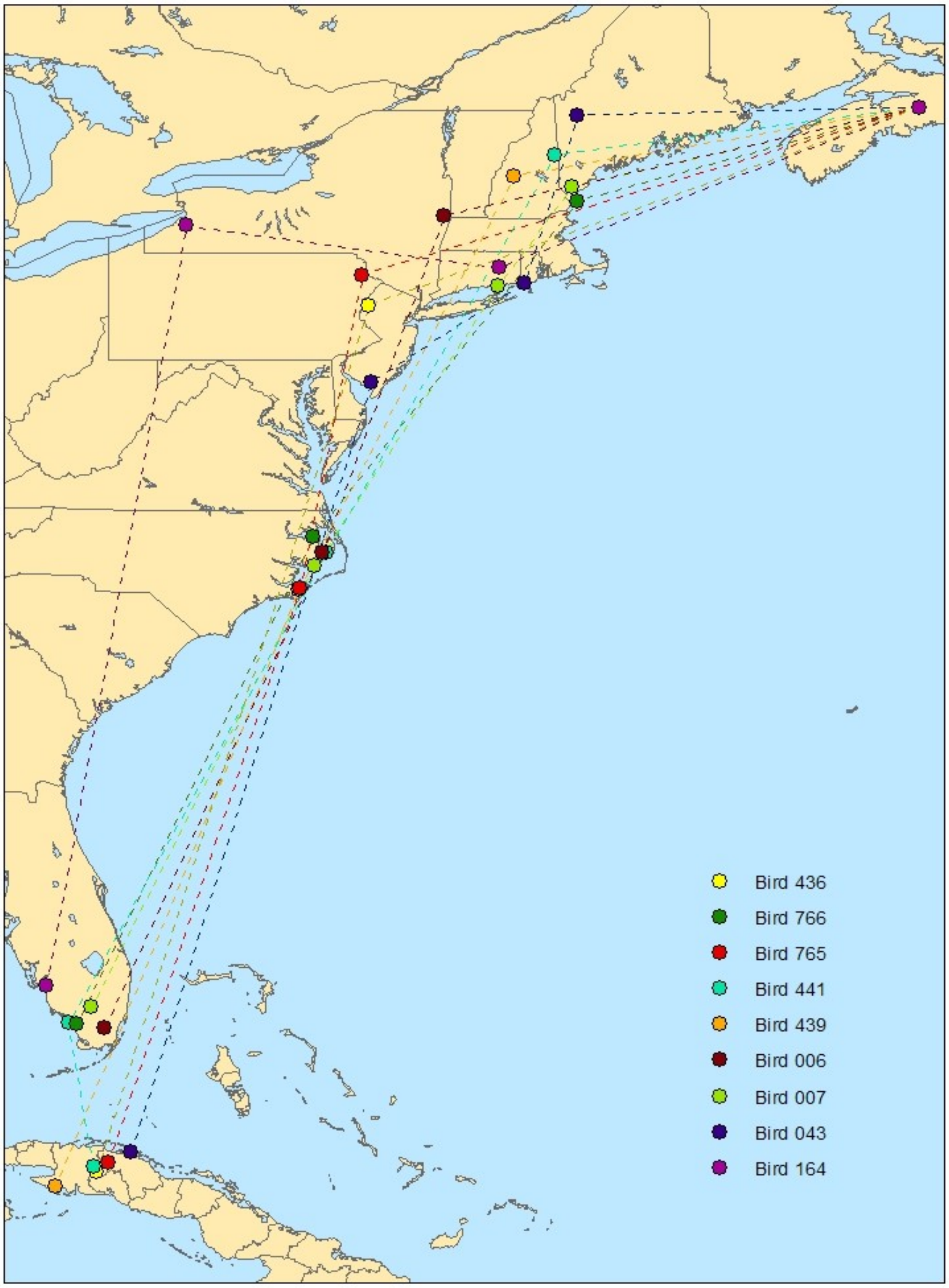

Figure 2.10: Autumn migration routes of all geolocator-tagged birds. Individually colour-coded points indicate the breeding grounds, stopover sites, and wintering sites.

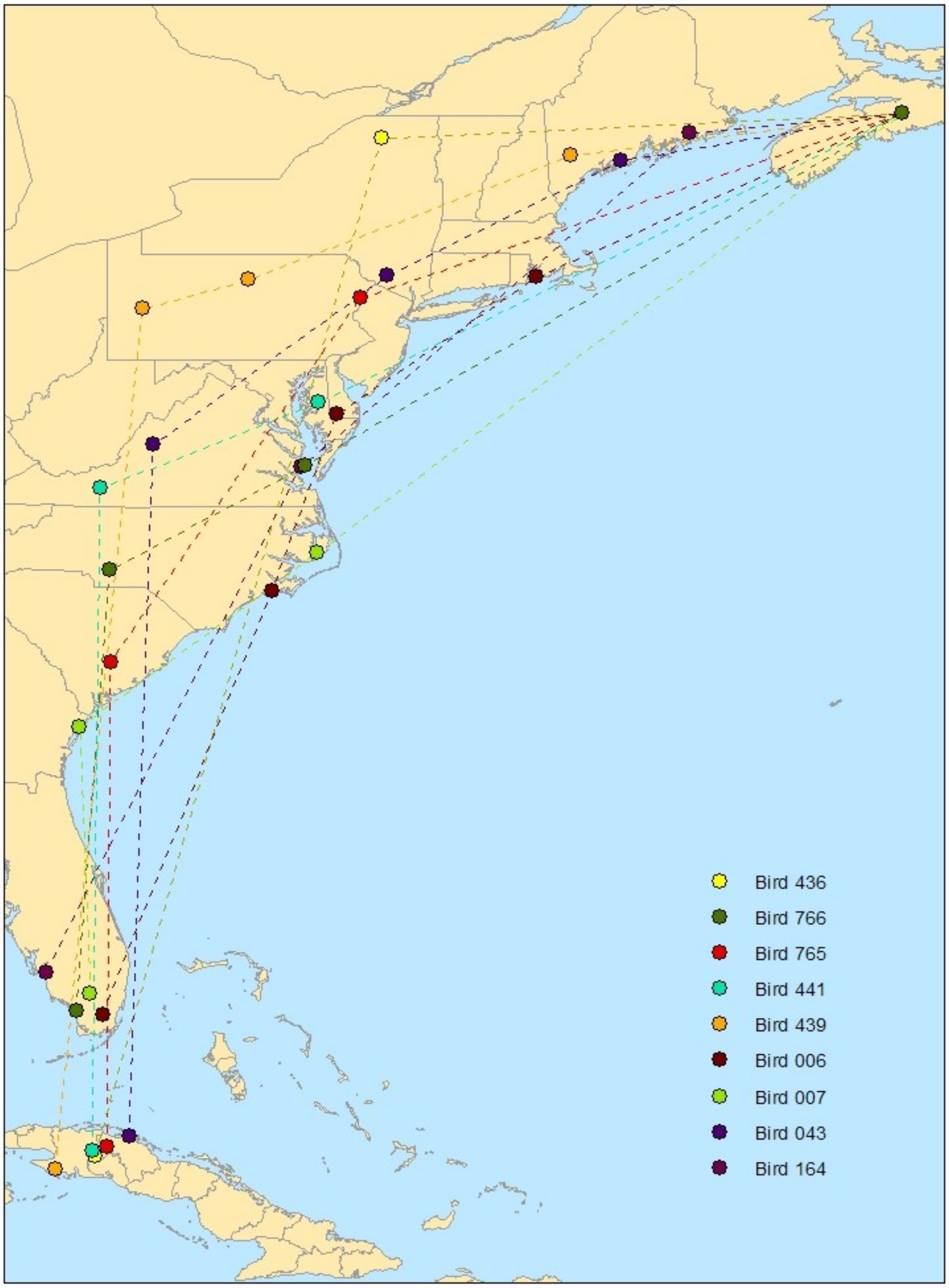

Figure 2.11: Spring migration routes of all geolocator-tagged birds. Individually colour-coded points indicate breeding grounds, stopover sites, and wintering sites.

2.4 Discussion

Tree swallows breeding in Nova Scotia began migration in July almost immediately post-breeding. All nine swallows had a long initial stopover in the northeastern United States from July until August or September, followed by a shorter stopover along the coast in October, before wintering in southern Florida or Cuba from November until March or April. Due to lengthy stopovers in the autumn, the duration of autumn migration is longer than the duration of spring migration, and consequently the rate of migration in spring is much faster than in autumn. No correlations between migratory events were found in this population.

The timing and location of autumn stopovers of birds in this study is consistent with a previous study that looked at the location of swallow roosts during autumn migration (Burney 2002). Swallows spend their nights in the non-breeding season in roosts. Roosts of 600 – 124 000 swallows (mostly tree swallows) in Montezuma National Wildlife Refuge, New York, were found from late July until late October (Burney 2002). Large roosts along the mid Atlantic coast were also noted in September, while Florida had many large roosts from December to March (Burney 2002). This study also supports Butler's (1988) hypothesis that northeastern populations migrate down the Atlantic coast to Florida and Cuba.

Although there are some similarities in migration strategy between individuals in the non-breeding season, there are also some interesting differences within and between individuals. First, unlike the females, the male swallow had only one autumn and spring stopover. The male also arrived back on the breeding grounds nine days earlier than the females in 2012. Although one male does not provide evidence of a pattern, male birds often arrive at the breeding grounds before females to claim good quality territories that will attract good quality mates (Morbey and Ydenberg 2001).

Second, four swallows wintered in Florida while five swallows continued on to Cuba. The swallows that wintered in Cuba spent one day flying from Florida to Cuba, so this decision does not seem to be energetically costly. Also, the average locations of individual tree swallows at each wintering site were not very far from one another (Figure 2.10), suggesting that tree swallows from this population may spend the winter together. However, due to the error inherent with geolocators it is impossible to know with any certainty at this time. Another study found that eight tree swallows breeding in Saskatchewan migrated to four different wintering locations (southern USA, the Bahamas, eastern Mexico, and the Yucatan Peninsula) while two swallows breeding in Wisconsin wintered at different sites (eastern Mexico and Florida), illustrating that not all individuals from the same breeding population use the same wintering grounds (Laughlin et al. 2013).

Third, it is interesting that spring migration routes are not as similar as autumn migration routes. Since spring migration occurs in 1-2 months rather than the 3-4 months of that in autumn, each swallow during spring migration may be moving as quickly as possible, only stopping when necessary due to poor weather or to refuel, resulting in the use of different stopover sites. The spring migration routes and stopovers of other species also often differ from their autumn migration routes and stopovers (Heckscher et al. 2011; Delmore et al. 2012; Callo et al. 2013), although the reasons are not clear.

Stopovers during migration are often necessary for birds to rest, refuel, or molt (Warnock 2010). The long autumn stopover (39-101 days) of the swallows in the study population may be related to molt, food availability, or poor condition. Tree swallows molt between mid-July and mid-November (Stutchbury and Rohwer 1990) and it is possible that molt of flight feathers in this population is mostly completed while stopping over in the northeastern US. The large numbers of roosting swallows in the northeastern US found by Burney (2002) also suggest there are many good quality roosting sites in this area with sufficient food to support many birds as they increase their energy stores for migration. Tree swallows from breeding populations in Saskatchewan, Ontario, and Wisconsin had an extended stopover of about one month in Louisiana, roosting in wetlands and sugarcane fields (Laughlin et al. 2013). At this time, however, molt was already complete, and most birds left during the sugarcane harvest, suggesting this location may be a good quality site for roosting (Laughlin et al. 2013). Other migrating aerial insectivores also have extended stopovers. For example, western kingbirds (*Tyrannus verticalis*) breeding in Oklahoma spent 62-85 days in northern Mexico before migrating to their wintering areas in central Mexico (Jahn et al. 2013). The stopover is thought to coincide with an increase in food due to the monsoon season, and is likely to co-occur with molt (Jahn et al. 2013). Purple martins (*Progne subis*) also spend about a month at pre-migratory roosts near their breeding grounds before rapidly migrating to Central America, likely to increase energy stores before continuing migration (Fraser et al. 2013). Based on these studies, long autumn stopovers seem to be a common occurrence for migrating aerial insectivores in North America.

Individual birds did not seem to consistently arrive late or early throughout the annual cycle, and migration rate was not correlated with migration distance or with date of departure from the breeding site. These findings are surprising, as other studies have found temporal relationships in passerine migration. For example, purple martins showed significant positive relationships between autumn migration initiation and arrival on the wintering grounds (Fraser et al. 2013). As well, red-backed shrikes (*Lanius collurio*) had a positive relationship between autumn migration initiation and arrival on the wintering grounds, as well as arrival on the breeding grounds the following spring, suggesting that individual birds are consistently early or late (Tottrup et al. 2012). Tree swallows may not show these relationships because their long stopovers in the northeastern US and along the mid-Atlantic coast may give even birds in poor condition enough time to improve their body condition so that they all arrive at their wintering grounds around the same date.

Understanding where swallows from different populations stop over and spend the winter may help us understand what is causing the differential decline of aerial insectivores across North America. This study identified important stopover sites in the northeastern US and North Carolina, and wintering sites in Florida and Cuba for birds breeding in Nova Scotia. If all swallows from Nova Scotia stop over and winter close together, they may be exposed to localized threats, and conservation efforts can be directed to these areas. If the migratory connectivity of different swallow populations can be determined through the use of geolocators, researchers can focus on protecting and improving the habitat of common areas in the hope of conserving and protecting swallow populations.

CHAPTER 3: CARRY-OVER EFFECTS IN TREE SWALLOWS

3.1 Introduction

In North America, much research on migratory birds is conducted during the breeding season. However, migratory birds spend only a few months on the breeding grounds, while the majority of the year is spent either at their wintering sites or on migration (e.g. Marra et al. 1998). Individuals are, however, likely to be affected by conditions throughout the annual cycle (Harrison et al. 2011); therefore, it is important to understand carry-over effects; that is, how conditions in one season affect fitness in a subsequent season (Norris and Marra 2007).

Carry-over effects from conditions on the wintering grounds may affect spring migration and reproduction the next summer. Birds overwintering in poorer environments who are unable to maintain their body mass (e.g. Studds and Marra 2005; Johnson et al. 2006) may begin spring migration later than those overwintering in good quality environments (e.g. Marra et al. 1998; Rockwell et al. 2012). This in turn can influence the timing of arrival on the breeding grounds (Marra et al. 1998; Rockwell et al. 2012) and the initiation of breeding (Sorensen et al. 2009). Breeding ground arrival time is especially important for males, who typically have to compete for territories and good quality mates (Morbey and Ydenberg 2001). Later arriving birds (Norris et al. 2004a; Rockwell et al. 2012) or birds in poor condition (Inger et al. 2010) are less likely to have high reproductive investment or successfully fledge their nestlings. Conditions on the wintering grounds can therefore affect both migration and reproductive success the following summer.

Similarly, events in the breeding season may also affect events following the breeding season, such as molt and migration. Delayed reproduction can cause an overlap of molt with reproduction (Morton 1992; Norris et al. 2004b), a faster molt before beginning migration (Conklin and Battley 2012), or a molt during migration (Norris et al. 2004b), which may negatively affect feather characteristics such as colour, symmetry, strength, and durability (Dawson et al. 2000; Norris et al. 2004b). Molting is energetically expensive (Dawson et al. 2000), and a faster molt that affects feather quality may affect flying ability, while a late molt may deplete energy needed for migration (Dawson et al. 2000). Delayed reproduction or poor body condition following breeding can also result in delayed migration (Morton and Pereyra 1994; Stutchbury et al. 2011; Camacho 2013), potentially affecting migration strategy, such as stopover length. Further, adults that lose their nests may be in better condition at the end of the breeding season and may migrate earlier and overwinter farther from the breeding grounds where conditions might be better (Bogdanova et al. 2011). Alternatively, unsuccessfully reproducing adults in better condition may be able to withstand harsher conditions, and thus may winter closer to the breeding grounds, allowing them an earlier return in the spring and better access to high-quality territories (Catry et al. 2013).

Carry-over effects can, therefore, potentially affect body condition and reproductive success, so it is important to understand how they impact bird populations. Understanding carry-over effects may be especially important for species such as aerial insectivores, which have experienced sharp declines in population size (McCracken 2008; Nebel 2010). Until recently, however, it has been difficult, if not impossible, to track small migratory birds such as aerial insectivores throughout the year. The advent of lightweight geolocators gives researchers the technology to uncover the full annual cycle of such birds and to therefore examine carry-over effects.

The little work that has been done on aerial insectivores suggests that carry-over effects from the wintering grounds on the breeding grounds also affect these species. For example, barn swallows (*Hirundo rustica*) followed over a number of years arrived on the breeding grounds earlier in years when wintering sites had high primary productivity (high normalized difference vegetation index [NDVI]) than in years with low primary productivity (low NDVI) (Saino et al. 2004b), and began breeding earlier and fledged more young (Saino et al. 2004a,b). House martin (*Delichon urbicum*) and common swift (*Apus apus*) populations were also positively related to primary productivity on the putative wintering grounds (Ambrosini et al. 2011). It is likely that events in the breeding season also carry-over into migration, but there have been no studies to examine whether this occurs in aerial insectivores.

The goal of this study was to examine the potential carry-over effects between breeding parameters and migration strategy in tree swallows breeding in Nova Scotia, Canada. Using geolocators, I determined if breeding parameters influenced migration by examining the relationships between brood size, fledging date, and female condition in the breeding season with autumn departure date, arrival on the wintering grounds, duration of migration, migration distance, migration rate, and the number of stopover days during autumn migration.

I predicted that adults with larger broods would have later departure dates and longer stopovers than adults with smaller broods. Adults raising larger broods may have smaller fat stores after raising their young than birds with smaller broods (e.g. Nur 1984), and if more time is required to increase energy stores, departure date and stopover length could be affected. I also predicted that adults with later fledging broods would depart the breeding grounds later and consequently arrive later on the wintering grounds than adults with early fledging broods. Finally, I predicted that birds in poor condition at the end of the breeding season would have delayed departure dates, longer stopovers, and slower migration rates than birds in better condition. Adults in poor condition at the end of the breeding season likely require more time to increase energy stores before migration than birds in good condition.

3.2 Methods

3.2.1 Study Site

I performed this study on box-nesting tree swallows at four study sites near Wolfville, Nova Scotia, Canada (45.07, -64.34; 45.07, -64.33; 45.07, -64.33; and 45.09, -64.29) from May to July 2011, 2012, and 2013 (see Leonard and Horn 1996 for details of the sites).

3.2.2 Breeding Parameters

I checked all nests every second day until the clutch was complete. I began checking nests again two days before the expected hatch day, and then I checked daily until all eggs had hatched. Nests were then checked every second day until day 18 (hatch day = day 1), when I checked nests daily until all nestlings had fledged. Fledging checks were done by covering the hole and opening the side just enough to see if there were nestlings inside. These late checks did not cause premature fledging.

3.2.3 Female Condition

In 2012, I removed 40 incubating females by hand from their nests two days before the expected hatch day of their eggs. I banded them with a Canadian Wildlife Service (CWS) band and a colour band to differentiate them from males later in the season. To determine female condition, I weighed the birds with a spring scale to the nearest 0.5 g and took tarsus measurements with digital calipers to the nearest 0.01 mm at this time and again when geolocators were deployed on 24 of these 40 females (see below). Using the weight and tarsus measurements, I used a scaled mass index (SMI) (see Peig and Green 2009) to assign a measure of condition during incubation and at time of deployment to each female. Females with a higher SMI were considered to be in better condition than females with a lower SMI. An additional 30 adult swallows were also tagged in 2011 (see below) as part of a different study but tarsus was not measured, so I do not have condition for these birds.

3.2.4 Geolocators

In 2011, 30 adult tree swallows (16 males and 14 females) were caught with nest box traps and tagged with geolocators (Lotek Wireless model MK12-S) when their nestlings were ~4 days old. The geolocators were attached using a leg loop harness made of 1 mm ethylenepropylene-diene rubber O-rings and weighed 0.96 g with the harness (≤5% of tree swallow body weight (~22 g)). Swallows were also weighed and banded with a CWS band at this time.

In 2012, 24 adult female tree swallows were caught with nest box traps and tagged with geolocators (Lotek Wireless model MK6740) when their nestlings were 12-

17 days old. I opted to tag females only because the recapture rate of males tagged the previous year was very low (see Chapter 4 for how females were selected). Geolocators were attached the same way as in 2011, but with the addition of a drop of cyanoacrylate adhesive (Krazy glue) on the geolocator to help secure it to the down. Geolocators with the harness weighed ≤1 g (≤5% of body weight).

I retrieved the geolocators in May and June of the year following deployment. All nesting females were checked for geolocators during incubation by removing the bird by hand from the nest. Forty-three males were also checked for geolocators during the nestling period in 2012 by trapping birds using nest box traps. When a tagged bird was recovered, I removed the geolocator and the bird was weighed and the tarsus measured.

Eight of the 30 (26.7%) swallows fitted with geolocators in 2011 returned to the study sites in 2012. Of these eight, two returned without their geolocators and one returned with geolocators that had unrecoverable data (2 males, 1 female). Nine of the 24 (37.5%) swallows tagged in 2012 returned to the study sites in 2013. Of these nine, four returned without geolocators, one returned with a geolocator that had unrecoverable data and one returned with a geolocator with such severe clock drift that it had to be excluded from the analyses. Therefore, in total, 17 of 54 (31.5%) tagged birds returned to the study sites, with eight geolocators (14.8%) providing data (1 male, 7 females).

3.2.5 Migration Parameters

Geolocator data were processed using BASTrack software (British Antarctic Survey) (see Chapter 2 for details). I considered the departure date for autumn migration to be the day when each bird moved 1 degree or more in longitude or latitude south/southwest (away from the breeding grounds), without returning to that location until the following year (Jahn et al. 2013). I considered arrival on the wintering grounds to be when latitude and longitude ceased to shift south or southwest and longitude fluctuated by no more than 4 degrees until the beginning of spring migration, which was defined as the bird moving 1 degree or more in longitude or latitude north/northeast (away from the wintering grounds) and not returning to that location until after the tag is recovered (Jahn et al. 2013; Stutchbury et al. 2011). Migration duration was defined as the number of days between the autumn migration departure date and arrival on the wintering ground (Tottrup et al. 2012), while migration distance was defined as the straight line distance between the breeding grounds, any stopovers, and the wintering grounds (Johnson et al. 2012). I calculated migration rate by dividing migration distance by migration duration, including stopover days (Fraser et al. 2013). I considered the birds to be at a stopover site when their location remained consistent for at least two days before migration continued in a southerly direction (Stutchbury et al. 2011). Because all birds had an initial stopover of 39 - 101 days in the northeastern US (see Chapter 2), I also looked at the number of stopover days in the northeastern US separately from the total number of stopover days.

3.2.6 Statistical Analysis

I tested for inter-correlations amongst breeding parameters and found that egg initiation date and fledging date were highly correlated ($r = 0.81$, $n = 28$, $P < 0.0001$) and, therefore, include only fledging date in the analyses. As the later event, it seems the more likely of the two variables to affect migration parameters. Clutch size and brood size were also highly correlated (r = 0.61, n = 35, P = 0.0001), so I restricted my analyses to examining only the effects of brood size on migration parameters. Condition at incubation and condition at deployment were also significantly correlated (r = 0.47, n = 24, P = 0.02) so I only include condition at deployment in my analyses. Although there are correlations between some of the migration parameters (e.g. departure date and migration duration), I included all parameters in the analyses, as I was interested in how each was affected by breeding parameters.

Because of the small sample size, I used Spearman's correlations to compare breeding parameters with each migration parameter. Although I potentially had information for eight tagged birds, for analyses involving brood size and fledging date I had a final sample size of six because the nests of two birds from 2011 were not monitored, so that information is not available. Also, I had information on condition for only three females, because only three birds tagged in 2012 returned with usable geolocator data in 2013. In the latter case, I did not analyze these data statistically, but rather graphed the data to look for trends.

3.3 Results

Brood size showed no significant relationships with any of the migration parameters that I measured (Table 3.1, Figure 3.1). Fledging date also showed no significant relationships with any of the migration parameters except autumn departure date (Table 3.1, Figure 3.2). Visual inspection of the graphs relating condition to migration parameters suggest that birds in better condition at deployment may spend less time at the stopover in the northeastern US than birds in poorer condition (Figure 3.3).

Table 3.1: Spearman correlations between breeding parameters (brood size, fledging date) and migration parameters (departure date, arrival date, duration, distance, rate, stopover length, and length of stopover in the northeastern United States [NE USA]). Significant P values are bolded.

Breeding Parameter	**Migration Parameter**	r_s	**n**	**P**
Brood size	Departure	-0.26	6	0.66
	Arrival	0.00	6	1.00
	Duration	0.17	6	0.71
	Distance	0.17	6	0.71
	Rate	-0.17	6	0.71
	Stopovers	0.17	6	0.71
	NE USA	-0.68	6	0.14
Fledging date	Departure	0.87	6	**0.03**
	Arrival	0.00	6	1.00
	Duration	-0.67	6	0.17
	Distance	-0.23	6	0.66
	Rate	0.38	6	0.50
	Stopovers	-0.67	6	0.18
	NE USA	0.64	6	0.18

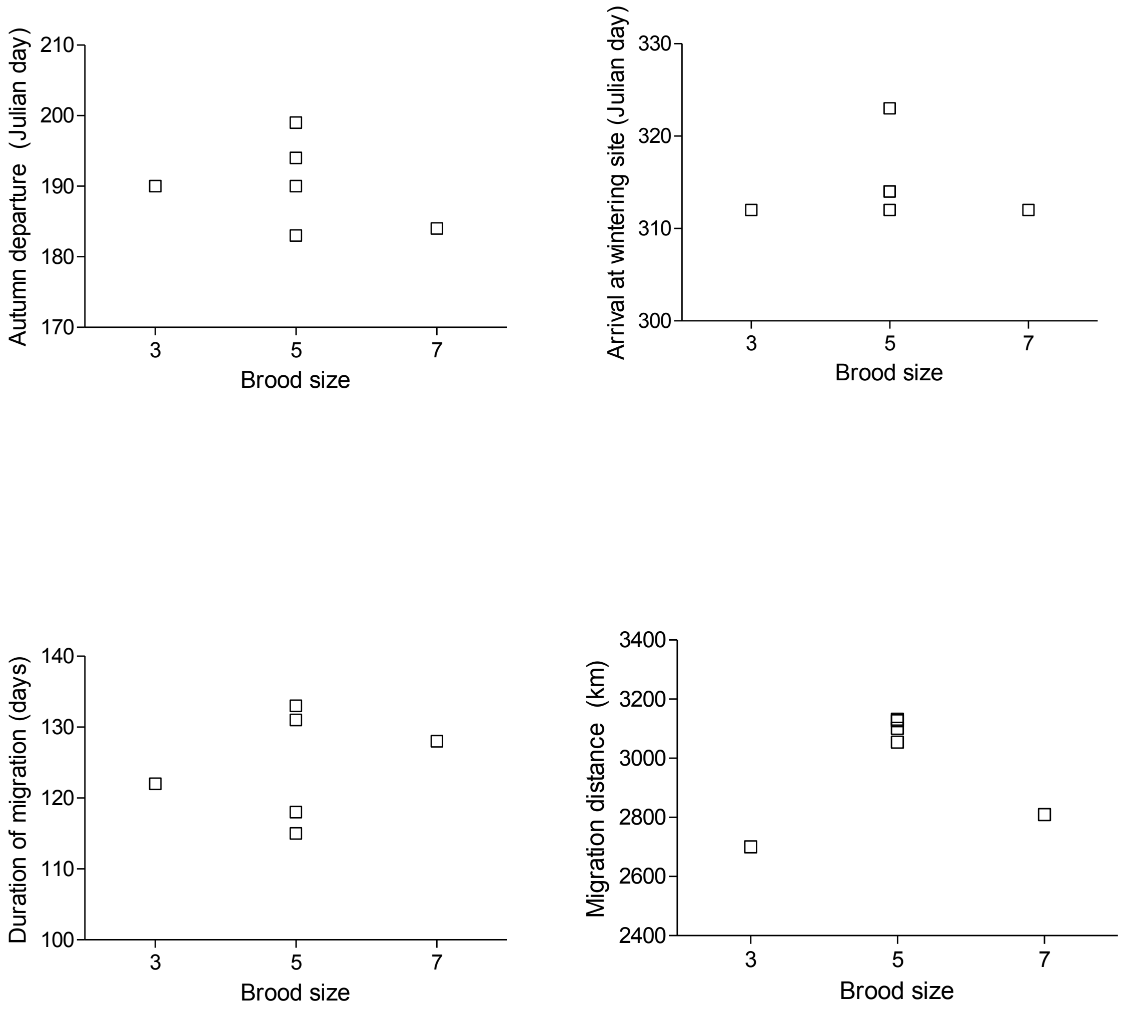

Figure 3.1: The relationship between brood size and autumn departure date (Julian day); arrival on the wintering site (Julian day); duration of migration; migration distance (km); rate of migration (km/day); number of stopover days; and number of stopover days in the northeastern US in geolocator-tagged tree swallows (*continued on page 48*).

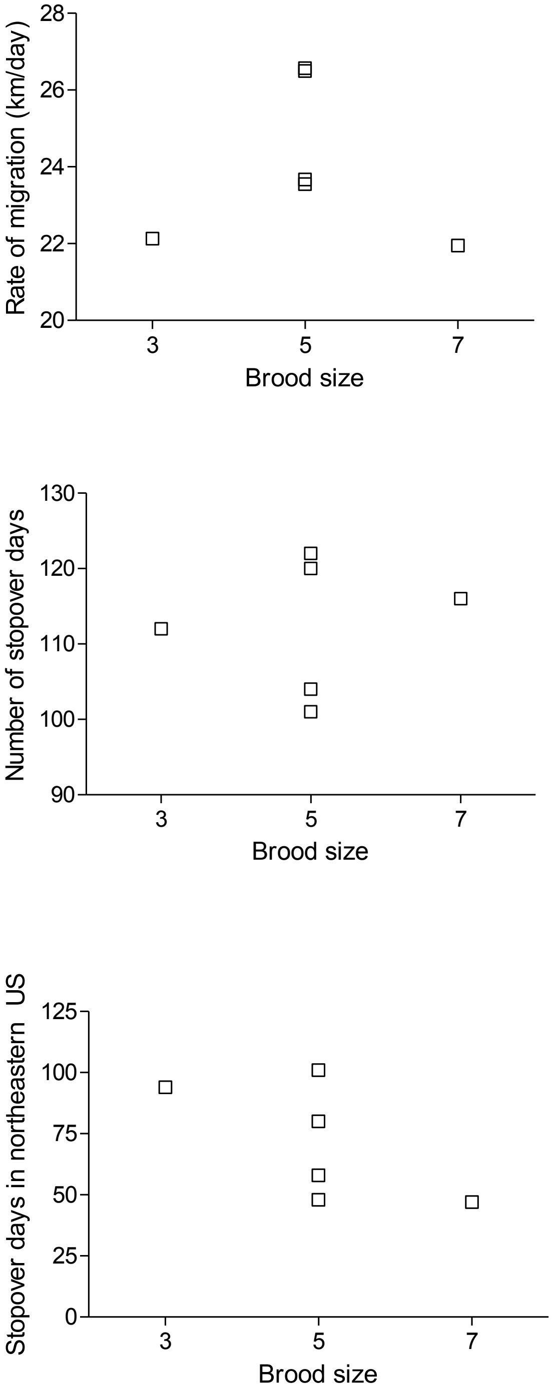

Figure 3.1 (*cont.*): The relationship between brood size and autumn departure date (Julian day); arrival on the wintering site (Julian day); duration of migration; migration distance (km); rate of migration (km/day); number of stopover days; and number of stopover days in the northeastern US in geolocator-tagged tree swallows.

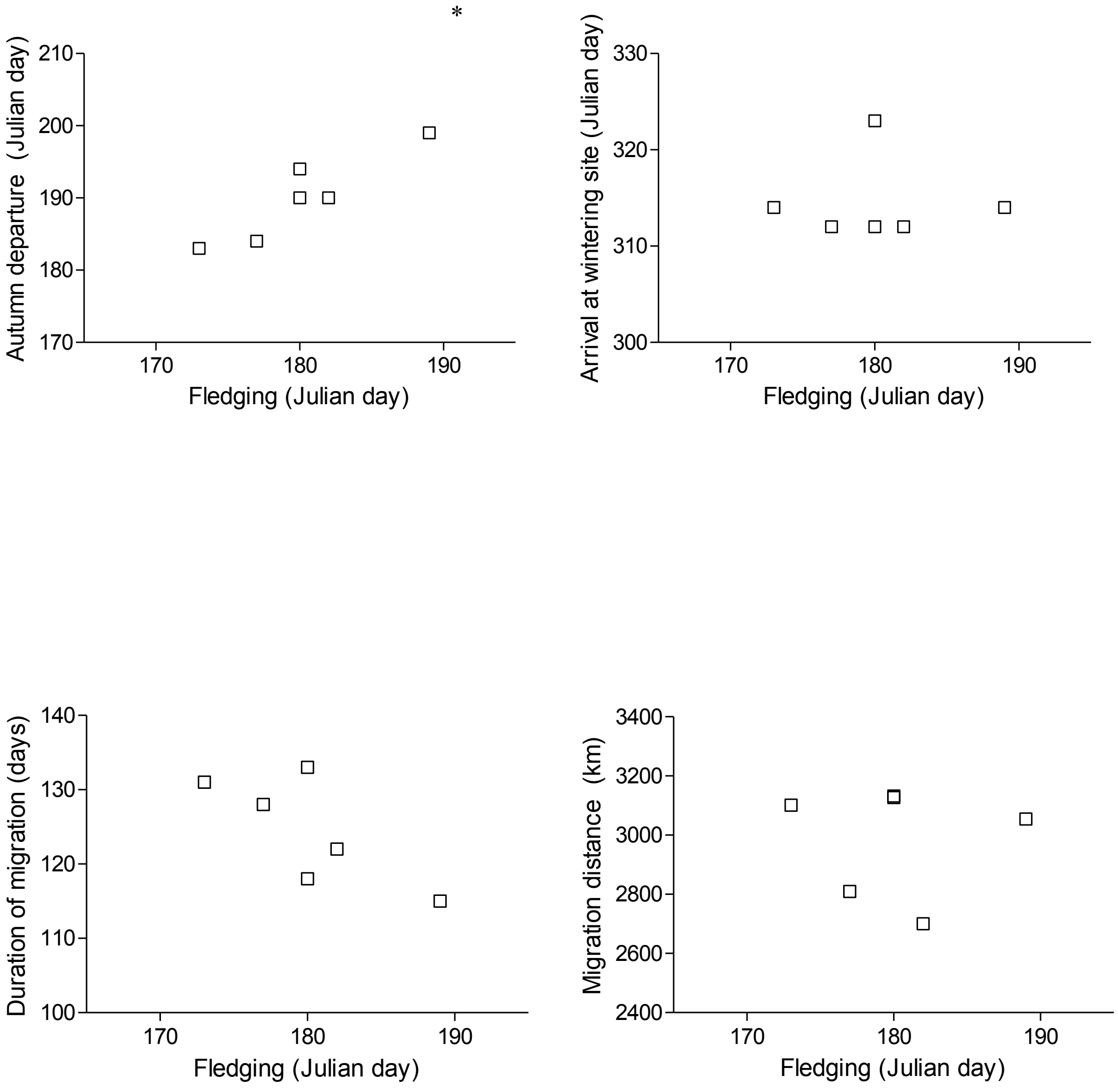

Figure 3.2: The relationship between fledging date (Julian day) and autumn departure date (Julian day); arrival on the wintering site (Julian day); duration of migration; migration distance (km); rate of migration (km/day); number of stopover days; and number of stopover days in the northeastern US in geolocator-tagged tree swallows (*continued on page 50*).

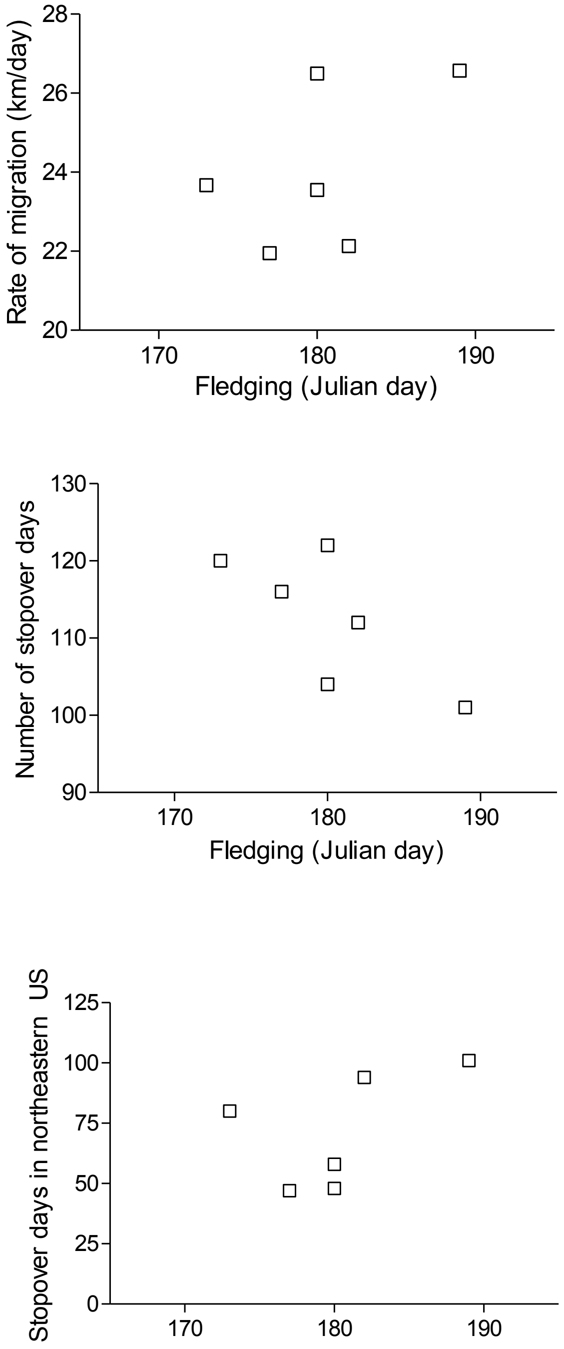

Figure 3.2 (*cont.*): The relationship between fledging date (Julian day) and autumn departure date (Julian day); arrival on the wintering site (Julian day); duration of migration; migration distance (km); rate of migration (km/day); number of stopover days; and number of stopover days in the northeastern US in geolocator-tagged tree swallows.

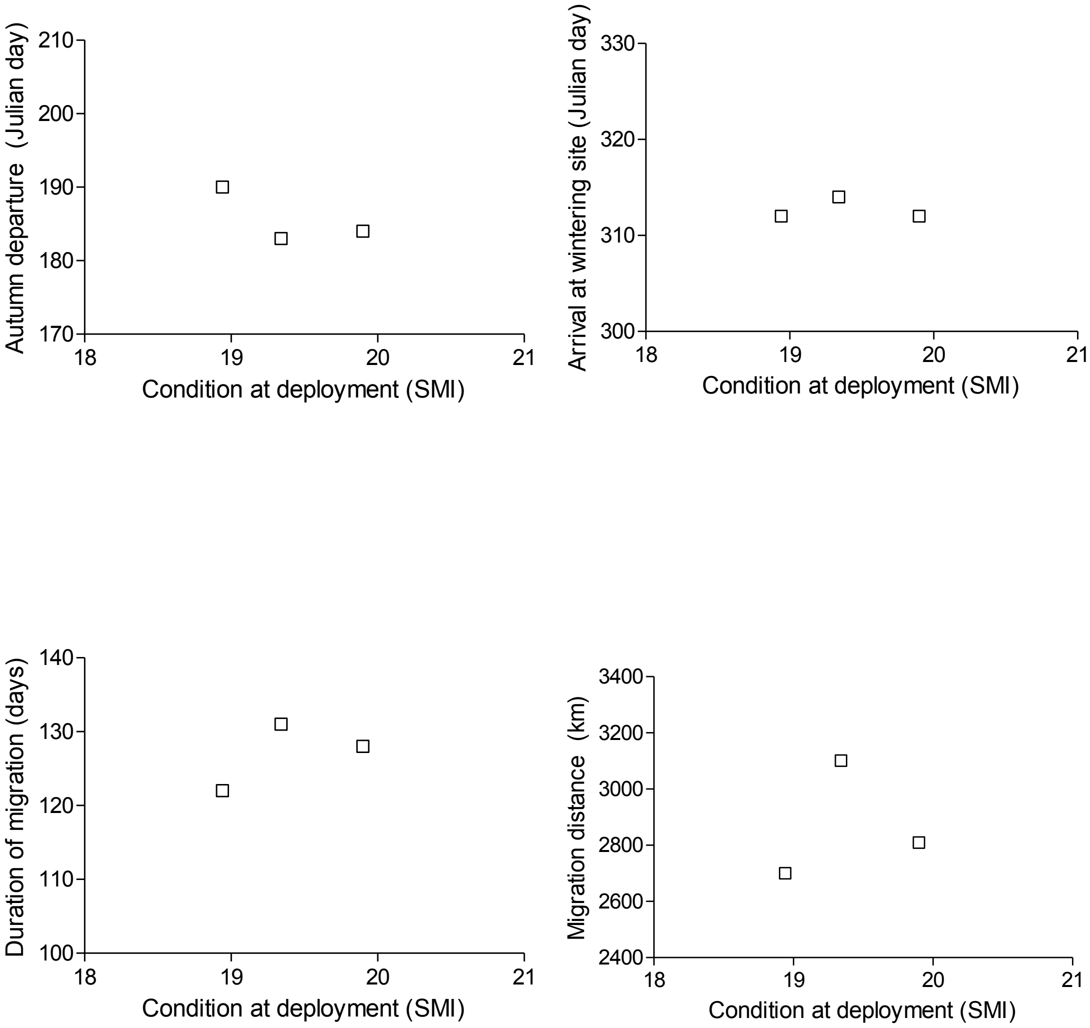

Figure 3.3: The relationship between condition at deployment and autumn departure date (Julian day); arrival on the wintering site (Julian day); duration of migration (days); migration distance (km); rate of migration (km/day); number of stopover days; and number of stopover days in the northeastern US in geolocator-tagged tree swallows. Condition is calculated using the scaled mass index (SMI) and is in grams. A higher SMI indicates better condition (*continued on page 52*).

Figure 3.3 (*cont.*): The relationship between condition at deployment and autumn departure date (Julian day); arrival on the wintering site (Julian day); duration of migration (days); migration distance (km); rate of migration (km/day); number of stopover days; and number of stopover days in the northeastern US in geolocator-tagged tree swallows. Condition is calculated using the scaled mass index (SMI) and is in grams. A higher SMI indicates better condition.

3.4 Discussion

I found that tree swallows with late-fledging nestlings began autumn migration significantly later than those with early-fledging nestlings. Although my sample size was very small, there was also some suggestion that swallows in better condition at deployment spent less time at the stopover in the northeastern US than those in poorer condition. Otherwise, there were no significant relationships among breeding and migration parameters.

To my knowledge there have been no studies examining the relationship between brood size and migration parameters. One possibility is that females only lay as many eggs and hatch as many young as they can care for, with better quality females laying more eggs earlier than poorer quality females (Nur 1986). My population showed a near significant relationship between condition during incubation and brood size ($r = 0.31$, $n = 34$, $P = 0.08$). If females limit their brood size according to their quality, larger broods may not cost good-quality females more than small broods cost poor-quality females, and therefore there might be no expectations for a relationship between brood size and migration parameters. Another possibility is that there may be a relationship but I do not have the power to detect a difference in the relationships between breeding parameters, such as brood size, and migration strategy.

Swallows with later fledging nestlings began autumn migration later than those with earlier fledging nestlings. This result is consistent with studies done on savannah sparrows (*Passerculus sandwichensis*) and white-crowned sparrows (*Zonotrichia leucophrys oriantha*) that showed departure from the breeding grounds was positively correlated with the date of breeding completion (Morton and Pereyra 1994; Mitchell et al.

2012). These studies, however, did not follow individuals during migration so it is unknown if fledging date had further effects on migration strategy.

Despite a later departure, birds with later fledging nestlings did not arrive later on the wintering grounds than birds with earlier fledging nestlings. Post-hoc tests reveal a negative relationship between departure date and duration of migration ($r = -0.77$, $n = 8$, $P = 0.025$) and between departure date and the number of stopover days ($r = -0.83$, $n = 8$, $P = 0.01$). This relationship suggests that swallows are able to compensate for a delayed departure during migration by spending less time at stopover sites rather than flying faster. Similarly, wood thrushes (*Hylocichla mustelina*) departing the breeding grounds later had shorter stopovers and arrived on the wintering grounds at the same time as earlier departing birds (Stuchbury et al. 2011). Late departing Cory's shearwaters (*Calonectris diomedea*) also arrived on the wintering grounds at the same time as early departing birds (Catry et al. 2013). In contrast, the arrival of purple martins (*Progne subis*) on the wintering grounds was largely predicted by departure date from the breeding grounds (Fraser et al. 2013).

The importance of an early arrival on the wintering grounds may depend on whether or not a species is territorial during the winter. If a species is territorial in the winter, it may be beneficial to arrive earlier on the wintering grounds to claim good quality winter territories (Brown and Sherry 2008). If a species is not territorial, like tree swallows, arrival time may not be as important. However, early departing swallows may benefit from increased time at stopovers in order to increase energy reserves and decrease the chance of mortality during migration (Stutchbury et al. 2011), thereby arriving at the wintering grounds at the same time as later departing swallows. Alternatively, swallows may quickly migrate to large roosts and then continue migration en masse when environmental conditions decline.

Swallows in better condition at the time of geolocator deployment seemed to spend fewer days at the stopover in the northeastern US. These results suggest an interesting pattern but with such a small sample size, more data are needed to say anything with certainty. Other studies have, however, shown similar results. For example, wood thrushes in better condition at the end of the breeding season crossed into the tropics earlier than those in poorer condition (Stutchbury et al. 2011). Similarly, adult bluethroats (*Luscinia svecica*) and spotted flycatchers (*Muscicapa striata*) with larger fat stores spent less time at stopovers than adults with smaller fat stores (Biebach 1985; Ellegren 1991). Swallows from my study population that were in better condition at the end of the breeding period tended to have earlier fledging dates ($r = -0.45$, $n = 19$, $P = 0.055$), so the shorter initial stopover is not likely related to making up time during migration. Instead, shorter stopovers may occur because swallows in better condition require less time at the first stopover to build energy reserves before continuing on with their migration (Biebach 1985).

This study revealed for the first time that breeding parameters have carry-over effects on migration in tree swallows. Fledging date especially seems to affect migration strategy, with adults raising late-fledging nestlings departing later in the autumn than those with early-fledged nestlings, but compensating for this by spending less time at stopover sites in order to arrive on the wintering grounds around the same time as earlier departing birds. Unfortunately, my sample size was small and so I was unable to explore some relationships in as much depth as originally planned. My results suggest that tree swallows may be able to adjust their migration strategy according to their circumstances. This might enable swallows to compensate during migration for shifts in the timing of breeding, for example due to poor weather or changes in insect availability.

CHAPTER 4: THE EFFECTS OF GEOLOCATORS ON TREE SWALLOWS

4.1 Introduction

Advances in technology have allowed researchers to probe further into the intricacies of the natural world. One area that has long been of interest is the movement of birds, both within the breeding season and during migration to wintering sites (Carlisle et al. 2009). Tracking birds visually is a difficult task due to their size and mobility, and it is nearly impossible to physically follow an individual during migration. However, various technologies have been developed to help researchers locate and track individual birds.

Simple approaches, such as banding, and more advanced approaches, including technology such as radio transmitters and satellite tags, have all contributed to our knowledge of bird movements. The earliest and most basic approach, banding, involves attaching metal or coloured bands to the bird's leg in the breeding season and then re-sighting or recapturing the banded birds in the non-breeding season. Banding has been used to identify migration routes and wintering locations (e.g. Butler 1988), but banded birds are re-sighted infrequently, reducing its effectiveness for tracking individuals. Radio transmitters, which transmit radio waves that can be picked up with an antenna, allow researchers to precisely locate tagged birds, but only within a limited range. Radio transmitters have revealed small-scale movements in the breeding season such as habitat use (e.g. Macias-Duarte and Panjabi 2013) and dispersal (e.g. King and Belthoff 2001), and helped determine home range size (e.g. Mrykalo et al. 2011). However, radio transmitters cannot be used for tracking birds over long distances or over physical barriers such as oceans. Alternatively, satellite tags, which transmit real time locations via satellite, allow researchers to determine the location of the bird over large spatial and temporal scales and have been used to identify migration routes and wintering sites of several species (e.g. Gschweng et al. 2008). Satellite tags are, however, heavy, and their use is limited to larger birds (>100 g). Although these various technologies have been successful in studying bird movements, they all have some limitations. In addition, they may have associated costs for the birds carrying the tags.

Reviews on the costs of tags have found mixed results (radio tags and data loggers: Calvo and Furness 1992; radio tags: Godfrey and Bryant 2003; all tags: Barron et al. 2010). Radio transmitters, for example, have been associated with decreases in survival in gray partridges (*Perdix perdix*) (Carroll 1990), reproductive success in spotted owls (*Strix occidentalis*) (Foster et al. 1992), and parental investment in northern cardinals (*Cardinalis cardinalis*) (Barron et al. 2013), as well as changes in behaviour in acorn woodpeckers (*Melanerpes formicivorus*) (Hooge 1991). Satellite tags have been associated with decreases in survival in common eiders (*Somateria mollissima*) (Fast et al. 2011) and changes in provisioning behaviour in Cory's shearwaters (*Calonectris diomedea*) (Villard et al. 2011). However, several other studies have found no effects of tags. For example, survival and body mass in Bicknell's thrushes (*Catharus bicknellii)* (Townsend et al. 2012), reproductive success in snowy owls (*Bubo scandiacus*) (Therrien et al. 2012), parental investment in hooded warblers (*Wilsonia citrina*) (Neudorf and Pitcher 1997), and behaviour in northern gannets (Hamer et al. 2007) did not appear to be affected by various kinds of tags. The impact of tags may, therefore, depend on a variety of factors including differences in life history, foraging style and body size. The mixed results of these studies suggest that it may take many studies across a variety of species to fully understand the effects of these tags, and that effects may be species-specific.

In the last few years, geolocators, which rely on light levels to estimate longitude and latitude, have been increasingly used to reveal the migration routes and wintering grounds of birds that are too small to carry satellite tags (e.g. Stutchbury et al. 2009). It appears that geolocators, like other tags, may also have some negative effects on the bearer. A recent review covering a broad range of species found that geolocators were associated with lower return rates and poorer condition (Constantini and Moller 2013), and short-distance migrants and small species seemed to be particularly affected (Bridge et al. 2013; Constantini and Moller 2013). Decreased hatching and fledging success have also been associated with parents carrying geolocators in lesser kestrels (*Falco naumanni*) and common terns (*Sterna hirundo*) (Rodriguez et al. 2009; Nisbet et al. 2011; but see northern wheatears (*Oenanthe oenanthe*), Schmaljohann et al. 2012). However, other reproductive measures such as nestling weight and nestling survival appeared not to be affected by tagged parents in common terns and red-backed shrikes (*Lanius collurio*) (Nisbet et al. 2011; Tottrup et al. 2012). Geolocators, like other tags, seem to have mixed effects across species.

Negative effects of tags are thought to be caused by increased energy requirements and changes in aerodynamics due to increased weight and drag (Barron et al. 2010; Constantini and Moller 2013). Heavier tags can decrease reproductive success (Sibly and McCleery 1980) and survival (Warner and Etter 1983), and change behaviour (Hooge 1991), likely because of increased energy requirements when carrying a heavy tag. Most researchers try to mitigate these effects by limiting the weight of their tags to less than 3 or 5% of the bird's body weight (e.g. Bachler et al. 2010; Nisbet et al. 2011; Arlt et al. 2013; Callo et al. 2013; Jahn et al. 2013). However, there seems to be no scientific reason for the adoption of this rule (Barron et al. 2010), and no difference in the effect size of a device weighing 3% of body weight vs. 5% of body weight (Barron et al. 2010). Tags have also been shown to significantly increase drag, irrespective of attachment type, at least when examined on a preserved common swift (*Apus apus*) (Bowlin et al. 2010). The drag was higher, however, with a harness that wrapped over the wings than with a leg-loop harness (Bowlin et al. 2010). Similarly, in another study using live rose-coloured starlings (*Sturnus roseus*), a harness alone increased drag as much as a harness with an attachment, but drag was higher with the attachment of an antenna (Pennycuick et al. 2012). Increases in energy expenditure and changes in aerodynamics may reduce flying and foraging ability, which may in turn affect fitness (Barron et al. 2010).

Increases in weight or drag associated with geolocators seem to particularly affect aerial foragers, including aerial insectivores (Constantini and Moller 2013). Geolocators have increasingly been used to gather information on the life history and habitat use of aerial insectivores. The benefits of obtaining this information are obvious, but may be outweighed by the costs to the bird, especially as aerial insectivores are declining across North America (McCracken 2008; Nebel et al. 2010). More information regarding potential negative effects of geolocators on the survival and reproduction of aerial insectivores is needed to determine the costs, if any, of carrying these tags.

The purpose of my study is to determine the effects of geolocators on female tree swallows breeding in Nova Scotia, Canada. Tree swallows are aerial insectivores that migrate to the southern United States, Cuba, and Central America (Butler 1988; Chapter 2). I compared return rates, reproductive success, and condition between geolocator-tagged and untagged swallows.

4.2 Methods

4.2.1 Study Site

I conducted this study from May to July 2012 and 2013 at two long-running study sites near Wolfville, Nova Scotia, Canada (45.07, -64.34; 45.07, -64.33; see Leonard and Horn 1996).

4.2.2 Breeding Parameters and Female Condition

I performed nest checks every two days starting on 7 May 2012 and 6 May 2013 to determine clutch initiation dates. Once incubation began, nests were not checked again until two days before the expected hatch date. I then checked nests daily until all eggs had hatched, after which I checked them every second day until day 18 post-hatch (hatch day = day 1), when I again checked them daily to determine fledging date. I checked for fledging by covering the hole with my hand and opening the nest box just enough to see if there were still nestlings inside. These late checks did not cause premature fledging.

I weighed nestlings with a spring scale to the nearest 0.5 g on day 6 or 7 post-hatch, when they were in a period of rapid growth, and then again at day 13 post-hatch, when they reached their peak mass (McCarty 2001). At day 13, I also banded each nestling with a Canadian Wildlife Service (CWS) band.

In 2012, 40 female swallows were weighed with a spring scale to the nearest 0.5 g and tarsus was measured with digital calipers to the nearest 0.01 mm two days before the expected hatch date of their eggs. In 2013, all recaptured birds were weighed and measured again during incubation. I used weight and tarsus length to determine female condition in 2012 and 2013 using a scaled mass index (SMI) (see Peig and Green 2009). This index provides a predicted body mass for each individual standardized to the same tarsus length, to account for natural differences in weight due to size. A higher SMI, therefore, indicates better condition than a lower SMI.

4.2.3 Geolocators

In 2012, I removed 40 females from their nest boxes two days before the expected hatch date of their eggs and banded them with a CWS band and a colour band, so they could be distinguished from males later in the season when geolocators were deployed. I only tagged females because the recapture rate of males from the previous year was low.

When nestlings were 12-17 days old, 24 of the 40 females were caught with nest box traps and tagged with geolocators. Due to the late arrival of the geolocators from the manufacturer and high rates of predation (see below), I could not select females at random for tagging. Therefore, once the tags arrived, I tagged the first 24 females I caught. I attached the geolocators (Lotek Wireless model MK6740) with a figure eight leg loop harness (≤1 g combined weight and ≤5% of adult body weight). Harnesses were made of 1mm ethylenepropylene-diene rubber O-rings. I used a drop of cyanoacrylate adhesive (Krazy glue) to attach the main body of the geolocator to the female’s down, and I arranged surrounding feathers to cover the geolocator and reduce drag.

In May and June 2013, I checked all incubating females for bands and geolocators once incubation began. I weighed and took tarsus measurements of all banded females; if the female had a geolocator it was removed before measurements were taken.

4.2.4 Statistical Analysis

My intention was to compare tagged and untagged birds that were matched for initiation dates and clutch sizes. Unfortunately, two problems occurred during the 2012 field season that made doing so difficult. The first was that the geolocators arrived when the earliest breeders were preparing to fledge their young, meaning that females that received tags tended to be later breeders. The second problem was that one field site experienced an unusually high level of predation and so eight of the original 40 females abandoned their nests following predation. Ultimately then, not all untagged females were available as controls because many either began breeding significantly earlier than tagged birds or suffered predation whereas the tagged birds had not. Therefore, to match tagged and untagged birds as closely as possible, I restricted my groups to tagged and untagged females that initiated their nests within two days of each other, leaving me 17 tagged and 15 untagged females before migration. Of these birds, 8 tagged and 4 untagged females returned following migration and were used for post-migration comparisons of reproductive success and condition. For return rates, I restricted the comparison to untagged females that had not experienced complete nest predation because predation in the previous season could negatively influence return rates (Nesbitt Styrsky 2005). In this analysis, I had 17 tagged and 7 untagged females for comparison.

To determine if the tagged and untagged females initially differed from one another in 2012, I used two-tailed t-tests or Mann-Whitney U tests (when data were not normally distributed) to compare egg initiation date, clutch size, and condition between tagged and untagged swallows in 2012. Tagged and untagged females did not differ significantly in egg initiation dates (mean ± SE, tagged: Julian day 137.12 ± 1.77, untagged: Julian day 135.93 ± 2.17; $U = 84.5$, $n_1 = 17$, $n_2 = 15$, $P = 0.11$), clutch size (mean ± SE, tagged: 5.94 ± 0.16 eggs, untagged: 5.73 ± 0.15 eggs; $t = 0.03$, $df = 30$, $P = 0.36$), or condition during incubation (mean ± SE, tagged: 22.79 ± 0.51 g, untagged: 23.25 ± 0.54 g; $t = 0.61$, $df = 29$, $P = 0.55$).

Then, to determine if tagged birds differed from untagged birds following migration, I used a chi-square test to examine if return rates differed between the two groups. I then used t-tests or Mann-Whitney U tests to compare egg initiation date, clutch size, fledging success (the proportion of nestlings fledged from the number of eggs laid), nestling weight at day 6/7 and day 13 post-hatch, and condition between tagged and untagged swallows in 2013. I also did within-individual comparisons using the subset of birds that returned from migration to look at variation between 2012 and 2013. I used repeated measures two-way ANOVAs with year and treatment (tagged, untagged) as variables to determine if egg initiation date, clutch size, and condition of tagged and untagged birds differed between 2012 and 2013. Fledging success and nestling weight were not included in this analysis because of the predation that occurred in 2012.

I used GraphPad Prism 5 (San Diego, California, GraphPad Software) to perform all statistical analyses. Data were tested for normality using the D'Agostino and Pearson omnibus normality test. All t-tests were two-tailed. Results were considered significant when $P \leq 0.05$. Averages are presented as mean ± SE. Four tagged swallows lost their geolocators sometime during the year. I therefore conducted two sets of analyses when examining the effects of the tags. I compared all birds that were initially tagged and returned to the site (i.e. all tagged) versus the untagged birds. I also compared only those birds that returned still carrying a tag (i.e. return with tag) versus the untagged birds.

4.3 Results

4.3.1 Return Rate

Return rates were not significantly different between tagged and untagged birds ($\chi^2 = 0.035$, df = 1, P = 0.85). Eight of 17 tagged females (47%) returned in 2013, with four still carrying geolocators, while three of seven untagged females (43%) returned.

4.3.2 Breeding Parameters and Female Condition

Across female comparison

Among females that returned, there was no significant difference in egg initiation date, clutch size, fledging success, or average nestling weight between tagged and untagged females in 2013, including only females that returned with tags (Table 4.1, Figures 4.1-4.4).

Table 4.1: Mann-Whitney U tests of egg initiation date, clutch size, fledging success, and average nestling weight on day 6/7 and day 13 for untagged and tagged females (all tagged) in 2013, as well as untagged females and females that returned still carrying their geolocators (return with tag) in 2013.

	All tagged			**Return with tag**		
	U	**n**	***P***	***U***	**n**	***P***
Egg initiation	12.0	8, 4	0.55	6.0	4, 4	0.69
Clutch size	10.0	8, 4	0.32	3.5	4, 4	0.23
Fledging success	11.5	8, 4	0.46	8.0	4, 4	0.88
Nestling weight D6/7	11.0	8, 3	0.92	2.0	4, 3	0.23
Nestling weight D13	8.0	7, 3	0.67	4.0	3, 3	1.00

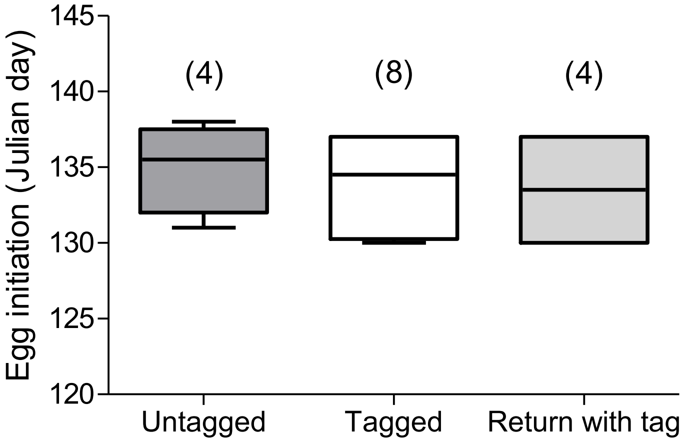

Figure 4.1: Egg initiation date in 2013 for female tree swallows without (untagged) geolocators, with (tagged) geolocators, and those still carrying the geolocator (return with tag). Boxes represent the range between the first and third quartile and the line inside the box represents the median. Whiskers represent the minimum and maximum values.

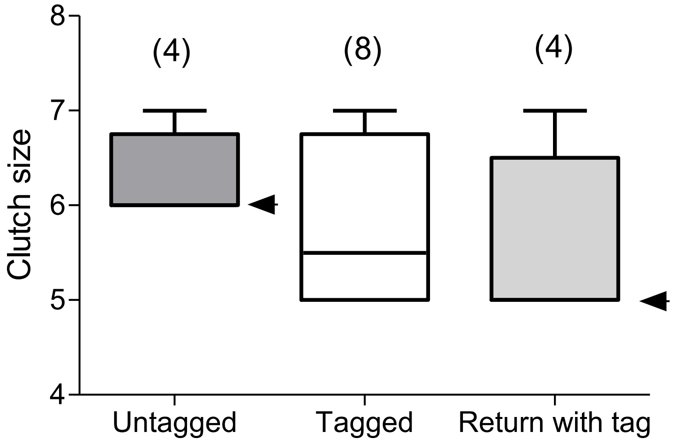

Figure 4.2: Clutch size in 2013 of female tree swallows without (untagged) geolocators, with (tagged) geolocators, and those still carrying the geolocator (return with tag). Boxes represent the range between the first and third quartile and the line inside the box represents the median. Whiskers represent the minimum and maximum values. Arrows point to median.

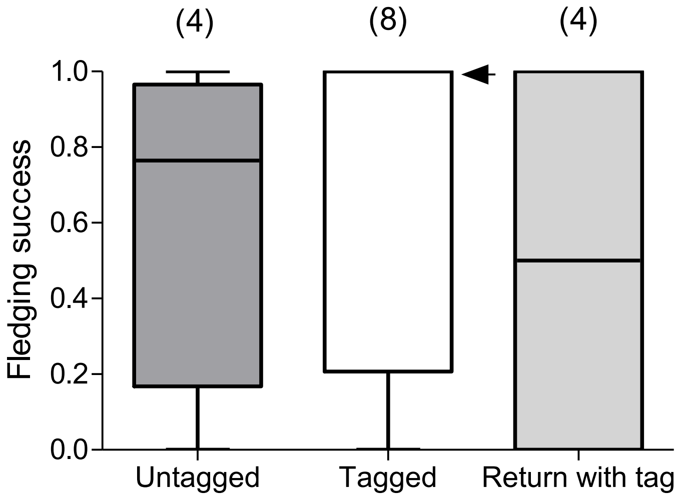

Figure 4.3: Fledging success (proportion of fledged nestlings from the number of eggs laid) in 2013 for female tree swallows without (untagged) geolocators, with (tagged) geolocators, and those still carrying the geolocator (return with tag). Boxes represent the range between the first and third quartile and the line inside the box represents the median. Whiskers represent the minimum and maximum values. Arrow points to median.

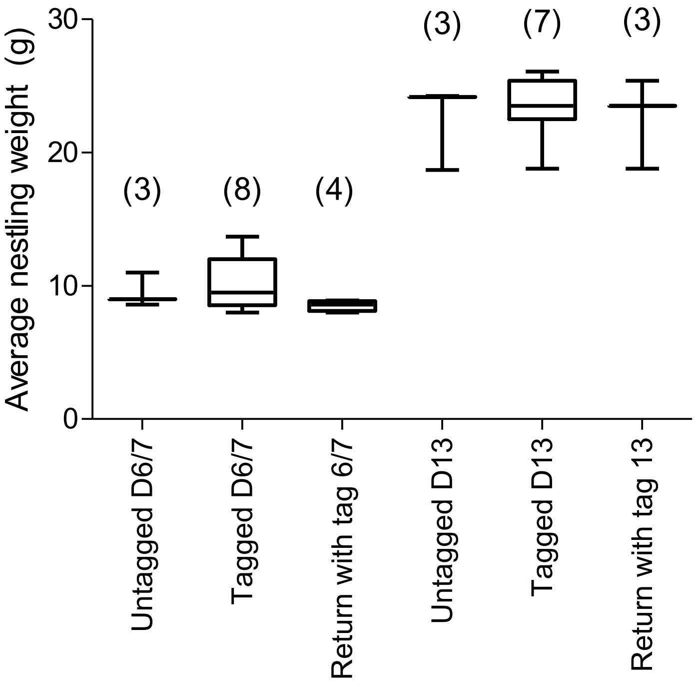

Figure 4.4: Average weight (g) per nestling in 2013 from nests of female tree swallows without (untagged) geolocators, with (tagged) geolocators, and those still carrying geolocators (return with tag) on day 6/7 post-hatch and day 13 post-hatch where hatch day = day 1. Boxes represent the range between the first and third quartile and the line inside the box represents the median. Whiskers represent the minimum and maximum values.

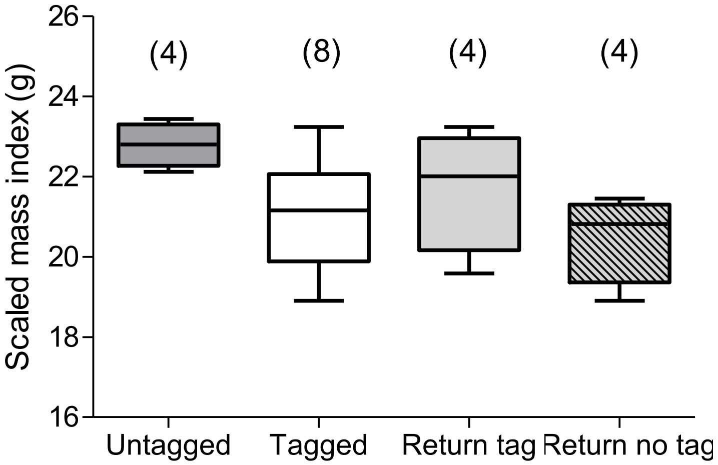

Figure 4.5: Condition (represented by the scaled mass index) during incubation in 2013 of female tree swallows without (untagged) and with (tagged) geolocators. Condition of tagged females that returned still carrying tags (return tag) and no longer carrying tags (return no tag) is also shown. Condition is represented by the scaled mass index (SMI), with higher numbers indicating better condition. Boxes represent the range between the first and third quartile and the line inside the box represents the median. Whiskers represent the minimum and maximum values.

The condition of tagged females did, however, differ significantly from untagged females ($U = 3.5$, $n_1 = 8$, $n_2 = 4$, $P = 0.04$), with tagged birds in poorer condition in 2013 than untagged birds (Figure 4.5). This result, however, appears to be based on the condition of the females that had been tagged but returned without their geolocators, which were in significantly poorer condition than untagged swallows ($U = 0.0$, $n_1 = 4$, $n_2 = 4$, $P = 0.03$) (Figure 4.5).

Within female comparison

There was no significant effect of year or treatment on egg initiation dates, but there was a significant interaction between year and treatment, with tagged females initiating nests later than untagged females in 2012 but earlier than untagged females in 2013 (Table 4.2, Figure 4.6).

There was no significant effect of year or treatment on clutch size, but there was a near significant interaction between year and treatment, with the mean clutch size similar for tagged and untagged females in 2012, but smaller for tagged females in 2013 and larger for untagged females in 2013 (Table 4.2, Figure 4.7).

Finally, there was a significant effect of year on condition, with both tagged and untagged females in poorer condition in 2013 than in 2012, and a near significant effect of treatment on condition, with tagged birds in poorer condition than untagged birds in both 2012 and 2013. There was, however, no significant interaction between year and treatment (Table 4.2, Figure 4.8).

Table 4.2: Repeated measures ANOVA for egg initiation date, clutch size and condition of tagged and untagged females in 2012 and 2013. Significant *P* values are bolded.

Variable		**Sum of squares**	**df**	***F***	***P***
Egg Initiation Date	Interaction	21.33	1, 10	9.64	**0.01**
	Year	0.33	1, 10	0.15	0.71
	Treatment	4.08	1, 10	0.32	0.58
	Subjects	126.40	10, 10	5.71	**0.006**
Clutch Size	Interaction	0.52	1, 10	3.97	0.07
	Year	0.02	1, 10	0.16	0.7
	Treatment	0.19	1, 10	0.19	0.67
	Subjects	9.81	10, 10	7.48	**0.002**
Condition	Interaction	0.01	1, 10	0.01	0.91
	Year	15.65	1, 10	14.00	**0.004**
	Treatment	16.14	1, 10	4.59	0.058
	Subjects	35.19	10, 10	3.15	**0.04**

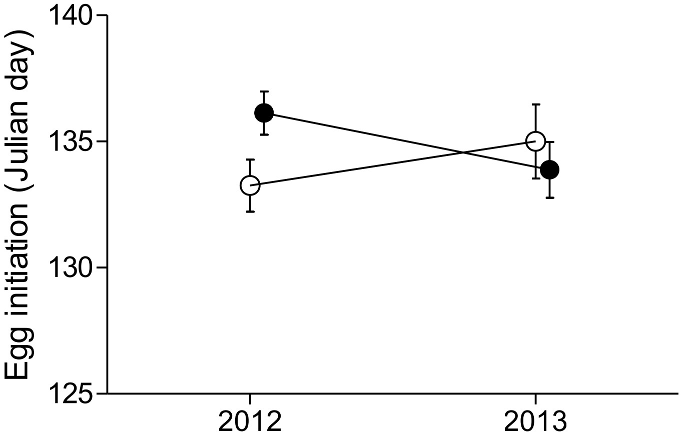

Figure 4.6: Egg initiation dates of tagged (filled circles) (n = 8) and untagged (open circles) (n = 4) females in 2012 and 2013 (mean ± SE).

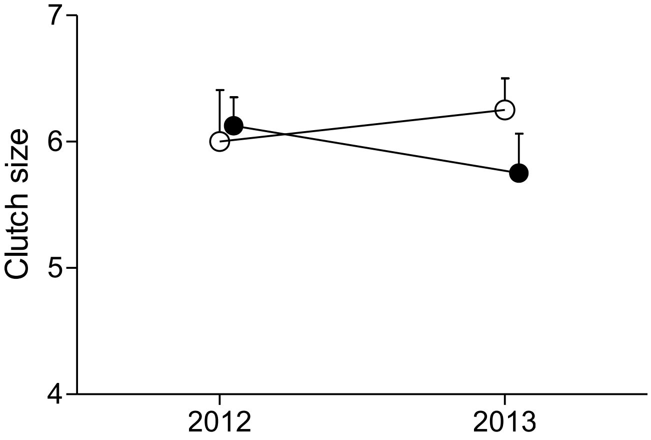

Figure 4.7: Clutch size of tagged (filled circles) (n = 8) and untagged (open circles) (n = 4) females in 2012 and 2013 (mean ± SE).

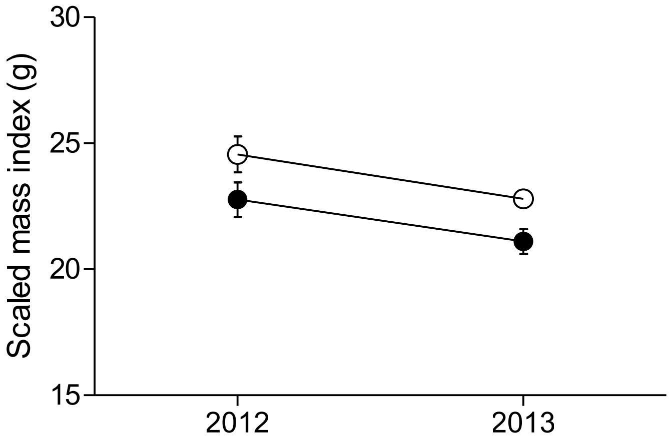

Figure 4.8: Condition of tagged (filled circles) (n = 8) and untagged (open circles) (n = 4) females in 2012 and 2013 (mean ± SE). Condition is represented by the scaled mass index (SMI), with higher numbers indicating better condition.

4.4 Discussion

The results of my study showed that return rate, egg initiation date, clutch size, fledging success, and nestling weight did not differ significantly between tagged and untagged females that returned after migration. However, egg initiation date for tagged females was earlier in 2013 than in 2012. Tagged females were in poorer condition than untagged females in 2013, although this difference is likely because the subset of tagged swallows that returned were also in poorer condition in 2012 than the subset of untagged birds that returned.

About half of the tagged birds that returned arrived without their geolocators. This was most likely due to the harness design. Harnesses were prepared in different sizes, with the intent to fit larger birds with larger harnesses. A few harnesses were, however, too large for even the largest swallows in this population, and so had to be modified, potentially creating a weak link in the harness. Other, unmodified harnesses may still have been too large, allowing the swallow to slip free of the geolocator.

I found no significant difference in the return rates of tagged and untagged females. Contrary to my results, a previous study found lower return rates for geolocator tagged tree swallows breeding in Saskatchewan and British Columbia, although this was not the case for birds in Ontario (Gomez et al. 2014). It is not clear why return rates differ across sites. One possibility is that because swallows from different breeding areas migrate to different winter locations (Laughlin et al. 2013; Chapter 2 of this study), they experience different conditions, thus differentially affecting return rates. Return rates of control birds also varied across sites (high in Ontario, intermediate in Saskatchewan, and low in British Columbia), suggesting that birds breeding in Saskatchewan and British

Columbia experienced harsher conditions during migration and on their wintering grounds than birds breeding in Ontario and Nova Scotia, which may be compounded for birds carrying tags.

Although egg initiation date did not differ between tagged and untagged females in 2013, I did find a significant interaction between year and treatment. Untagged birds began laying earlier than tagged birds in 2012, but there was no difference between egg initiation dates of tagged and untagged birds in 2013. This result is consistent with tagged red-backed shrikes (*Lanius collurio*) that began breeding earlier upon return to the breeding site than the previous year (Tottrup et al. 2012). This result is not, however, consistent across all studies. Northern wheatears (*Oenanthe oenanthe*) carrying geolocators arrived on the breeding grounds on average three days later, and initiated egg laying on average six days later than control birds (Arlt et al. 2013). Differences in the initiation of breeding may be caused by tagged and untagged birds wintering in different locations or in different quality habitats, resulting in different arrival times on the breeding grounds or different body conditions after migration (Arlt et al. 2013).

I found no difference in clutch size, fledging success, or mean nestling weight between tagged and untagged swallows in 2013. To date, the few studies that have examined the effect of geolocators on reproductive success have also found no effect. For instance, clutch sizes of male northern wheatears tagged with geolocators the previous year did not differ significantly from those of untagged birds (Schmaljohann et al. 2012). Similarly, mean nestling weights and fledging success of tagged male and female tree swallows in Saskatchewan did not differ significantly from those of untagged swallows prior to migration (Gomez et al. 2014). One explanation for why tagged birds have similar reproductive success to untagged birds may be that only good quality tagged females were able to survive the winter and return to breed, resulting in similar reproductive output between tagged and untagged birds.

Tagged swallows were in poorer condition than untagged swallows upon recapture in 2013. A significant effect of year and a nearly significant effect of treatment were, however, observed between tagged and untagged birds between 2012 and 2013, with both tagged and untagged birds returning in poorer condition in 2013, and the subset of tagged birds that returned being in poorer condition in both 2012 (before being tagged) and 2013 than the subset of untagged birds that returned. Therefore, the poor condition of tagged birds is likely not due to the geolocators. However, these results should be interpreted cautiously, as my sample size was small and a recent study suggested aerial insectivores may be particularly sensitive to changes in aerodynamics because of the amount of time they spend on the wing. Increases in drag may decrease foraging success or cause the bird to expend more energy in flight, resulting in poorer body condition (Barron et al. 2010; Constantini and Moller 2013). Poor body condition was also seen in common terns (*Sterna hirundo*) tagged with geolocators that lost so much body mass after tagging that the geolocators had to be removed (Nisbet et al. 2011). However, red-backed shrikes showed no difference in mass after returning from migration compared to other untagged birds or from the their weight the previous year (Tottrup et al. 2012).

Overall, my results suggest that geolocators do not have a strong negative effect on tree swallow reproduction and condition in the short term. This conclusion should, however, be viewed with caution because my sample sizes were small, which limited the power of my tests to detect small differences. Studies examining the welfare of a species, especially those in decline, should weigh the potential costs against the benefits of obtaining more information. Although no costs were detected in this study, it is recommended that new models of geolocators work to reduce drag, as well as weight, in order to have the least effect on the study species and provide the most realistic migration data.

CHAPTER 5: GENERAL DISCUSSION

5.1 Summary

The purpose of my study was to record the migration routes and wintering grounds of tree swallows breeding in Nova Scotia, Canada (Chapter 2), examine if breeding events have carry-over effects on autumn migration (Chapter 3), and determine if geolocators have a negative effect on tree swallows (Chapter 4).

In Chapter 2, I show that tree swallows breeding in Nova Scotia, Canada, begin autumn migration in July and migrate along the east coast of North America. The beginning of autumn migration is characterized by an extended stopover in the northeastern US. Many swallows have a second stopover in North Carolina. The swallows arrive at their wintering sites in Florida and Cuba in October and November. Spring migration is faster than autumn migration, beginning in March or early April and ending in late April to early May when birds arrive on the breeding grounds. Spring migration is also less uniform than autumn migration, with individuals using many different stopover sites. Tree swallows from this population show no temporal patterns in migration strategy; for example, autumn departure date does not predict arrival date on the wintering grounds, suggesting birds may individually adjust their migratory strategy.

In Chapter 3, I find that my study population shows little evidence of carry-over effects from the breeding season on autumn migration. The only significant finding is that swallows with later fledging dates began migration later than swallows with earlier fledging dates. It is also possible that birds in poor condition spend more time stopped over in the northeastern US compared to birds in better condition, but these results are based on a very small sample size, so must be viewed with caution. Overall, the results of this chapter suggest that late breeders and birds in poor condition at the end of the breeding season may require more time than early breeders and birds in better condition to recover energy stores before migration.

Finally, in Chapter 4, I show that tree swallows tagged with geolocators had similar return rates and clutch sizes, fledging success, and nestling weights as untagged swallows after returning from migration. However, tagged swallows initiated egg laying earlier in 2013 than in 2012. Also, although tagged swallows were in poorer condition than untagged swallows after migration, the subset of tagged birds that returned were also in poorer condition than the subset of untagged birds that returned in 2012. Both tagged and untagged swallows showed declines in condition in 2013 compared to 2012. These results suggest geolocators may not have short term effects on survival and reproduction. However, these results should be interpreted cautiously due to a small sample size.

5.2 Limitations

This study had some challenges due to the limitations of geolocators. I required the use of geolocators as they are currently the only tags capable of tracking small passerines through the annual cycle. However, because geolocators use light to estimate location, they do not give precise locations, resulting in daily errors of 143-400 km from the true location (Shaffer et al. 2005; Fudickar et al. 2011). This error means I was only able to give a broad estimate of the location of stopover sites and wintering sites. Using light to estimate location also results in problems around the autumn and spring equinoxes because day length is the same everywhere and, consequently, latitude estimates are unreliable. I was, therefore, unable to determine when the swallows began spring migration, thereby preventing the determination of spring migration duration, rate, and speed. Furthermore, changes in aerodynamics due to the weight and drag of the geolocator may cause increases in energy expenditure which could in turn cause tagged birds to stopover more frequently or change where they overwinter, affecting the very information of interest (Bowlin et al. 2010). Unfortunately, this cannot be assessed because the migration routes and strategy of untagged birds are currently unknown.

Another limitation of the study is that migration routes and migration strategy (e.g. timing, speed) of male tree swallows is largely unknown. In 2011, geolocators were deployed on 16 males and 14 females. However, due to the low recapture rate of males, only females were tagged in 2012. This means that the migration routes and migration strategy of males is largely unknown and I was not able to compare males and females.

The small sample size of returning birds also imposed some limitations on my study. I was not able to statistically analyze the relationship between condition and migration parameters, and even the analyses involving brood size and fledging date did not have much power to detect a difference.

5.3 Future Work

This study followed tree swallows over two years and similar migration schedules and routes were seen in both annual cycles. However, it would be interesting to follow the same individuals over more than one year to determine if they are consistent in their use of stopover sites and wintering sites from year to year. Swallows with late fledging dates had late departure dates, but there was no relationship between departure date and arrival on the wintering grounds, suggesting that individuals may adjust their migration strategy. If swallows have a flexible migration strategy, they may be better able to adapt to climate shifts due to climate change or change their use of stopover sites and wintering sites due to habitat loss.

Males and females may use different migration strategies and wintering sites (e.g. Bachler et al. 2010), so a larger study with more males may reveal interesting migration patterns between the sexes. Similarly, swallows from different breeding populations use different migration routes and stopover sites (Laughlin et al. 2013). In light of evidence that swallows breeding in the northeast are declining at a faster rate than elsewhere (Nebel et al. 2010, Shutler et al. 2012), comparing migration routes and wintering sites may reveal important stressors on birds from this area. A larger study would also help to further explore if there are other carry-over effects from the breeding season on migration.

REFERENCES

Afanasyev, V. 2004. A miniature daylight level and activity data recorder for tracking animals over long periods. *Mem Natl Inst Polar Res* 58: 227-233.

Alerstam, T., A. Hedenstrom, and S. Akesson. 2003. Long distance migration: evolution and determinants. *Oikos* 103: 247-260

Ambrosini, R., V. Orioli, D. Massimino, and L. Bani. 2011. Identification of putative wintering areas and ecological determinants of population dynamics of common house martin (*Delichon urbicum*) and common swift (*Apus apus*) breeding in northern Italy. *Avian Conserv Ecol* 6: 3

Arlt, D., M. Low, and T. Part. 2013. Effect of geolocators on migration and subsequent breeding performance of a long-distance passerine migrant. *PLoS ONE* 8: e82316.

Bachler, E., S. Hahn, M. Schaub, R. Arlettaz, L. Jenni, J.W. Fox, V. Afanasyev, and F. Liechti. 2010. Year-round tracking of small trans-Saharan migrants using light-level geolocators. *PLoS One* 5: e9566.

Bairlein, F. 2001. Results of bird ringing in the study of migration routes. *Ardea* 89: 7-19.

Barron, D.G., J.D. Brawn, and P.J. Weatherhead. 2010. Meta-analysis of transmitter effects on avian behaviour and ecology. *Method Ecol Evol* 1: 180-187.

Barron, D.G., P.J. Weatherhead, and J.D. Brawn. 2013. A test of radio-transmitter effects on parental investment and productivity in the northern cardinal. *The Condor* 115: 669-676.

Bauer, S., B.A. Nolet, J. Giske, J.W. Chapman, S. Akesson, A. Hedenstrom, and J.M. Fryxell. "Chapter 6: Cues and decision rules in animal migration." *Animal Migration: a synthesis.* Eds. E.J. Milner- Gulland, J.M. Fryxell, and A.R.E. Sinclair. New York: Oxford University Press, 2011. 68-87.

Biebach, H. 1985. Sahara stopover in migratory flycatchers: fat and food affect the time program. *Experientia* 41: 695-697.

Bogdanova, M.I., F. Daunt, M. Newell, R.A. Phillips, M.P. Harris, and S. Wanless. 2011. Seasonal interactions in the black-legged kittiwake, *Rissa tridactyla*: links between breeding performance and winter distribution. *Proc R Soc B* 278: 2412-2418.

Bohning-Gaese, K., M.L. Taper, and J.H. Brown. 1993. Are declines in North American insectivorous songbirds due to causes on the breeding range? *Conserv Biol* 7: 76-86.

Bowlin, M.S., P. Henningsson, F.T. Muijres, R.H.E. Vleugels, F. Liechti, A. Hedenstrom. 2010. The effects of geolocator drag and weight on the flight ranges of small migrants. *Method Ecol Evol* 1: 398-402.

Bridge, E.S., J.F. Kelly, A. Contina, R.M. Gabrielson, R.B. MacCurdy, and D.W. Winkler. 2013. Advances in tracking small migratory birds: a technical review of light-level geolocation. *J Field Ornithol* 84: 121-137.

Brown, D.R., and T.W. Sherry. 2008. Alternative strategies of space use and response to resource change in a wintering migrant songbird. *Behav Ecol* 19: 1314-1325.

Burney, C.W. 2002. A study of swallow roosts found in the eastern United States. M.S. thesis, Cornell University, Ithaca, New York.

Butler, R.W. 1988. Population dynamics and migration routes of tree swallows, *Tachycineta bicolor*, in North America. *J. Field Ornithol.* 59: 395-402.

Caccamise, D.F., and R.S. Hedin. 1985. An aerodynamic basis for selecting transmitter loads in birds. *Wilson Bull* 97: 306-318.

Canadian Council on Animal Care (CCAC) Guidelines on: the care and use of wildlife. 2003. www.ccac.ca. Accessed February 18, 2014.

Callo, P.A., E.S. Morton, B.J.M. Stutchbury. 2013. Prolonged spring migration in the red-eyed vireo (*Vireo olivaceus*). *The Auk* 130: 240-246.

Calvert, A.M., P.D. Taylor, and S. Walde. 2009. Cross-scale environmental influences on migratory stopover behaviour. *Glob Change Biol* 15:744-759.

Camacho, C. 2013. Tropical phenology in temperate regions: extended breeding season in a long-distance migrant. *The Condor* 115: 830-837.

Carlisle, J.D., S.K. Skagen, B.E. Kus, C. van Riper III, K.L. Paxton, and J.F. Kelly. 2009. Landbird migration in the American west: Recent progress and future research directions. *The Condor* 111: 211-225.

Carroll, J.P. 1990. Winter and spring survival of radio-tagged gray partridge in North Dakota. *J Wildlife Manage* 54: 657-662.

Catry, P., M.P. Dias, R.A. Phillips, J.P. Granadeiro. 2013. Carry-over effects from breeding modulate the annual cycle of a long-distance migrant: an experimental demonstration. *Ecology* 94: 1230-1235.

Calvo, B., and R.W. Furness. 1992. A review of the use and the effects of marks and devices on birds. *Ringing & Migration* 13: 129-151.

Chapman, F.M. 1966. *Tree Swallow*, in Handbook of Birds of Eastern North America. Pages 282-283. Dover Publications Inc., New York, New York.

Conklin, J.R., and P.F. Battley. 2012. Carry-over effects and compensation: late arrival on non-breeding grounds affects wing moult but not plumage or schedules of departing bar-tailed godwits *Limosa lapponica baueri*. *J Avian Biol* 43: 252-263.

Constantini, D., and A.P. Moller. 2013. A meta-analysis of the effects of geolocator application on birds. *Curr Zool* 59: 697-706.

Croxall, J.P., J.R.D. Silk, R.A. Phillips, V. Afanasyev, D.R. Briggs. 2005. Global circumnavigations: Tracking year-round ranges of nonbreeding albatrosses. *Science* 307: 249-250.

Dawson, A., S.A. Hinsley, P.N. Ferns, R.H.C. Bonser, and L. Eccleston. 2000. Rate of moult affects feather quality: a mechanism linking current reproductive effort to future survival. *Proc R Soc B* 267: 2093-2098.

Delmore, K.E., J.W. Fox, D.E. Irwin. 2012. Dramatic intraspecific differences in migratory routes, stopover sites and wintering areas, revealed using light-level geolocators. *Proc R Soc B* 279: 4582-4589.

Ellegren, H. 1991. Stopover ecology of autumn migrating bluethroats *Luscinia s. svecica* in relation to age and sex. *Ornis Scand* 22: 340-348.

Environment Canada, 2013. North American Breeding Bird Survey - Canadian Trends Website, Data-version 2011. Environment Canada, Gatineau, Quebec, K1A 0H3. Accessed March 29, 2014.

Fair, J.M., E. Paul, and J. Jones, eds. The Ornithological Council. “Guidelines to the use of wild birds in research.” 3rd ed. BIRDNET, Aug 2010. Web. 18 Dec 2013.

Fast, P.L.F., M. Fast, A. Mosbech, C. Sonne, H.G. Gilchrist, S. Descamps. 2011. Effects of implanted satellite transmitters on behavior and survival of female common eiders. *J Wildlife Manage* 75: 1553-1557.

Foster, C.C., E.D. Forsman, E.C. Meslow, G.S. Miller, J.A. Reid, F.F. Wagner, A.B. Carey, and J.B. Lint. 1992. Survival and reproduction of radio-marked spotted owls. *J Wildlife Manage* 56: 91-95.

Fraser, K.C., B.J.M. Stutchbury, C. Silverio, P.M. Kramer, J. Barrow, D. Newstead, N. Mickle, B.F. Cousens, J.C. Lee, D.M. Morrison, T. Shaheen, P. Mammenga, K. Applegate, and J. Tautin. 2012. Continent-wide tracking to determine migratory connectivity and tropical habitat associations of a declining aerial insectivore. *Proc R Soc B* 279: 4901-4906.

Fraser, K.C., B.J.M. Stutchbury, P. Kramer, C. Silverio, J. Barrow, D. Newstead, N. Mickle, T. Shaheen, P. Mammenga, K. Applegate, E. Bridge, and J. Tautin. 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: 291-296.

Fryxell, J.M., Milner-Gulland, E.J., and Sinclair, A.R.E. "Chapter 1: Introduction." *Animal Migration: a synthesis.* Eds. E.J. Milner- Gulland, J.M. Fryxell, and A.R.E. Sinclair. New York: Oxford University Press, 2011. 1-3.

Fudickar, A.M., M. Wikelski, and J. Partecke. 2011. Tracking migratory songbirds: accuracy of light-level loggers (geolocators) in forest habitats. *Method Ecol Evol* 3: 47-52.

Godfrey, J.D., and D.M. Bryant. "Effects of radio transmitters: review of recent radio tracking studies." Pp. 83-95 in Williams, M. (Comp.) 2003: Conservation applications of measuring energy expenditure of New Zealand birds: assessing habitat quality and costs of carrying radio transmitters. *Sci for Conserv* 214.95

Gomez, J., C.I. Michelson, D.W. Bradley, D.R. Norris, L.L. Berzins, R.D. Dawson, and R.G. Clark. 2014. Effects of geolocators on reproductive performance and annual return rates of a migratory songbird. *J Ornithol* 155: 37-44.

Gschweng, M., E.K.V. Kalko, U. Querner, W. Fiedler, and P. Berthold. 2008. All across Africa: highly individual migration routes of Eleonora's falcon. *Proc R Soc B* 275: 2887-2896.

Hamer, K.C., E.M. Humphreys, S. Garthe, J. Hennicke, G. Peters, D. Gremillet, R.A. Phillips, M.P. Harris, and S. Wanless. 2007. Annual variation in diets, feeding locations and foraging behaviour of gannets in the North Sea: flexibility, consistency and constraint. *Mar Ecol Prog Ser* 338: 295-305.

Harrison, X.A., J.D. Blount, R. Inger, D.R. Norris, and S. Bearhop. 2011. Carry-over effects as drivers of fitness differences in animals. *J Anim Ecol* 80: 4-18.

Heckscher, C.M., S.M. Taylor, J.W. Fox, and V. Afanasyev. 2011. Veery (*Catharus fuscescens*) wintering locations, migratory connectivity, and a revision of its winter range using geolocator technology. *The Auk* 128: 531-542.

Hooge, P.N. 1991. The effects of radio weight and harnesses on time budgets and movements of acorn woodpeckers. *J Field Ornith* 62: 230-238.

Inger, R., X.A. Harrison, G.D. Ruxton, J. Newton, K. Colhoun, G.A. Gudmundsson, G. McElwaine, M. Pickford, D. Hodgson, and S. Bearhop. 2010. Carry-over effects reveal reproductive costs in a long-distance migrant. *J Anim Ecol* 79: 974-982.

Jahn, A.E., V.R. Cuerto, J.W. Fox, M.S. Husak, D.H. Kim, D.V. Landoll, J.P. Ledezma, H.K. LePage, D.J. Levey, M.T. Murphy, and R.B. Renfrew. 2013. Migration timing and wintering areas of three species of flycatchers breeding the Great Plains of North America. *The Auk* 130: 247-257.

Johnson, J.A., S.M. Matsuoka, D.F. Tessler, R. Greenberg, and J.W. Fox. 2012. Identifying migratory pathways used by rusty blackbirds breeding in southcentral Alaska. *Wilson J Ornithol* 124: 698-703.

Johnson, M.D., T.W. Sherry, R.T. Holmes, and P.P. Marra. 2006. Assessing habitat quality for a migratory songbird wintering in natural and agricultural habitats. *Conserv Biol* 5: 1433-1444.

Kelly, J.F. and D.M. Finch. 1998. Tracking migrant songbirds with stable isotopes. *Trends Ecol Evol* 13: 48-49.

Ketterson, E.D., and V. Nolan Jr. “Chapter 12: The evolution of differential bird migration.” *Current Ornithology Vol 1* Ed. R.F. Johnston. Springer, 1983. 357-403.

King, R.A., and J.R. Belthoff. 2001. Post-fledging dispersal of burrowing owls in southwestern Idaho: characterization of movements and use of satellite burrows. *The Condor* 103: 118-126.

Landers, T.J., M.J. Rayner, R.A. Phillips, and M.E. Hauber. 2011. Dynamics of seasonal movements by a trans-Pacific migrant, the westland petrel. *The Condor* 113: 71-79.

Laughlin, A.J., C.M. Taylor, D.W. Bradley, D. LeClair, R.G. Clark, R.D. Dawson, P.O. Dunn, A. Horn, M. Leonard, D.R. Sheldon, D. Shutler, L.A. Whittingham, D.W. Winkler, D.R. Norris. 2013. Integrating information from geolocators, weather radar, and citizen science to uncover a key stopover area of an aerial insectivore. *The Auk* 130: 230-239.

Leonard, M., and A. Horn. 1996. Provisioning rules in tree swallows. *Behav Ecol Sociobiol* 38: 341-347.

Lincoln, F.C. 1935. The waterfowl flyways of North America. U.S. Department of Agriculture, circular no. 342.

Lisovski, S., C.M. Hewson, R.H.G. Klaassen, F. Korner-Nievergelt, M.W. Kristensen, and S. Hahn. 2012. Geolocation by light: accuracy and precision affected by environmental factors. *Method Ecol Evol* 3: 603-612.

Macias-Duark, A., and A.O. Panjabi. 2013. Association of habitat characteristics with winter survival of a declining grassland bird in Chihuahuan Desert grasslands of Mexico. *The Auk* 130: 141-149.

Marra, P.P., K.A. Hobson, and R.T. Holmes. 1998. Linking winter and summer events in a migratory bird using stable-carbon isotopes. *Science* 282: 1884-1886.

McCarty, J.P. 2001. Variation in growth of nestling tree swallows across multiple temporal and spatial scales. *The Auk* 118: 176-190.

McCracken, J. Are aerial insectivores being 'bugged out'? *Bird Watch Canada* Winter 2008: 4-7.

Mitchell, G.W., A.E. M. Newman, M. Wikelski, and D.R. Norris. 2012. Timing of breeding carries over to influence migratory departure in a songbird: An automated radiotracking study. *J Anim Ecol* 81: 1024-1033.

Morbey, Y.E., and R.C. Ydenberg. 2001. Protandrous arrival timing to breeding areas: a review. *Ecol Lett* 4: 663-673.

Morton, M.L. 1992. Control of postnuptial molt in the mountain white-crowned sparrow: a perspective from field data. *Ornis Scand* 23: 322-327.

Morton, M.L. and M.E. Pereyra. 1994. Autumnal migration departure schedules in mountain white-crowned sparrows. *The Condor* 96: 1020-1029.

Mrykalo, R.J., M.M. Grigione, and R.J. Sarno. 2011. Home range and dispersal of juvenile Florida burrowing owls. *Wilson J Ornithol* 119: 275-279.

Nebel, S., A. Mills, J.D. McCracken, and P.D. Taylor. 2010. Declines of aerial insectivores in North America follow a geographic gradient. *Avian Conserv Ecol* 5: 1-14.

Nesbitt Styrsky, J. 2005. Influence of predation on nest-site reuse by an open-cup nesting neotropical passerine. *The Condor* 107: 133-137.

Neudorf, D.L., and T.E. Pitcher. 1997. Radio transmitters do not affect nestling feeding rates by female hooded warblers. *J Field Ornithol* 68: 64-68.

Newton, I. *The Migration Ecology of Birds*. London: Elsevier, 2008. Book.

Nisbet, I.C.T., C.S. Mostello, R.R. Veit, J.W. Fox, and V. Afanasyev. 2011. Migrations and winter quarters of five common terns tracked using geolocators. *Waterbirds* 34:32-39.

Norris, D.R. 2005. Carry-over effects and habitat quality in migratory populations. *Oikos* 109: 178-186.

Norris, D.R. and C.M. Taylor. 2006. Predicting the consequences of carry-over effects for migratory populations. *Biol Lett* 2: 148-151.

Norris, D.R. and P.P. Marra. 2007. Seasonal interactions, habitat quality, and population dynamics in migratory birds. *The Condor* 109: 535-547.

Norris, D.R., P.P. Marra, T.K. Kyser, T.W. Sherry, and L.M. Ratcliffe. 2004a. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proc R Soc B.* 271: 59-64.

Norris, D.R., P.P. Marra, R. Montgomerie, T.K. Kyser, and L.M. Ratcliffe. 2004b. Reproductive effort, molting latitude, and feather color in a migratory songbird. *Science* 306: 2249-2250.

Norris, D.R., M.B. Wunder, and M. Boulet. 2006. Perspectives on migratory connectivity. *Ornithol Monographs* 61: 79-88.

Nur, N. 1984. The consequences of brood size for breeding blue tits I. Adult survival, weight change and the cost of reproduction. *J Anim Ecol* 53: 479-496.

Nur, N. 1986. Is clutch size variation in the blue tit (*Parus caeruleus*) adaptive? An experimental study. *J Anim Ecol* 55: 983-999.

Peig, J., and A.J. Green. 2009. New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. *Oikos* 118: 1883-1891.

Pennycuick, C.J., and P.L.F. Fast. 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. *J Ornithol* 153: 633-644.

Phillips, R.A., J.R.D. Silk, J.P. Croxall, V. Afanasyev, and D.R. Briggs. 2004. Accuracy of geolocation estimates for flying seabirds. *Mar Ecol Prog Ser* 266: 265-272.

Rockwell, S.M., C.I. Bocetti, and P.P. Marra. 2012. Carry-over effects of winter climate on spring arrival date and reproductive success in an endangered migratory bird, Kirtland's warbler (*Setophaga kirtlandii*). *The Auk* 129: 744-752.

Rodriguez, A., J.J. Negro, J.W. Fox, and V. Afanasyev. 2009. Effects of geolocator attachments on breeding parameters of lesser kestrels. *J Field Ornith* 80:399-407.

Ryder, T.B., J.W. Fox, and P.P. Marra. 2011. Estimating migratory connectivity of gray catbirds (*Dumetella carolinensis*) using geolocator and mark–recapture data. *The Auk* 128: 448-453.

Saino, N., T. Szep, R. Ambrosini, M. Romano, and A.P. Moller. 2004a. Ecological conditions during winter affect sexual selection and breeding in a migratory bird. *Proc R Soc B* 271: 681-686.

Saino, N., T. Szep, M. Romano, D. Rubolini, F. Spina, and A.P. Moller. 2004b. Ecological conditions during winter predict arrival date at the breeding quarters in a trans-Saharan migratory bird. *Ecol Lett* 7: 21-25.

Sanderson, F.J., P.F. Donald, D.J. Pain, I.J. Burfield, and F.P.J. van Bommel. 2006. Long-term population declines in Afro-Palearctic migrant birds. *Biol Conserv* 131: 93-105.

Schmaljohann, H., M. Buchmann, J.W. Fox, and F. Bairlein. 2012. Tracking migration routes and the annual cycle of a trans-Sahara songbird migrant. *Behav Ecol Sociobiol* 66: 915-922.

Schneider, D.C., and B.A. Harrington. 1981. Timing of shorebird migration in relation to prey depletion. *The Auk* 98: 801-811.

Shaffer, S.A., Y. Tremblay, J.A. Awkerman, R.W. Henry, S.L.H. Teo, D.J. Anderson, D.A. Croll, B.A. Block, and D.P. Costa. 2005. Comparison of light- and SST-based geolocation with satellite telemetry in free-ranging albatrosses. *Mar Biol* 147: 833-843.

Shutler, D., D.J.T. Hussell, D.R. Norris, D.W. Winkler, R.J. Robertson, F. Bonier, W.B. Rendell, M. Belisle, R.G. Clark, R.D. Dawson, N.T. Wheelwright, M.P. Lombardo, P.A. Thorpe, M.A. Truan, R. Walsh, M.L. Leonard, A.G. Horn, C.M. Vleck, D. Vleck, and A.P. Rose. 2012. Spatiotemporal patterns in nest box occupancy by tree swallows across North America. *Avian Conserv Ecol* 7: 1-9.

Sibly, R.M., and R.H. McCleery. 1980. Continuous observation of individual herring gulls during the incubation season using radio tags: an evaluation of the technique and a cost-benefit analysis of transmitting power. Pp. 345-352, in C. J. Amlaner and D. W. Macdonald, eds. A handbook on biotelemetry and radio tracking. Pergamon Press, Oxford, United Kingdom.

Slagsvold, T., and J.T. Lifjeld. 1990. Influence of male and female quality on clutch size in tits (*Parus* spp.). *Ecology* 71: 1258-1266.

Sorensen, M.C., J.M. Hipfner, T.K. Kyser, and D.R. Norris. 2009. Carry-over effects in a Pacific seabird: stable isotope evidence that pre-breeding diet quality influences reproductive success. *J Anim Ecol* 78: 460-467.

Studds, C.E., and P.P. Marra. 2005. Nonbreeding habitat occupancy and population processes: an upgrade experiment with a migratory bird. *Ecology* 86: 2380-2385.

Stutchbury, B.J.M., and S. Rohwer. 1990. Molt patterns in the tree swallow (*Tachycineta bicolor*). *Can J Zool* 68: 1468-1472.

Stutchbury, B.J.M., S.A. Tarof, T. Done, E. Gow, P.M. Kramer, J. Tautin, J.W. Fox, and V. Afanasyev. 2009. Tracking long-distance songbird migration by using geolocators. *Science* 323: 896.

Stutchbury, B.J.M., E.A. Gow, T. Done, M. MacPherson, J.W. Fox, and V. Afanasyev. 2011. Effects of post-breeding moult and energetic condition on timing of songbird migration into the tropics. *Proc R Soc B* 278: 131-137.

Therrien, J., G. Gauthier, and J. Bety. 2012. Survival and reproduction of adult snowy owls tracked by satellite. *Popul Ecol* 76: 1562-1567.

Tottrup, A.P., R.H.G. Klaassen, R. Strandberg, K. Thorup, M.W. Kristensen, P.S. Jorgensen, J. Fox, V. Afanasyev, C. Rahbek, and T. Alerstam. 2012. The annual cycle of a trans-equatorial Eurasian-African passerine migrant: different spatio-temporal strategies for autumn and spring migration. *Proc R Soc B* 279: 1008-1016.

Townsend, J.M., C.C. Rimmer, and K.P. McFarland. 2012. Radio-transmitters do not affect seasonal mass change or annual survival of Bicknell's thrushes. *J Field Ornithol* 83: 295-301.

Villard, P., C. Bonenfant, and V. Bretagnolle. 2011. Effects of satellite transmitters fitted to breeding Cory's shearwaters. *J Wildl Manage* 75: 709-714.

Warner, R.E., and S.L. Etter. 1983. Reproduction and survival of radio-marked hen ring necked pheasants in Illinois. *J Wildl Manage* 47: 369-375.

Warnock, N. 2010. Stopping vs. staging: The difference between a hop and a jump. *J Avian Biol* 41: 621–626.

Webster, M.S., P.P. Marra, S.M. Haig, S. Bensch, and R.T. Holmes. 2002. Links between worlds: Unraveling migratory connectivity. *Trends Ecol Evol* 17: 76-83

Winkler, D.W., K.K. Hallinger, D.R. Ardia, R.J. Robertson, B.J. Stutchbury and R.R. Cohen. 2011. Tree swallow (*Tachycineta bicolor*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Web. 2 Feb 2012.