Foraging and Roosting Habitat Use of Nesting Bank Swallows in Sackville, NB

by

Sarah Saldanha

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

at

Dalhousie University
Halifax, Nova Scotia
August 2016

DEDICATION PAGE

This thesis is dedicated to my parents Carlos Saldanha and Carol Mordy who have always supported my love of nature and everything wild.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

Habitat loss and degradation caused by agricultural intensification is considered to play a leading role in the declines of aerial insectivores, making the understanding of habitat dynamics critical for protection of this bird guild. Of all aerial insectivores, Bank Swallows are declining at the fastest rate and little is known about their foraging and roosting habitat requirements on the breeding ground. Therefore, the goal of my thesis was to identify the foraging and roosting habitat of breeding Bank Swallows and to determine how both intrinsic and extrinsic factors affect this species' habitat use. Using automated and manual radio telemetry I tracked the movements of 68 breeding Bank Swallows from three colonies in Sackville, NB. Foraging was concentrated near the colony and in salt marshes and foraging distance increased with chick age, was greater in birds with inactive nests and increased in cold and humid weather. Furthermore, the likelihood of Bank Swallows roosting communally in distant cattail wetlands was higher in males than in females and when chicks were young and decreased with relative humidity and ambient light. Moreover, Bank Swallows left the colony to roost earlier as chicks aged, when ambient light was low and when they traveled to further roosts and returned later as their chicks aged, when temperature and wind speeds were low and when they used distant roosts. Finally, the likelihood of roosting at the major roost site was higher when chicks aged, relative humidity was high and ambient light was low. These findings on Bank Swallow foraging and roosting habitat use can aid in the identification of critical habitat for this declining species.

LIST OF ABBREVIATIONS AND SYMBOLS USED

AICc   Aikaike's Information Criterion corrected for sample size

CI   Confidence Interval

COSEWIC   Committee On the Status of Endangered Wildlife in Canada

DAC   Diurnal Activity Center

km   Kilometer

m   Meter

QGIS   Quantum GIS

SARA   Species At Risk Act

SD   Standard Deviation

SE   Sackville Engineering Colony

TB   Tantramar Bridge Colony

TN   Tantramar North Colony

VHF   Very High Frequency

β Model Parameter Estimate

ACKNOWLEDGEMENTS

CHAPTER 1: INTRODUCTION

1.1 Introduction

Habitat loss and degradation are major factors contributing to global species population declines and extinctions (Fahrig 1997, Owens & Bennett 2000, Foley et al. 2005). By encroaching on and degrading natural habitats, anthropogenic activities such as urbanization, deforestation and agriculture are considered the major drivers for global biodiversity loss and extinction (Sala et al. 2000, Foley et al. 2005, Fischer & Lindenmayer 2007). Through the direct loss of habitat, habitat fragmentation, pollution and the introduction of invasive species, these activities negatively impact virtually all taxonomic groups ranging from plants to vertebrates (Hobbs & Yates 2003, Donald et al. 2001, Foley et al. 2005). Therefore, understanding and mitigating the effects of habitat loss has become a major theme in conservation biology (Haila 2002, Foley et al. 2005).

Today, agriculture is considered one of the main causes of habitat loss and degradation worldwide (Foley et al. 2005). During the 1960's the need to increase productivity to match growing human consumption led to the development of intensive agricultural practices (Tilman et al. 2011). This marked the shift from diverse mixed-farming systems to crop expansion and homogenisation paired with increased fertilization, irrigation, and pesticide use (Matson et al. 1997). Together, these changes led to the loss of heterogeneity and the degradation of habitat within agricultural landscapes (Benton et al. 2003, Ghilain & Belisle 2008). As a result, many farmland species have suffered steep population declines and reduced distributions (Donald et al. 2001, Flohre et al. 2011, Paquette et al. 2013).

Agricultural intensification has had an especially large impact on farmland (grassland) birds (Fuller et al. 1995, Donald et al. 2001, 2006). Over the last 40 to 50 years, the decline in the distribution and abundance of farmland birds has been greater than in any other group (Fuller et al. 1995, Donald et al. 2001, Sauer et al. 2012). Agricultural intensification can impact farmland birds in two ways: 1) directly from mortality caused by farming machinery and insecticide poisoning and 2) indirectly through the reduction and degradation of habitat (Chamberlain et al. 1999, Evans et al. 2007, Perlut et al. 2011). While direct mortality can have severe effects on specific groups such as ground-nesting birds (Perlut et al. 2011), habitat loss and degradation have the potential to cause more wide-scale declines (Chamberlain et al. 1999, Evans et al. 2007). Habitats used by nesting and foraging farmland birds, such as pastureland, wetlands, scrubland and hedgerows have all declined with agricultural intensification and as a result, the range and abundance of farmland birds has declined (Altieri 1999, Møller 2001, Evans et al. 2003, Grüebler et al. 2008, Wuczyński et al. 2011, Jeliazkov 2016). Furthermore, the use of pesticides in intensive agriculture may further degrade these habitats by reducing the abundance of insect prey (Boatman et al. 2004, Goulson 2014, Sotherton & Holland 2002). Therefore, the wide-scale declines of farmland birds is mainly considered to be caused by the loss and degradation of habitat with intensive farming.

Aerial insectivores, a group of birds which commonly occupy agricultural landscapes and forage for insects in flight, have suffered from especially strong population declines (Nebel et al. 2010). While increased predation (Ydenberg et al. 2004, Baines et al. 2008) and mortality caused by weather events (Sauer et al. 1996, Stokke et

al. 2005, Dionne et al. 2008) may play a role in these declines, habitat degradation caused by the reduction of insect prey is considered to be the most probable explanation (Andren 1994, Robinson et al. 1995, MacHunter et al. 2006, Nebel et al. 2010).

Of all aerial insectivores, Bank Swallows, *Riparia riparia*, are experiencing the steepest population decline. In North America, Breeding Bird Survey data indicate that Bank Swallow populations have declined at an average rate of 8.84% per year since the 1970s, which has resulted in a population loss of 98% over the last 40 years (COSEWIC 2013). Bank Swallows were assessed as Threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) in May 2013 and formal protection under the Species At Risk Act (SARA) is currently being considered. If, like other aerial insectivores, habitat loss and degradation are the major drivers of this decline, a thorough understanding of this species' habitat requirements will be needed to identify and protect important habitat.

On the breeding grounds, Bank Swallows are thought to use distinct nesting, foraging and roosting habitats (the habitat used for nightly rest or sleep) (Mofatt et al. 2005, Falconer et al. 2016). Although Bank Swallow nesting habitat requirements have been well described (Heneberg 2009, Silver & Griffin 2009), knowledge about their foraging and roosting habitats is lacking.

1.2 Use of Small Tracking Devices and Automated Telemetry to Monitor Habitat Use

Habitat use can be exceptionally difficult to monitor in small, highly mobile species, such as Bank Swallows, and observational data alone often fails to capture the full extent of individual movements (Hagen & Hodges 2006).

To counter this difficulty, recent studies have used small tracking devices such as light level geolocators and Very High Frequency (VHF) radio tags to collect information on habitat use in such species (Burger & Shaffer 2008, Bridge et al. 2011). These tracking devices have overcome many of the limitations of previous techniques to identify patterns of habitat use in small and mobile species and can be used to fill key knowledge gaps and to identify habitat requirements.

In combination with the use of small radio tags, automated telemetry (a new tracking method), has proven to be highly efficient for monitoring both broad and fine scale movements in small, highly mobile species (Dossman et al. 2016, Crysler et al. 2016). Automated telemetry systems continuously scan and record coded signals emitted by radio tags using a stationary automated receiver (such as Lotek SRX 600 or SensorGnomes) and a combination of either omnidirectional or Yagi antennas (Falconer et al. 2016, Crysler et al. 2016). As opposed to traditional radio telemetry, which requires manual tracking using hand held devices, these systems work remotely, allowing for continuous (24 hrs/day, 7 days/week) recordings of tagged individuals. Furthermore, the detection range of these systems can be adjusted based on the type of antennas used. While the maximum detection range of omnidirectional antennas rarely exceeds one kilometer, that of Yagi antennas can range from ~200 m to 12 km in the direction of the Yagi antennas only (Taylor et al. 2011). Therefore, by using an array of several automated telemetry systems, not only the presence and absence of individual birds can be detected but also the direction and timing of their movements.

1.3 Study Species

1.3.1 Bank Swallow Nesting Habitat Selection and Biology

Bank swallows are small aerial insectivores that breed in freshly eroded banks of unconsolidated materials (Peck & James 1987, Garrison 1999). They prefer to nest in natural or human-made banks composed of fine sandy-loam soils, with low vegetation cover and a steep slope (Silver & Griffin 2009). Within these banks, Bank Swallows form colonies ranging from one to several thousand nests (Moffatt et al. 2005). Breeding is highly synchronized within colonies and restricted to the months of May through August (Emlen & Demong 1975, Turner & Rose 1989). At the beginning of the breeding season, older, more experienced birds arrive at the colony first, and then are followed by the first-year breeders 1-2 weeks later (Kuhnen 1985). Pairs are socially monogamous, although both males and females seek-out extra-pair copulations (Hoogland & Sherman 1976, Garrison 1999). Females lay 3-6 eggs and assume the majority of incubation, although males also participate (Garrison 1999). Eggs are incubated for 14 days (range: 12 - 16 days) before hatch (Garrison 1999). Once hatched, brooding is almost continuous for the first two to three days and then declines slowly before ceasing at 7 to 10 days (Petersen 1955). Females conduct the majority of the brooding although males and sometimes both sexes have been found to brood young simultaneously (Petersen 1955). Both males and females provision the young (Turner & Rose 1989, Garrison 1999). The young are fed at a rate of 22.1-28.2 visits/h before they fledge at 18-22 days and are fed irregularly for a week after this (Petersen 1955, Emlen & Demong 1975, Hickman 1979, Peck & James 1987). Fledged young may roost in nest burrows for up to one week after first leaving their nest (Garrison 1999). Overall, nesting success is high, with up to 70% of eggs

resulting in fledged young (Asbirk 1976, Sieber 1980). Success is highest in longer burrows located at the center of the colony and is usually higher for early broods (Freer 1977, Sieber 1980).

Bank Swallows display high colony site fidelity with 46-59 % of surviving juveniles and 56-92 % of adults returning to their previous-years' range (MacBriar & Stevenson 1976, Petersen & Mueller 1979, Freer 1979, Szep 1990). Furthermore, neighbouring birds in one year tend to settle near each other in subsequent years (Szabo & Szep 2010).

1.3.2 Foraging Habitat

Observational data suggest that breeding Bank Swallows are central-place foragers that hunt for insect prey in open terrestrial and aquatic habitats (e.g. wetlands, open water, grasslands, hayfields, pastures, croplands and scrubland) usually within 200-500 meters of their nest, but occasionally up to 1 km away (Turner 1980, Garrison 1999, Mofatt et al. 2005). However, to date, there have been no systematic studies on Bank Swallow foraging habitat use and range, and nothing is known about whether these change throughout the breeding season. In other swallow species, foraging habitat use and range were found to be affected by both extrinsic factors (factors that are not inherent such as weather) and intrinsic factors (inherent factors such as sex and breeding stage), however nothing is known about whether these factors affect the foraging habitat use of Bank Swallows (Brown & Brown 1999, Evans et al. 2003, McCarty & Winkler 1999a).

1.3.3 Roosting Habitat

Although Bank Swallow roosting behaviour and habitat use during winter and migration has been well described (Bijlsma & van den Brink 2005, Winkler 2006), little is known about this behaviour during the breeding season (for an exception see Falconer et al. 2016). During winter and migration, Bank Swallows roost communally (i.e. congregate at night for rest or sleep) with other swallow species in large wetlands, reed or cane beds, or other dense vegetation over water (Winkler 2006). At this time, roosts may number from a few individuals up to 3 million birds (Bijlsma & van den Brink 2005). On the breeding grounds, however, there have been fewer studies on communal roosting. Adults were previously assumed to be occupied by nesting duties at night and therefore unable to join communal roosts (Garrison 1999). However, a pair of radio-tagged Bank Swallows were found roosting overnight in agricultural crops when their young were 9–17 days old (Alves & Johnson 1994), suggesting that this may not always be the case. Similarly, radio-tagged male and female Bank Swallows in Ontario occasionally left their nest at night and travelled up to 35km away in the direction of large cattail wetlands (Falconer et al. 2016). In this study, some male Bank Swallows roosted away from the colony every night throughout the nestling period. Females, on the other hand, only roosted away once the chicks were about 8 days old, suggesting sex-based differences in roosting behaviour and also, possible constraints imposed by caring for young (Falconer et al. 2016).

1.4 Chapter Outlines

The goal of my study was to identify the foraging and roosting habitat of breeding and pre-migratory Bank Swallows and to measure how both extrinsic and intrinsic factors affect this habitat use throughout the breeding season. In the remainder of this chapter, I describe my general methods, including a description of my study site, nest monitoring, the capture and radio-tagging of Bank Swallows and the position of the automated telemetry array. In chapter 2, I used a combination of manual tracking and automated telemetry to identify the foraging habitats used by breeding Bank Swallows and to determine how intrinsic (e.g. sex, chick age) and extrinsic (e.g. weather conditions) factors affected habitat use. In chapter 3, using the same tracking techniques, I identified how these same factors affect i) the probability of Bank Swallows roosting communally during the breeding season, ii) the timing and the duration of the commute between the breeding colony and roost sites and iii) the prevalence of use of different potential roosts sites. Finally, in chapter 4 I summarize my results, discuss the limitations of my study, and end with suggestions for future work.

1.5 General Methods

1.5.1 Study Site

My study was conducted at three breeding colonies near the towns of Sackville, New Brunswick and Amherst, Nova Scotia from 12 May to 12 August 2014 and 16 May to 26 August 2015. The study area is mainly composed of flat pastureland, hayfields and marshlands and is serpentined by the Tantramar River.

In 2014 and part of 2015 (see below), I monitored the colony Tantramar Bridge (TB) of 91 pairs of breeding Bank Swallows**,** situated in a sandy-clay bank along the Tantramar River (45.8980°, -64.3430°). In 2015, I also monitored a colony Tantramar North (TN) of 76 breeding pairs that was also located 0.9 km north of TB on the Tantramar River (45.9051°, -64.3380°). In June 2015, before any tags were deployed, 90% of the nests at TB were lost when high rainfall caused the bank to collapse. At that point, I began to study a third breeding colony Sackville Engineering (SE) of 54 breeding pairs situated 1.2 km south of TB in an aggregate pile on the property of Sackville Public Works (45.89059°, -64.35377°). The birds nesting at SE had later incubation dates than those at TB or TN and, therefore, may have been re-nesting birds from collapsed colonies.

1.5.2 Nest Monitoring

I checked nesting burrows every two to three days beginning when I first observed nests being excavated and ending 12 days post-hatch. At each check, I inserted a flashlight and dental mirror attached to a long pole into the burrow. I recorded clutch initiation date, clutch size, hatching dates, hatching success and nestling survival until day 12.

Poor weather conditions and poor views of nest contents prevented me from recording hatching date for 44 nests across the two years and three colonies. For each of these nests, I estimated a unique hatching date by calculating the average between the earliest (i.e. last day eggs were recorded in this nest) and latest (e.g. first day nestlings were recorded in this same nest) day the nestling may have hatched.

In total, I followed 71 (78%) nests at TB, 51 (67%) at TN and 23 (43%) at SE that were active for at least some of the breeding season and accessible.

1.5.3 Banding and Tagging

I captured 49 adults (33 females and 16 males) at TB, 45 (26 females and 19 males) at TN and 23 (15 females and 8 males) at SE, using a combination of tube traps (Morris 1942) and mist nests, starting when the pairs were in late incubation. All birds were banded with a Canadian Wildlife Service aluminum band and sexed based on the presence of a brood patch or cloacal protuberance (Pyle 1997).

I randomly selected 11 males and 13 females at TB, 17 males and 15 females at TN and 4 males and 8 females at SE to be tagged with VHF transmitters. Although all tagged birds from TB and SE were from distinct nests, at TN, 10 pairs from the same nest were tagged in addition to 12 birds from distinct nests to determine whether both parents left the nest at night. I used Lotek NTQB-1 radio transmitters that weighed 0.29 g (2.2 ± 0.2 % of the body weights of tagged individuals and below the 3% recommended maximum weight (Phillips et al. 2003) and the 5% limit suggested by the Canadian Council on Animal Care). Tags had a guaranteed life expectancy (80% of total life expectancy) of 33 days with a burst rate of 10 sec. All birds that were captured and banded, but not tagged were used as a control group to assess the effects of tagging on nest success (see Chapter 2).

Individuals selected to carry transmitters were fitted with a VHF tag using the glue-on method developed by Raim (1978). This method was selected because there have been no reports of ill-effects, apart from minor local plumage damage (Sykes et al. 1990,

Naef-Daenzer et al. 2001, Schulz et al. 2001, Bowman et al. 2002, Dunn & Whittingham 2005, Mong & Sandercock 2007, Hansbauer & Pimentel 2008). Also, the tags have a relatively short retention time (average 5-40 days) and therefore, were expected to drop off before migration (Sykes et al. 1990, Johnson et al. 1991, Bowman et al. 2002, Mong & Sandercock 2007). The attachment process took 10 minutes (Schulz et al. 2001) and the total handling time/ bird was less than 20 minutes.

1.5.4 Automated Telemetry Array

To monitor Bank Swallow movements throughout the study I tracked the tagged birds with an array of 11, 6 m high automated telemetry towers. Each tower contained a data logging receiver (Sensorgnome; www.sensorgnome.org) and 1-3 omnidirectional and/or 9-element Yagi antennas. When a tagged swallow was within ~1 km of an omnidirectional tower or ~12 km of a Yagi tower (in the direction of the Yagi antennas only) (Taylor et al. 2011), its unique code, the time of the detection and the strength of the signal were recorded by the receiver.

In both 2014 and 2015, one tower equipped with omnidirectional antennas was erected at the top of the bank at each of the breeding colonies and the additional towers were placed in the open area surrounding the colony sites (Figure 1.1, 1.2). In both years, the array consisted of 11 towers and was designed to capture the direction of the birds as they left or returned to the colony from roost sites, as well as the presence of birds at the colonies and the roost sites. In 2014, before roost sites were located, the towers were positioned to capture the time, signal strength and direction of a tagged bird's movements as it left or entered its nesting burrow. After identifying two roosts in cattail marshes in July 2014 (EDDY and AMMAR), two towers at the edge of the array (FVIEW and

11

COW) were relocated to these marshes to directly monitor the presence or absence of birds at the roost sites (Figure 1.1). In 2015, I used a combination of ground truthing and satellite imagery to identify and place towers at all cattail marshes within 30 km of the colonies (Figure 1.2).
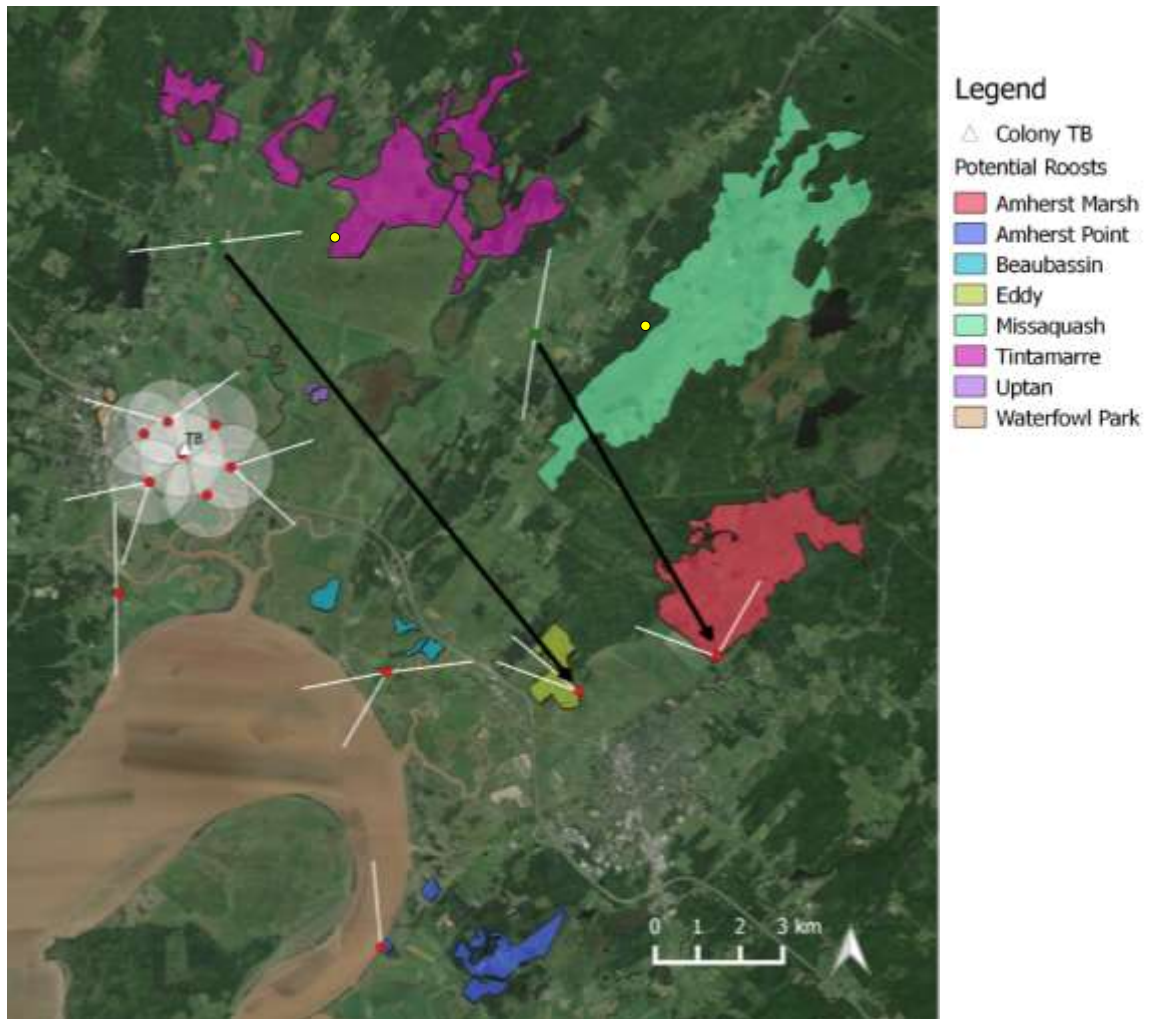
Figure 1.1 Map of the study site, roost sites (polygons) and tower placement (points) in 2014. Red points show towers that remained in place during the entire season and yellow points show the towers that were moved. Black arrows indicate where towers were moved to. White triangles indicate breeding colony locations. The large white circles indicate the maximum detection range of omnidirectional antennas (1 km) and white lines indicate the direction of directional antennas.
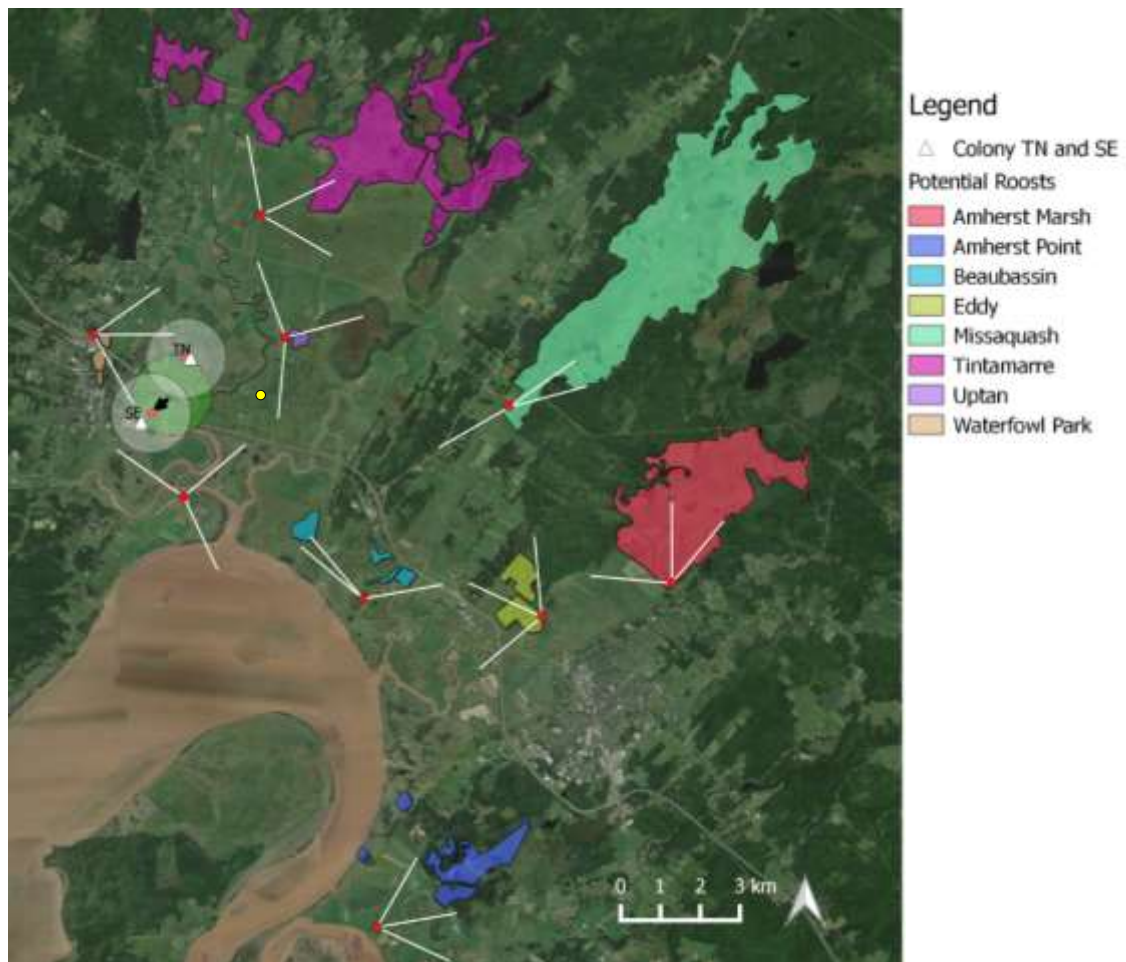
Figure 1.2 Map of the study site, roost sites (polygons) and tower placement (points) in 2015. Red points show towers that remained in place during the entire season and yellow points show the towers that were moved. Black arrows indicate where towers were moved to. White triangles indicate breeding colony locations. The large white and green circles indicate the maximum detection range of omnidirectional antennas (1 km) (with green circles indicating a moved tower) and white lines indicate the direction of directional antennas.

CHAPTER 2: BANK SWALLOW FORAGING HABTIAT USE

2.1 Introduction

Farmland (grassland) birds are one of the fastest declining groups of birds in both Europe and North America (Donald et al. 2001). An increase in agricultural intensification since the early 1960's is considered one of the major contributors to these declines (Møller 2001, Vickery & Herkert 2001, Robinson & Sutherland 2002, Murphy 2003, Donald et al. 2006). Agricultural intensification uses farmland expansion, crop homogenization, fertilization, irrigation, and pesticides to optimize food production (Matson et al. 1997). As a consequence, agricultural habitats have become more homogenous, and many habitats traditionally found within these landscapes such as pastureland, wetlands, scrubland and hedgerows have declined (Altieri 1999, Jeliazkova 2016). With this loss of diversity, agricultural landscapes can no longer support many farmland species (Altieri 1999, Jeliazkova 2016). Understanding these effects is especially important given that farmlands represent one of the major land-covers of our world (Meyer & Turner 1992, Krebs et al. 1999).

One family of birds that are commonly found within agricultural landscapes, Hirundinidae or swallows, have suffered from especially strong population declines (Møller 2001, Blancher et al. 2009, Nebel et al. 2010). Swallows are aerial insectivores, meaning that they forage for insects in flight, and therefore require open spaces, such as those found in agricultural landscapes, to feed (Evans et al. 2003, Nakano et al. 2007, Kang & Kaller 2013, Stanton 2015). A recent study found that the abundance of one swallow species, the Tree Swallow (*Tachycineta bicolor*), decreased with the proportion

of intensive agriculture in the surrounding landscape, suggesting a link between swallow declines and farming practices (Ghilain & Belisle 2008). Agricultural intensification may be responsible for population declines in swallows by causing the reduction of their insect prey. This could occur in two ways 1) directly by killing insects via insecticide use and 2) indirectly via the loss or degradation of suitable habitat for their insect prey (Nebel et al. 2010). Although research on the direct effects of insecticide use is limited by the lack of long-term data on insect abundance, studies suggest that both arthropod abundance and diversity decline with increasing agricultural intensity (Benton et al. 2002, Attwood et al. 2008, Grüebler et al. 2008). In one study, the abundance of flies (Diptera), a major food source for swallows, was negatively affected by the proportion of intensive agriculture within 500 m of sampling points (Paquette et al. 2013). Swallow populations may also be suffering from loss or degradation of foraging habitat. Barn Swallows (*Hirundo rustica*) for instance, prefer to forage in active dairy farms and hedge rows, two habitats that are becoming rarer with intensive agriculture (Møller 2001, Evans et al. 2003). Identifying foraging habitat for swallows within agricultural environments may help identify which habitats must be conserved to protect these species.

Of all the swallow species in North America, Bank Swallows (*Riparia riparia*) have declined at the steepest rate. In Canada, Breeding Bird Survey data indicate that this species has declined by 98% over the last 40 years (COSEWIC 2013). Although the main driver for these declines still remains unclear, habitat loss and degradation are considered potential causes (COSEWIC 2013).

Bank Swallow nesting habitat has been well described (Petersen 1955, Heneberg 2009, Silver & Griffin 2009), however, little is known about their foraging habitat

requirements during the breeding season. The available anecdotal evidence suggests that breeding Bank Swallows are central place foragers that feed on aerial insects in open habitats within 200-500 m of their nesting colonies (Garrison 1999, Mofatt et al. 2005). Furthermore, there is little known about whether Bank Swallows select for specific types of open habitats or if their habitat use changes through the breeding season, as has been shown for other swallow species (Brown & Brown 1999, Evans et al. 2003, Dunn & Whittingham 2005). Barn Swallows forage farther from nest sites and close to vegetative boundaries or warm water bodies in poor weather conditions (Brown & Brown 1999, Evans et al. 2003) and Tree Swallows can forage up to 10 km from their nest site during the pre-laying period (Dunn & Whittingham 2005), but remain within a few hundred meters of their nests during the egg and nestling periods (McCarty & Winkler 1999a). If Bank Swallow habitat use also changes throughout the breeding season, understanding and predicting these changes be important in the identification of habitat requirements for this species.

The goal of my study, therefore, was to identify Bank Swallow foraging habitat during the breeding season. I first measured where individuals from three colonies breeding in Sackville, NB foraged. Then, to measure how Bank Swallow foraging habitat use changes throughout the breeding season, I measured the effect of intrinsic factors (inherent factors such as sex and breeding stage) and extrinsic factors (non-inherent factors such as weather) on the distance Bank Swallows travelled to forage. Since Bank Swallows are believed to be central place foragers, understanding how foraging distance changes throughout the breeding season can indicate differences in either foraging requirements or the quality of foraging habitat over time.

2.2 Methods

For information on nest monitoring, trapping and tagging and the collection of intrinsic factors (see Chapter 1 general methods).

2.2.1 Identifying Bank Swallow Foraging Habitat

To identify Bank Swallow foraging habitat, I measured the presence or absence of radio tagged birds at 29 pre-determined points across various habitat types in 2014 and 52 points in 2015 (Figure 2.1). These points were positioned at the intersection of lines that made up a 600 × 600 m grid centered at colony TB (the position grid was expanded in 2015 to cover colonies TN and SE but remained centered at TB for consistency). I selected a grid size of 600 m based on the maximum detection range of the manual tracking radio antenna (300 m in each direction). This detection range was also used to map 300 m radius circular plots around each point that represented the area in which individuals could be detected. Moreover, all points were further than 300 m from the colonies to avoid detecting birds at their nests. To fully incorporate the foraging range of this species (estimated as ~ 1 km from colonies; Garrison 1999, Mofatt et al. 2005), all tracking points were within 2 km of one of the colonies. When an assigned tracking point was inaccessible because of obstacles, I conducted the tracking session at the closest accessible position.

Figure 2.1 Position of tracking points (yellow) in 2014 (left) and 2015 (right). Colonies indicated as white triangles.

Between 4 July and 1 August 2014 and 5 July and 18 August 2015, I visited each tracking point every one to three days until all were visited at least ten times. To control for the effect of time of day, each tracking point was visited at least three times in the morning (06:00 to 10:00), mid day (10:00 to 14:00) and afternoon (14:00 to 18:00) throughout the breeding season. At each point, I noted the time, wind speed (km/h), temperature (°C), cloud cover (%) and precipitation (Y/N) using a hand-held weather meter (Kestrel). I then pointed the antenna in each of eight cardinal directions (N, NE, E, SE, S, SW, W and NW) for 30 seconds each for a total of four minutes at each point. During each of these sessions, I recorded the tag identification number of each detection, the direction of the recording, and, thirdly, the signal intensity (which is a predictor of the proximity to the tag). When a tag was detected multiple times during a session, I selected the detection with highest signal intensity to be included in the analysis. At the end of

each tracking session, I also counted the number of Bank Swallows that were visible with binoculars within 300 m of the sampling point and noted whether they were foraging (characterised as individuals with erratic circling flights; Møller 1987).

2.2.2 Distance Between the Foraging Plots and the Colonies

Since breeding Bank Swallows are central-place foragers, I measured the distance from each point and the colonies using Quantum GIS (QGIS) to take into account the effect of distance on foraging habitat use.

2.2.3 Habitat Composition

To determine the habitat composition within 300 m plots surrounding each of the tracking points, I first classified the habitat within each parcel of land within 2 km of each colony. I then mapped these habitat types onto the satellite images using QGIS and calculated the proportion of the area covered by each habitat type within each of these 300 m plots.

In total, I recorded 11 habitat types (crop, forest, hay, highway, pasture, saltmarsh, scrub, stagnant water, river, urban, wet grassland; Table 2.1, Figures 2.2, 2.3). Because highway and urban habitats had similar characteristics, these two habitats were combined for the analysis.

Table 2.1 Description of potential Bank Swallow foraging habitats within 2 km of the breeding colonies.

Habitat	Description
Crop	Agricultural row crops including corn and wheat
Forest	Habitat dominated by trees
Hay	Hay field harvested at least once per summer
Highway	Highway
Pasture	Grassland grazed by cows or sheep
Salt Marsh	Coastal grassland that is regularly flooded by seawater
Scrub	Habitat dominated by shrubs
Stagnant Water	Body of water having no current or flow
River	Stream of flowing water
Urban	Area occupied by a city or town
Wet Grassland	Periodically flooded grassland (ungrazed)
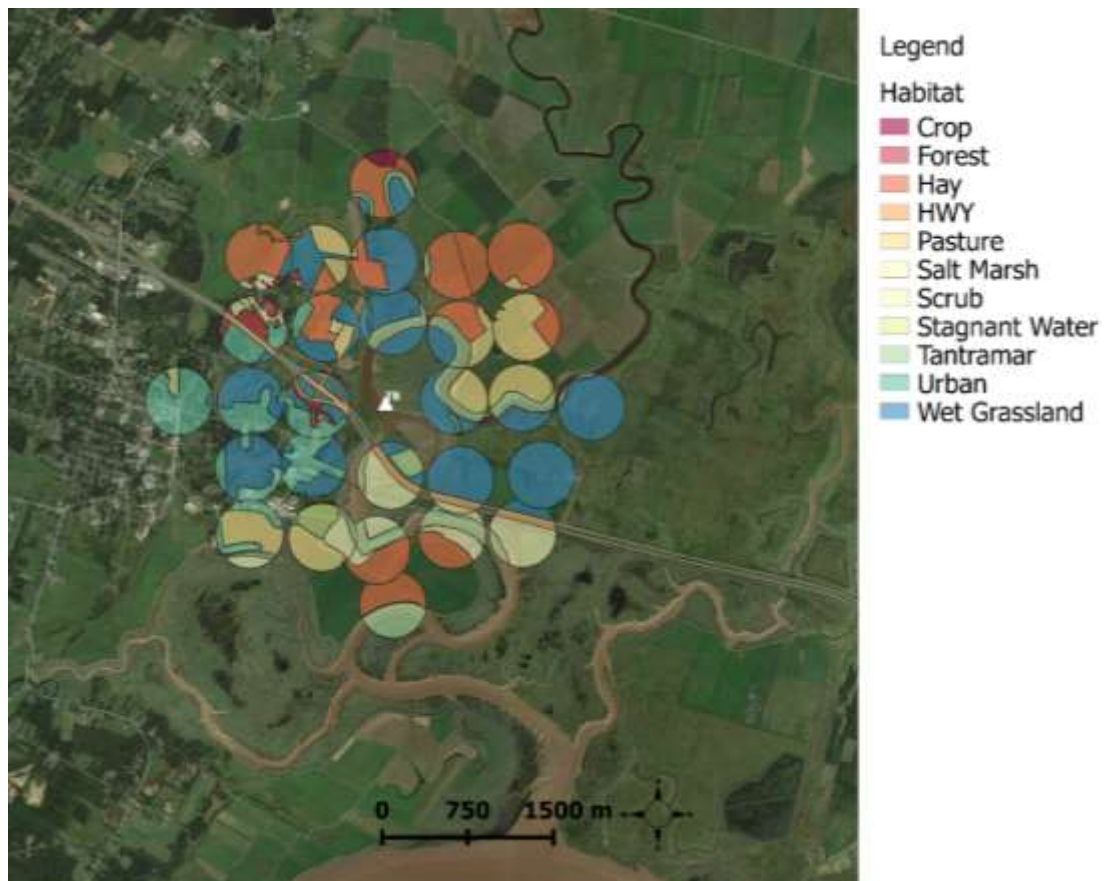
Figure 2.2 Position of colony TB and 300 m habitat plots surrounding Bank Swallow tracking points in 2014. Colony TB indicated as a white triangle.
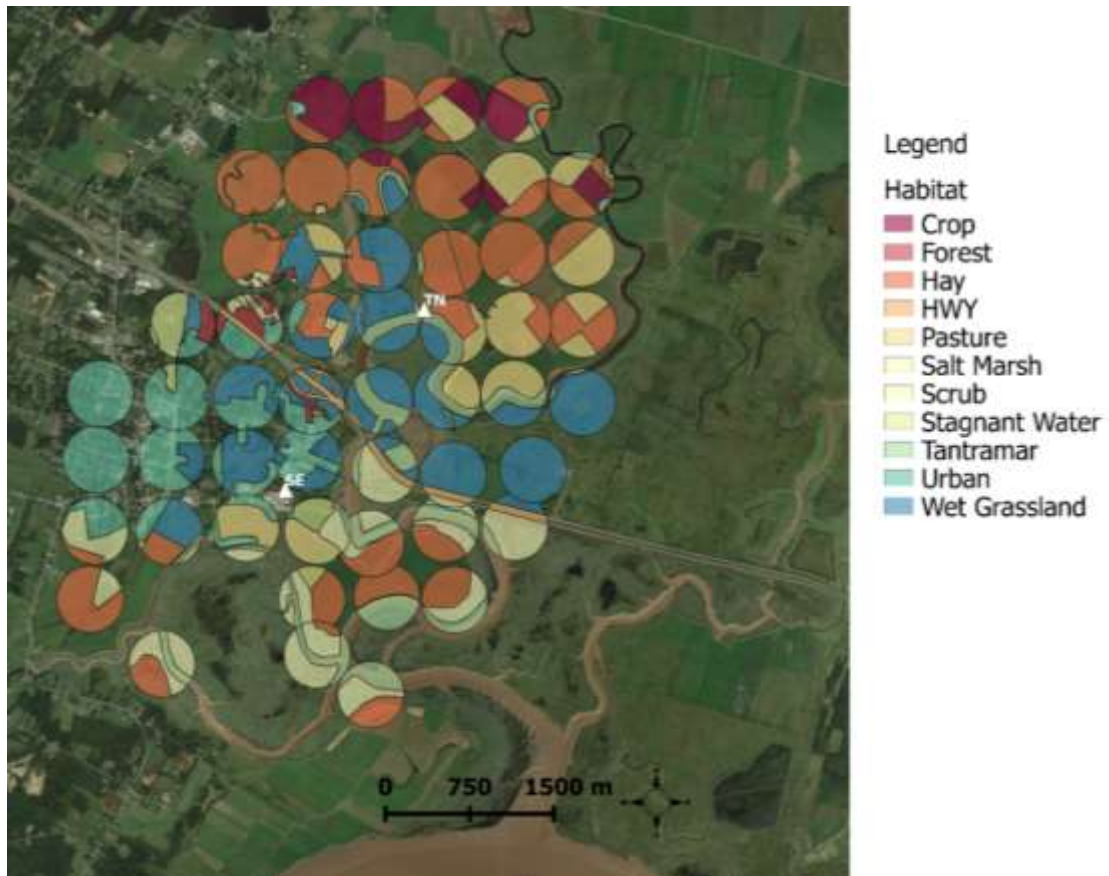
Figure 2.3 Position of colonies TN and SE and 300 m habitat plots surrounding Bank Swallow tracking points in 2015. Colonies TN and SE are indicated as white triangles.

Then, to account for differences in how common particular habitats were within the 300 m plots, the proportion of all habitats within each 300 m plot was divided by the proportion of the same habitat within 2 km of the colonies. Therefore, any habitat that had a value higher than one was more common at this given point than in the 2 km surrounding area and values below one signified that it was less common. I then used this measure, termed "relative abundance of habitat", for the analysis of Bank Swallow habitat use (see bellow).

Finally, to map how the proportion of different habitat types changed with distance from the colony, I measured the proportion of all habitat types by plotting a series of 20 concentric circles centred at each of the colonies and increasing in radii of 100 m increments. Then the relative proportion of habitats within each of these circles was measured.

2.2.4 Habitat Use Beyond Two Kilometers

To determine the extent that Bank Swallows use the area beyond the 2 km radius around their colonies, I used an array of 11 automated telemetry towers to record the presence of birds up to 15 km away.

To estimate the minimum distance travelled from a breeding colony by a tagged bird, I used the tower positions relative to the colonies, the maximum detection ranges of the antennas and the antenna directions associated with each detection (Figure 2.4). When the bird was detected by an omnidirectional antenna, I calculated the minimum distance travelled by measuring the distance a bird had to travel from its colony before entering a 1 km radius circle around the tower at which it was detected. When the bird was detected by a tower with directional antennas, I measured the minimum distance between its colony and a 12 km line which extended from the tower in the direction of the antenna that detected the bird. These ranges are, however, likely an underestimate since the structure and topography of the environment can reduce the detection range of the antennas.

Since tags emitted a signal every 10 seconds, I distinguished between different foraging bouts by measuring the time lag between detections. If a bird was detected twice

at the same location within less than 1 minute, I assumed this was part of the same trip. However, if the time lag between detections was over 1 minute, I assumed that these were two distinct trips, because swallows are highly mobile and can travel ~350 m within 1 minute (Blake & Chan 2006).
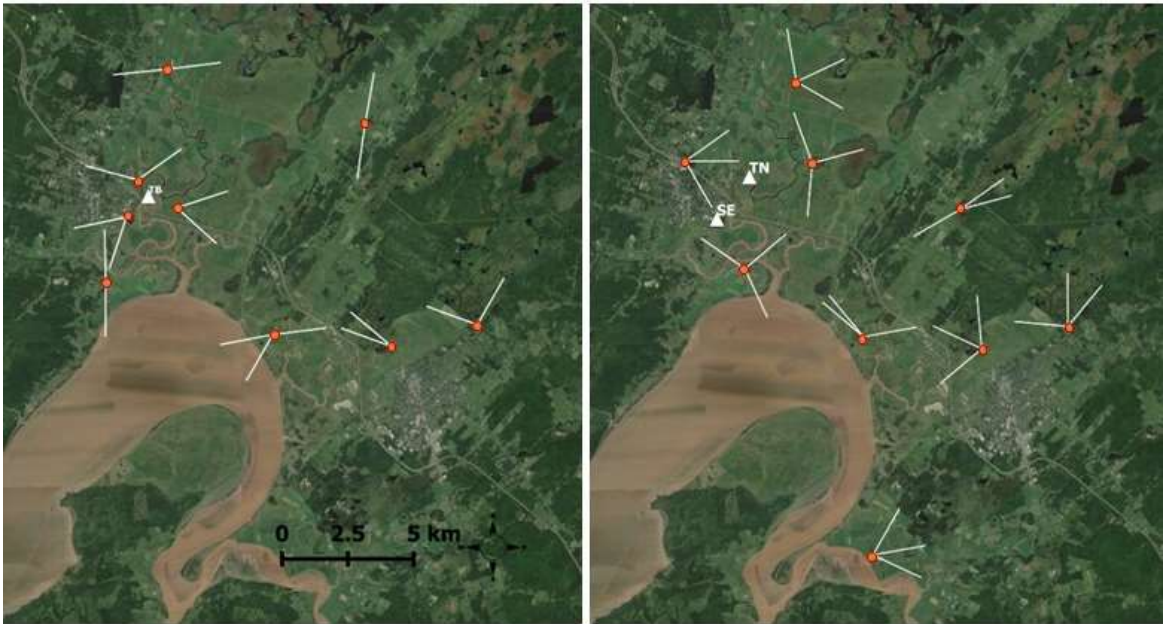
Figure 2.4 Position of colonies TB, TN and SE and the positon of the automated telemetry towers and their antenna directions in 2014 (left) and 2015 (right). Antenna directions shown as 2 km white lines and tower position shown as orange points.

2.2.5 Statistical Analyses

Collinearity between model variables was tested using Pearson's correlation coefficients (r). Crop and Hay were collinear for colony TB (r = 0.70). Since Hay had a bigger distribution than Crop, Crop was not included in the analysis for this colony.

All statistical modelling was done in R 3.1.2 and I visually assessed the fit of all models using residual plots.

To measure whether the nest success of the 68 tagged Bank Swallows differed from 69 untagged controls, I created three Generalized Linear Models (GLM) with the response variables: the proportion of eggs hatched, the number of fledged chicks and nest survival (nests with at least one fledged chick). Each model tested the response variable tagged/untagged bird while also controlling for burrow length and clutch initiation date, which are known to affect Bank Swallow nest success (Garrison 1999).

To measure habitat use, I modelled whether the number of times a bird was detected at a tracking point could be predicted by the distance, habitat type and the habitat heterogeneity of the 300 m plots. Distance and habitat heterogeneity (measured as the number of habitats within each plot) were included because both strongly affect the habitat use of other central place foragers (Bontadina et al. 2002, Benton 2003). To do this, I split my data by colony and produced three series of Zero Inflated Generalized Mixed Models (ZIMMS) with the response variable "number of sessions in which an individual was detected at given point" (Package glmmADMB). Each model had a Poisson distribution, the random effect "individual id", and the offset "log of the number of tracking sessions at a given point in which this individual was available". I analysed each colony separately instead of using colony as a nested random effect to compare the habitat use of individuals from different colonies. For each colony, I first created a full model with the variables distance, habitat heterogeneity, the relative abundance of each of the 10 habitat types and the interaction between distance and the abundance these habitat types. The interaction between distance and habitat was included to test whether

there was a relationship between distance and habitat type (Mysterud & Ims 1998). Then, to select the most parsimonious model for each colony, I compared all possible subsets of this full model using AICc (Akaike's information criterion corrected for small sample size, MuMIn package; Aho 2014).

To determine if foraging distance of tagged birds was affected by weather conditions, colony, sex, chick age, the interaction between sex and chick age and whether a nest was active, I fit a series of Generalized Mixed Effect Models (GLMM) with gamma distributions, the response variable "distance from the colony" and the random effect "individual id" (Package lmer). To remedy convergence issues, continuous predictor variables for this model (i.e. temperature, wind speed, cloud cover and chick age) were standardized and centered at 0 (Zuur et al. 2013). To select the model with the best fit, I also compared all nested models using AICc statistics (MuMIn package).

In the case where the AICc statistics of multiple models differed by less than two, the most parsimonious model was selected because this does not suggest substantial differences between the models (Burnham & Anderson 2002).

2.3 Results

2.3.1 General Results

Whether a bird was tagged (1) or not (0) had no significant effect on nest survival (Model Parameter Estimate (β) = 0.16, 95% CI = -0.64, 0.99), proportion of hatched chicks (β = 0.00, 95% CI = -0.29, 0.29) or the number of chicks fledged (β = 0.04, 95% CI = -0.19, 0.28) suggesting that the tags had no effect on Bank Swallow nest success.

In total, I conducted 323 tracking sessions in 2014 and 616 tracking sessions in 2015. At least one Bank Swallow was detected in 58% of the tracking sessions and observed in 33%. Of the 2903 Bank Swallows that were observed during the tracking sessions (1425 in 2014 and 1478 in 2015), all were foraging except for one record of a bird flying by (direct flight) and one record of a flock of 75 individuals perched in a tree preening. Therefore, I assumed that any bird that was detected using radio telemetry, but not observed, was foraging.

Overall, 66 of the 68 tagged birds were detected at least once. The tags of the two undetected birds were believed to have fallen off prematurely since they suddenly stopped being detected after 1 and 4 days although their nests remained active. The number of times each individual was detected was highly variable (mean: $34.9 \pm SD$ 22.0) and, overall, individuals from colony SE were detected less often ($22.3 \pm SD$ 17.9) than individuals from TB ($45.3 \pm SD$ 21.8) and TN ($31.6 \pm SD$ 19.4). Moreover, the number of points at which they were detected foraging was also highly variable ($15.13 \pm SD$ 7.14), suggesting variable foraging ranges (Figures 2.5.-2.10).
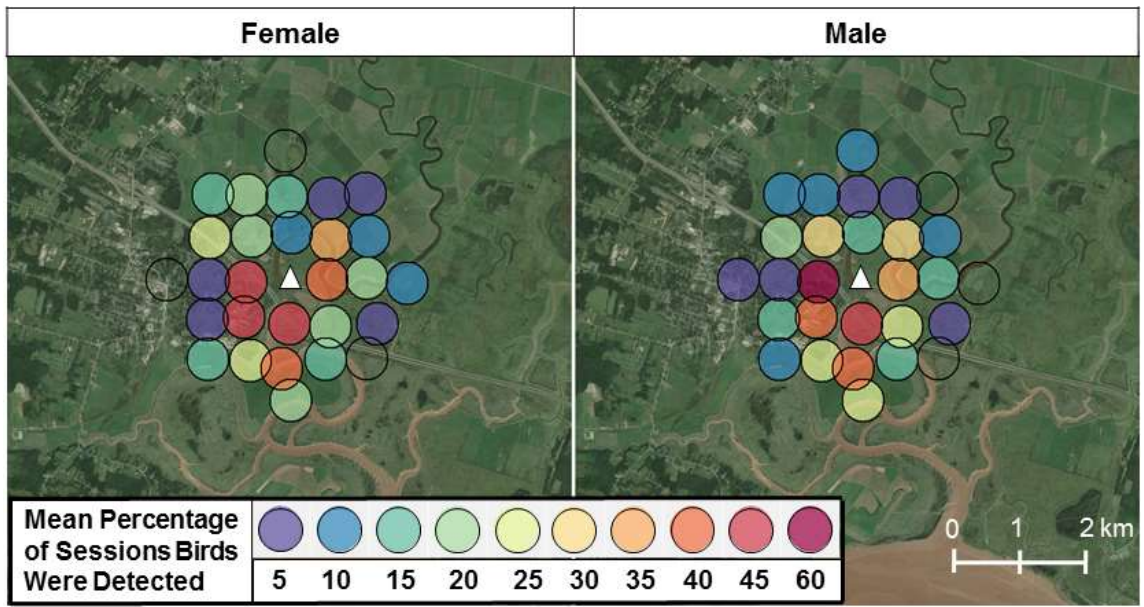
Figure 2.5 Mean percentage of tracking sessions in which individual female and male Bank Swallows from colony TB were detected at each of the 29 tracking points in 2014. The colony TB is indicated by the white triangle and circles represent each of the 300 m plots surrounding the tracking points.
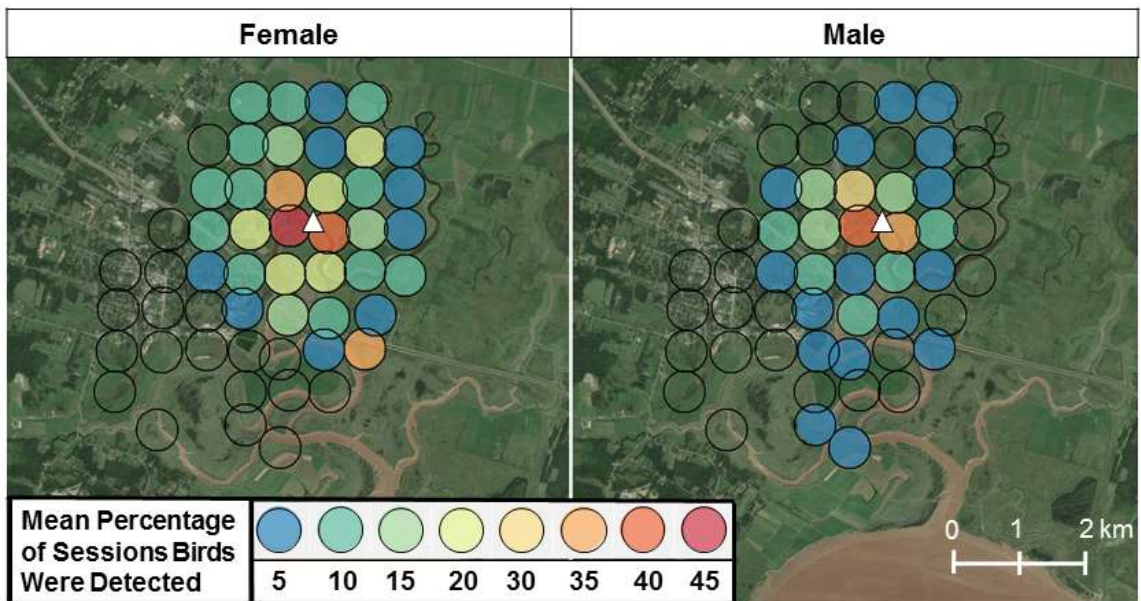
Figure 2.6 Mean percentage of tracking sessions in which individual female and male Bank Swallows from colony TN were detected at each of the 52 tracking points in 2015. The colony TN is indicated by the white triangle and circles represent each of the 300m plots surrounding the tracking points.
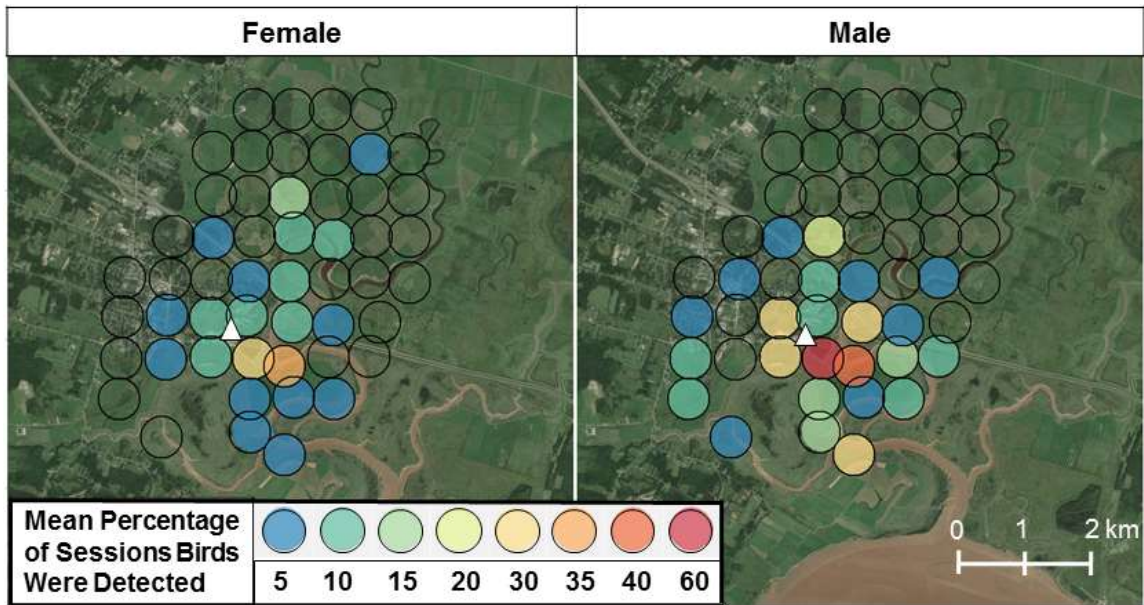
Figure 2.7 Mean percentage of tracking sessions in which individual female and male Bank Swallows from colony SE were detected at each of the 52 tracking points in 2015. The colony SE is indicated by the white triangle and circles represent each of the 300m plots surrounding the tracking points.
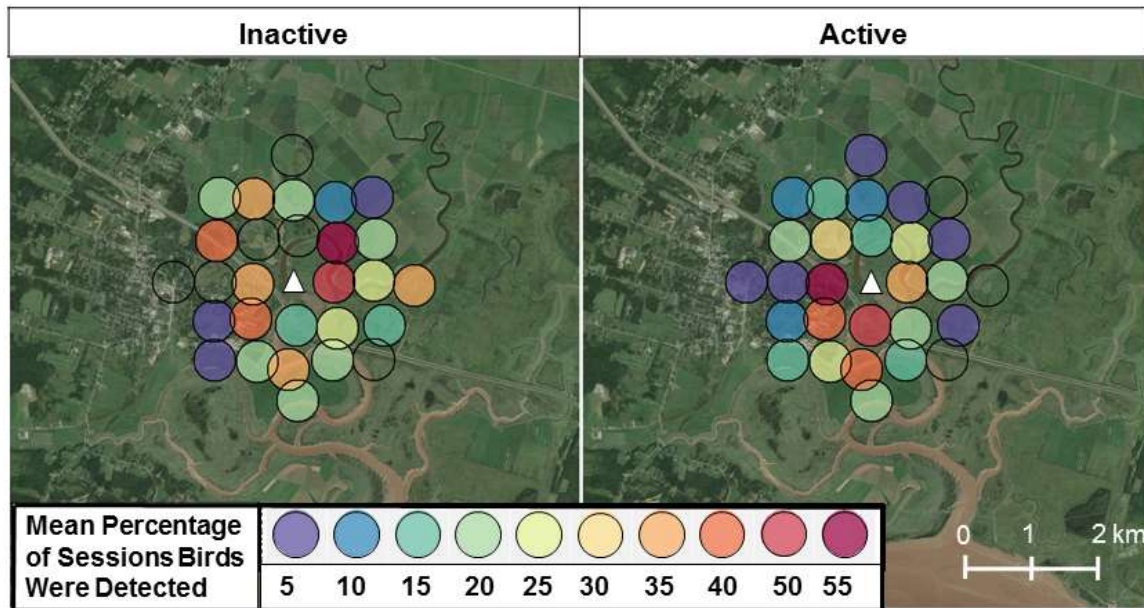
Figure 2.8 Mean percentage of tracking sessions in which individual Bank Swallows with inactive and active nests from colony TB were detected at each of the 29 tracking points in 2014. The colony TB is indicated by the white triangle and circles represent each of the 300m plots surrounding the tracking points.
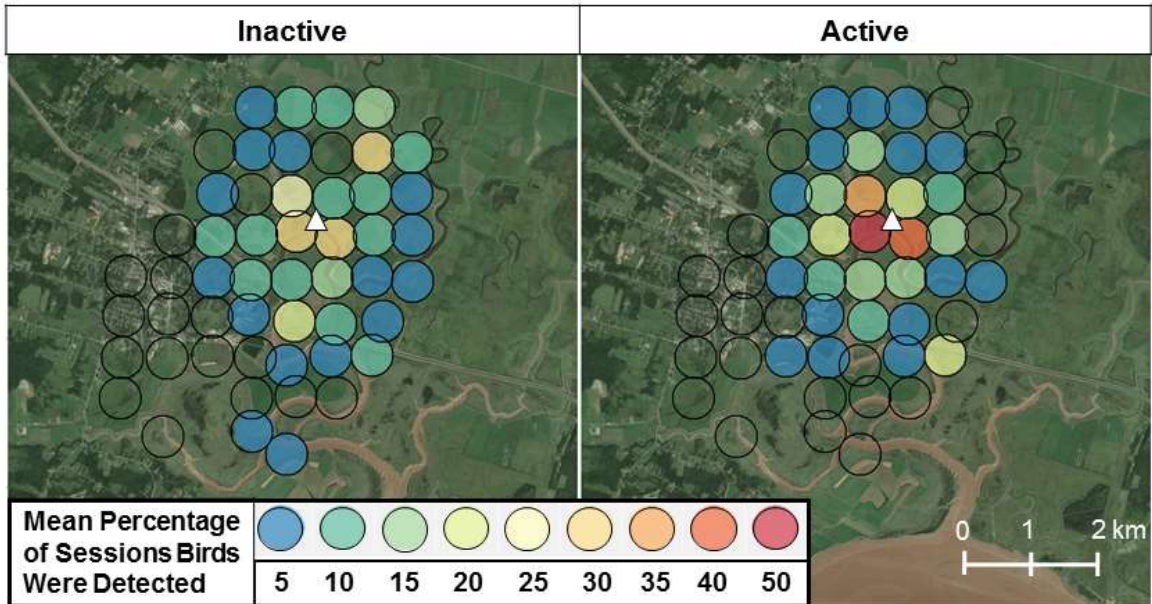
Figure 2.9 Mean percentage of tracking sessions in which individual Bank Swallows with inactive and active nests from colony TN were detected at each of the 52 tracking points in 2015. The colony TN is indicated by the white triangle and circles represent each of the 300m plots surrounding the tracking points.
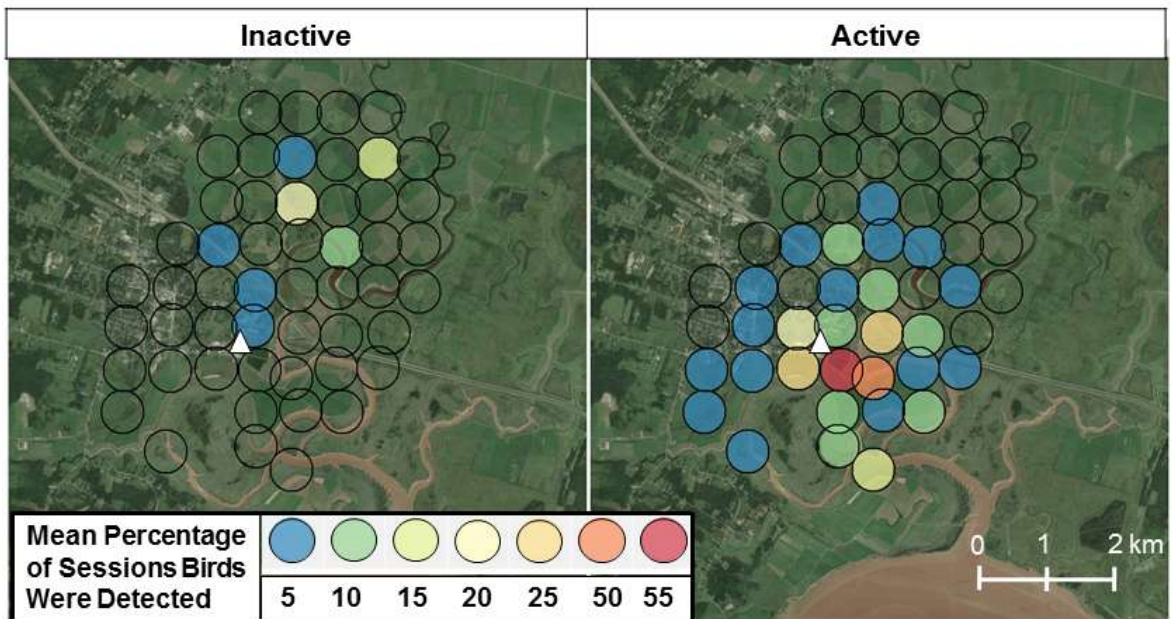
Figure 2.10 Mean percentage of tracking sessions in which individual Bank Swallows with inactive and active nests from colony SE were detected at each of the 52 tracking points in 2015. The colony SE is indicated by the white triangle and circles represent each of the 300m plots surrounding the tracking points.

2.3.2 Habitat Composition

All habitats were not equally distributed within the environment and therefore, the proportion of different habitat types changed with distance from the colonies (Figure 2.11).
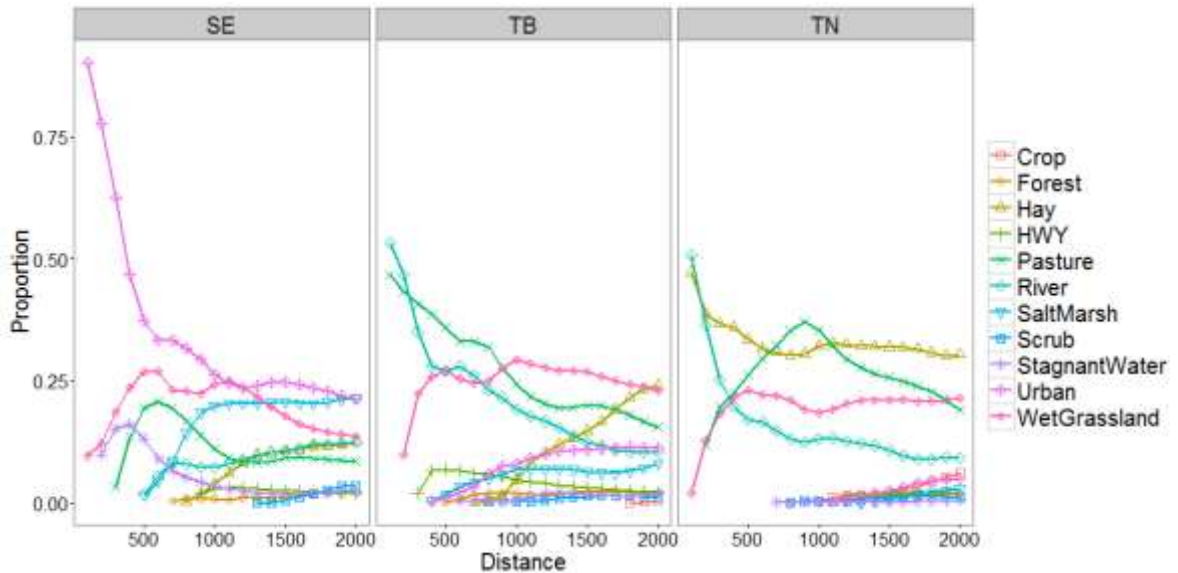
Figure 2.11 Proportion of the 11 habitat types at different distances from Bank Swallow breeding colonies.

2.3.3 Habitat Use Beyond Two Kilometers

Of the 117,186 distinct trips that were recorded at the automated telemetry towers, 80.3% were within 2 km, 19.7% were greater than 2 km from its nesting colony and 1.2% were greater than 5 km (Figure 2.12). One individual was detected foraging over 15 km from its colony. Moreover, these long distance movements occurred throughout the breeding season and in both males and females (Figure 2.13). In total, I detected 7 birds (3 females, 4 males) over 2 km from the colony during the day while incubating eggs, 44 (22 females and 22 males) while caring for chicks and 49 birds (24 females and 25 males) after their nests had either failed or their chicks had fledged.
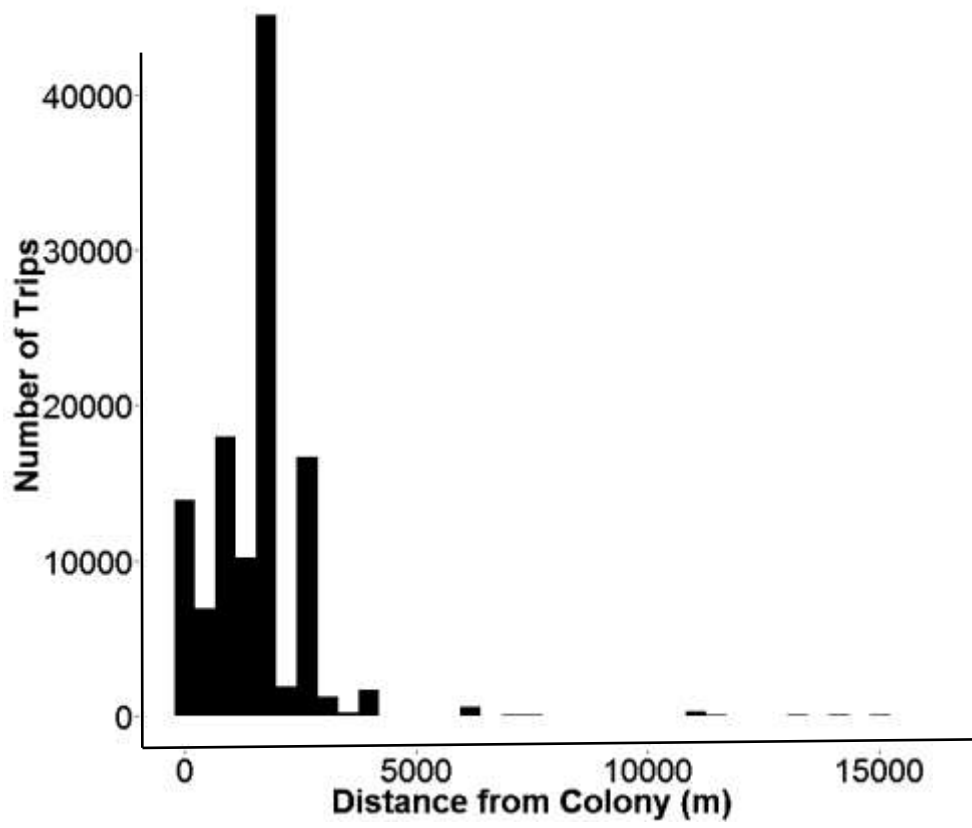
Figure 2.12 Number of detections with automated telemetry at different distances from Bank Swallow breeding colonies.
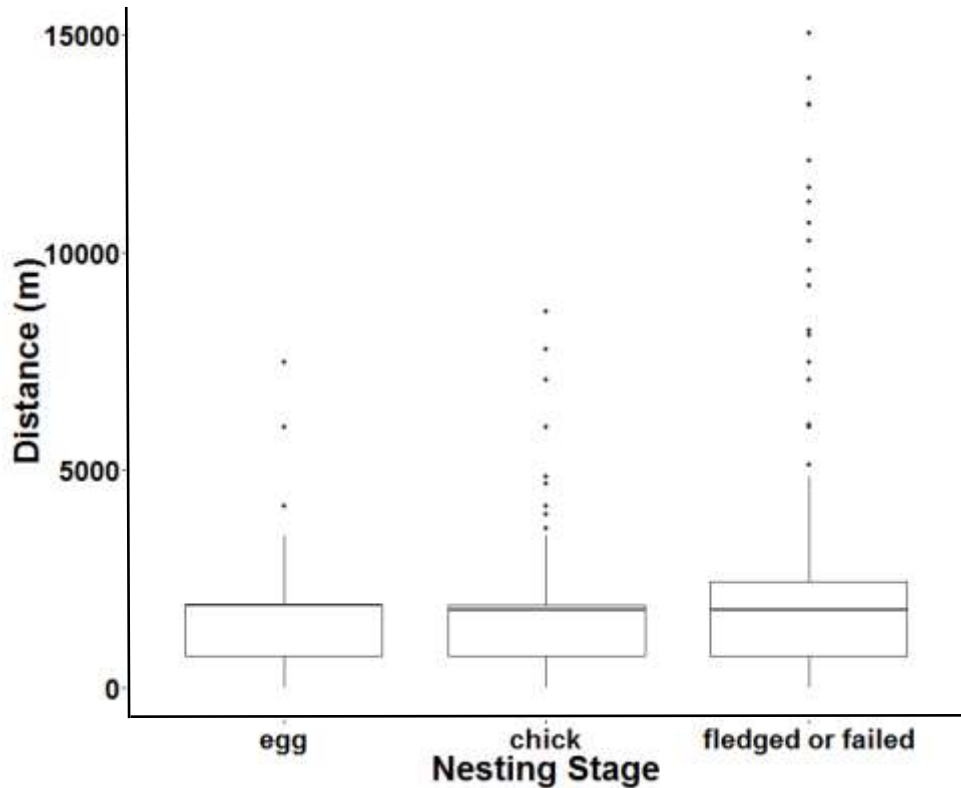
Figure 2.13 Distance from the colony and number of detections with automated telemetry of Bank Swallow at different nest stages.

2.3.4 Foraging Habitat Use

For all three colonies, the strongest predictor for the number of times a bird was detected at a tracking point was distance. However, habitat heterogeneity, habitat type and the interaction between habitat type and distance also had effects.

For colony TB, the best fit model suggests that Bank Swallows selectively foraged in plots close to the colony (β = -2.67, 95% CI = -3.04, -2.3), plots with high habitat heterogeneity (β = 0.14, 95% CI = 0.08, 0.20) and salt marsh (β = 0.06, 95% CI = -0.03, 0.15) and they selected against plots with river (β = -0.59, 95% CI = -0.73, -0.45) and wet grassland (β = -1.21, 95% CI = -1.58, -0.84; Table 2.2). However, the best fit

model also included interaction terms between salt marsh (β: 0.77, 95% CI: 0.52,1.03), river (β: 0.57, 95% CI: 0.46, 0.69) and wet grassland (β: 0.77, 95% CI: 0.52, 1.03) with distance, suggesting that these habitat relationships may be in part caused by their positions relative to the colony.

For colony TN, the best fit model suggests that Bank Swallows selectively foraged in plots close to the colony (β: -1.31, 95% CI: -1.55, -1.08), plots with high habitat heterogeneity (β: 0.10, 95% CI: 0.03, 0.16) and salt marsh (β: 0.15, 95% CI: 0.08, 0.21), wet grassland (β: 0.28, 95% CI: 0.19, 0.37), urban (β: 0.46, 95% CI: 0.08, 0.85) and crop (β: 0.07, 95% CI: 0.04, 0.10) (Table 2.3). However, like TB, the best fit model for TN also included the interaction terms for wet grassland (β: -1.62, 95% CI: -0.25, -0.08) and urban (β: -0.24, 95% CI: -0.47, -0.01) with distance, suggesting again that these habitat relationships may be in part caused by their positions relative to the colony.

Finally, for colony SE, the best fit model suggests that Bank Swallows selectively foraged in nearby plots (β: -1.63, 95% CI: -1.86, -1.4) and plots with high salt marsh (β: 0.09, 95% CI: 0.03, 0.15), and they selected against plots with urban habitat (β: -0.26, 95% CI: -0.36, -0.16; Table 2.4).

Table 2.2 Bank Swallow foraging habitat use model comparison for colony TB showing all models within 95% cumulative weight. Model selection shown in bold.

Model	Parameters	df	logLik	AICc	Δ	weight
TB 1	(river + wet grassland + salt marsh) * distance + pasture + urban + hay + habitat heterogeneity + offset(availability) + (1 | tag)	14	-949.2	1927.1	0	0.26
TB 2	**(river + wet grassland + salt marsh) * distance + habitat heterogeneity+ offset(availability) + (1 | tag)**	**11**	**-952.4**	**1927.2**	**0.1**	**0.25**
TB 3	(river + wet grassland + salt marsh) * distance + pasture + habitat heterogeneity + offset(availability) + (1 | tag)	12	-951.4	1927.3	0.2	0.24
TB 4	(river + wet grassland + salt marsh + hay) * distance + pasture + habitat heterogeneity + offset(availability) + (1 | tag)	14	-950.2	1929	1.9	0.1
TB 5	(river + wet grassland + salt marsh + hay) * distance + pasture + urban + habitat heterogeneity + offset(availability) + (1 | tag)	15	-949.1	1929	1.9	0.1

Table 2.3 Bank Swallow foraging habitat use model comparison for colony TN showing all models within 95% cumulative weight. Model selection shown in bold.

Model	Parameters	df	logLik	AICc	Δ	weight
TN 1	**(wet grassland + urban) * distance + salt marsh + crop + habitat heterogeneity + offset(availability) + (1 | tag)**	**11**	**-1125**	**2272.1**	**0**	**0.44**
TN 2	(wet grassland + urban) * distance + pasture + salt marsh + crop + habitat heterogeneity + offset(availability) + (1 | tag)	12	-1124.6	2273.5	1.3	0.23
TN 3	(wet grassland + urban) * distance + pasture + hay + salt marsh + crop + habitat heterogeneity + offset(availability) + (1 | tag)	13	-1123.6	2273.6	1.5	0.21
TN 4	(wet grassland + urban) * distance + river + pasture + hay + salt marsh + crop + habitat heterogeneity + offset(availability) + (1 | tag)	14	-1123.6	2275.6	3.5	0.08

Table 2.4 Bank Swallow foraging habitat use model comparison for colony SE showing all models within 95% cumulative weight. Model selection shown in bold.

Model	Parameters	df	logLik	AICc	Δ	weight
SE 1	(stagnant water + hay) * distance + urban + wet grassland + pasture + river + salt marsh + offset(availability) + (1 | tag)	13	-350.8	728.2	0	0.21
SE 2	**distance + urban + salt marsh + offset(availability) + (1 | tag)**	**6**	**-358.1**	**728.3**	**0.1**	**0.2**
SE 3	distance + hay + urban + salt marsh + offset(availability) + (1 | tag)	7	-357.1	728.3	0.1	0.2
SE 4	distance + hay + urban + pasture + river + salt marsh + offset(availability) + (1 | tag)	9	-355.6	729.6	1.4	0.1
SE 5	(stagnant water + wet grassland + hay) * distance + urban + pasture + river + salt marsh + offset(availability) + (1 | tag)	14	-350.6	729.8	1.7	0.09
SE 6	distance + river + urban + salt marsh + offset(availability) + (1 | tag)	7	-358	730.2	2.1	0.07
SE 7	distance + hay + urban + wet grassland + pasture + river + salt marsh + offset(availability) + (1 | tag)	10	-355.5	731.3	3.2	0.04
SE 8	(stagnant water + wet grassland + hay + urban) * distance + pasture + river + salt marsh + offset(availability) + (1 | tag)	15	-350.5	731.9	3.7	0.03

2.3.5 Foraging Distance

Although several foraging distance models showed substantial support (delta AICc < 2), model D 3 was considered to be the best model due to its low AICc and simplicity (Table 2.5). This model found that foraging distance increased with chick age ($\beta = 0.04$, 95% CI = 0.01, 0.06), wind speed ($\beta = 0.05$, 95% CI = 0.03, 0.08), and cold temperatures ($\beta = -0.04$, 95% CI =-0.06, -0.02) and generally was lower in males ($\beta = -0.08$, 95% CI= -0.18, 0.01) and in birds with active nests (β: -0.21, 95% CI: -0.40, -0.02).

Table 2.5 Bank Swallow foraging distance model comparison showing all models within 95% cumulative weight. Model selection shown in bold.

Model	Parameters	df	logLik	AICc	Δ	weight
D 1	chick age + temperature + wind + sex + act/inactive + sex * chick age + (1 | tag)	9	-14700	29417.5	0	0.32
D 2	chick age + temperature + wind + sex + act/inactive + sex * chick age + cloud + (1 | tag)	10	-14699	29418.7	1.2	0.17
D 3	**chick age + temperature + sex + act/inactive +wind + (1 | tag)**	**8**	**-14702**	**29419.3**	**1.9**	**0.13**
D 4	chick age + temperature + wind + sex + act/inactive + sex * chick age + precipitation + cloud + (1 | tag)	11	-14699	29420	2.5	0.09
D 5	chick age + temperature + act/inactive + wind + (1 | tag)	7	-14703	29420.2	2.7	0.08
D 6	chick age + temperature + sex + act/inactive +wind + cloud + (1 | tag)	9	-14701	29420.5	3.1	0.07
D 7	chick age + temperature + sex + act/inactive + wind + precipitation + (1 | tag)	9	-14702	29421.2	3.7	0.05
D 8	chick age + sex + act/inactive + temperature + wind + cloud + precipitation + (1 | tag)	10	-14701	29422	4.5	0.03

2.4 Discussion

Bank Swallows from all three colonies preferentially foraged near their respective colonies. There are two main hypotheses that may explain this behaviour. First, Bank Swallows may forage nearby to avoid the costs associated with travelling further from the colony to find food. This could include reducing the energetic costs and predation risk associated with travelling as well as the loss of time that could be used for other behaviours such as caring for young (Bryant & Turner 1982, Kacelnik 1984, Johst et al. 2001). Alternatively, Bank Swallows may select the location of their colony based on its proximity to suitable foraging habitat and thus the distance between the colony and the foraging areas would necessarily be short (Horn 1968). However, because Bank Swallows have very specific nesting requirements (Peck & James 1987, Garrison 1999,

Silver & Griffin 2009) and forage for aerial insects, a spatiotemporally variable food source (Grüebler 2008), the second hypothesis alone is unlikely to fully explain this relationship (Brown et al. 1991). Furthermore, I found that Bank Swallows foraging from all three colonies appeared to be associated with habitats such as saltmarsh (all colonies) or wet grassland (colony TN), that were either nonexistent or poorly represented in the habitats directly adjacent to the colonies (Figure 2.10), suggesting that colonies were not centered on preferred foraging habitat. In addition, the models for colonies TN and TB included interaction terms between habitat types and distances suggesting that distance from the colony influences the use of certain habitat types. For example, birds from colony TB selectively foraged in salt marsh but the strength of this relationship decreased with increasing distance from the colony. Therefore, Bank Swallows appear to forage near their colonies to avoid the costs associated with the commute to further foraging sites and not because their colonies were located at the center of preferred habitat.

While Banks Swallows from all colonies consistently selected for some habitats, the relationship with other habitats differed between the colonies. All Bank Swallows, irrespective of their breeding colony, selectively foraged in salt marshes. This result is consistent with many previous reports that suggested that salt marshes are high-quality foraging habitat for swallows and other aerial insectivores (Jacobson et al. 1983, Clarke et al. 1984, Brawley 1995, Lewis & Casgrande 1997). Despite common association with salt marshes, there were specific differences in the habitat use across colonies. For example, individuals from TN were associated to wet grassland, while individuals from TB avoided this habitat. Since habitat use depends on the availability of particular

habitats, these discrepancies may have resulted from differences in composition of habitat types surrounding each of the colonies.

Birds from the three colonies also differed in whether they selected for habitat heterogeneity. While TB and TN selectively foraged at plots with high habitat heterogeneity, this habitat was not commonly used by birds from SE. This, again, can be explained by differences in habitat composition surrounding the three colonies. While colonies TN and TB were located in agricultural fields, colony SE was located in an urban area. Within agricultural areas, habitat heterogeneity is considered beneficial for aerial insectivores as it is commonly associated with the presence of structural habitat such as hedgerows, buildings and scrubland which harbour aerial insects in these otherwise open, wind swept environments (Karg 1994, Evans et al. 2003). However, in urban environments, structural habitats do not provide food in the same way as in agricultural environments and insect diversity is generally lower within urban areas (Coleman & Barclay 2013). Therefore, birds from colonies TB and TN may have selected for habitat heterogeneity within the open area surrounding these colonies while colony SE may have avoided heterogeneous habitat as it was associated with urban areas.

Although Bank Swallows selectively foraged near their colonies, I found that Bank Swallows occasionally foraged further from their colonies than previously recorded through visual observations. Using automated telemetry, I found that Bank Swallows mostly foraged within 2 km of their colony, although they also were detected up to 15 km from the colony. This is substantially further than the 1 km maximum foraging range previously described (Garrison 1999, Mofatt et al. 2005). In Tree Swallows, Dunn and Whittingham (2005) recorded female movements up to 10 km away from their nest in the

pre-laying period and attributed these long distance movements to females seeking extra-pair copulations. Unlike this study, I observed long distance movements throughout the breeding season (with the highest rates when chicks were fledged or nest had failed) and in both males and females. Hence, Bank Swallow long distance movements cannot be attributed to extra-pair copulations alone.

Another potential explanation for these long distance movements is prospecting for future breeding opportunities (Brown & Brown 2000). The Cliff Swallow (*Petrochelidon pyrrhonota*), a closely related species that is also colonial, visits active colonies near the end of the breeding season to apparently evaluate the colony's success (Brown & Brown 2000). Since Bank Swallows long distance movements were more common later in the breeding season, this leads to the hypothesis that this may also be the case. However, further research would be needed to substantiate this claim.

I found that Bank Swallows foraged further from the colony in poor weather conditions, as their chicks aged, when they were female and their nests were inactive. There are a variety of explanations for these patterns.

In poor weather conditions, insect prey become less abundant in the air column because they cannot fly in cold temperatures and high wind (Taylor 1963, Grüebler et al. 2008, Dunn et al. 2011). Therefore, in these conditions, the food near the colony may become depleted, forcing Bank Swallows to forage further away in an attempt to find food. This result agrees with previous work that recorded Bank Swallows and other swallow species foraging further from their nests in poor weather conditions (Turner & Rose 1989, Winkler et al. 2006). Moreover, Swallows are also known to forage in two thermally stable areas during poor weather conditions: low over open water (Winkler et

al. 2006) and in sheltered hedgerows (Evans et al. 2003), both of which have been found to support higher abundances of aerial insects in poor weather conditions (Evans et al. 2003, Grüebler et al. 2008, Winkler et al. 2006). In this study, although the proportion of open water (River and Stagnant Water combined) decreased with distance from the colonies, the proportion of forest increased, suggesting that Bank Swallows may have travelled further in poor weather conditions to forage near hedgerows (Figure 2.11).

Bank Swallows in my study also foraged further from the colony as their young grew older. This is consistent with the results of other studies that found increases in foraging range as the nestling period advanced (Adams et at. 1994, Falconer et al. 2008, Sokolov et al. 2014). Birds often increase their foraging range to compensate for the lack of food availability (Bryant & Turner 1982, Adams et at. 1994), so, an increase of foraging distance during this period may reflect heightened pressure to find food for their growing offspring.

Female Bank Swallows tended to forage further from the colony than males (although this result was non-significant). This result is unexpected because female Bank Swallows undertake the majority of brooding and incubation and would therefore need to be closer to the nest than males during these times (Garrison 1999). However, this result might be biased by the number of foraging detections of males and females in the early breeding season. Since females spent more time at the nest for incubation and brooding, they were less likely to be detected early in the breeding season than males. Therefore, there were more detections of foraging females later in the breeding season, when chicks were older and foraging distances were greater (see above). However, the introduction of

an interaction term between sex and chick age did not improve the model fit, suggesting that further investigation is required.

Bank Swallows also foraged further from the colony when their nests were inactive, which included both failed and fledged nests. When nests became inactive, Bank Swallows were no longer required to return to the colony to care for young and could therefore take advantage of more distant foraging habitat without compromising the care of their young. This result is consistent with work on female Peregrine Falcons (*Falco peregrinus*) that extended their home ranges after their chicks fledged (Sokolov et al. 2014).

Although this study found strong individual and colonial variability in Bank Swallow foraging behaviour, the found patterns concerning foraging habitat use and distance are the first step in the identification of the foraging habitat requirements for this species. Although foraging habitat use is dependent on habitat availability (i.e. Bank Swallows in landlocked areas will not selectively forage in salt marsh), further studies may focus on whether habitats with similar structures are also commonly used. Furthermore, because foraging distance was influenced by both intrinsic and extrinsic factors, understanding how this translates into specific habitat use may be important in understanding Bank Swallow foraging requirements throughout the breeding season and in a changing environment. Overall, the foraging patterns identified in this study can help both inform future studies and provide insight into the management practices required to protect this declining species.

CHAPTER 3: BANK SWALLOW ROOSTING HABITAT USE

3.1 Introduction

Animal aggregations are one of the most remarkable events in nature. These synchronized groupings of individuals can vary greatly in their size and composition (Allee 1931). While some aggregations number only a few individuals, others number in the hundreds of thousands and even in the millions (Allee 1931). Moreover, animal aggregations can be composed of mixed or same-species groups and can be further divided by sex, age or body size (Allee 1931, Krause & Ruxton 2002). Despite these differences, aggregations are hypothesized to benefit individual group members by reducing thermoregulation costs (Beauchamp 1999) and predation risk (Lack 1968) and increasing mating opportunities (Bondel & Brooks 1999) and foraging efficiency (Ward & Zahavi 1973, Caccamise & Morrison 1988). In turn, these benefits are balanced by costs such as increased conspicuousness (Beauchamp 1999), disease transmission (Yom-Tov 1979) and increased competition (Beauchamp 1999, Bondel & Brooks 1999). Since the size and composition of animal aggregations can influence both the benefits and costs associated with this behaviour, balancing these trade-offs explains the great diversity of aggregations observed in nature (Beauchamp 1999).

In birds, one common aggregation type is communal roosting, where individuals congregate at night for rest and sleep (Laughlin et al. 2014). In these aggregations, anywhere from a few to millions of individuals gather just before sunset and spend the night together before dispersing again at sunrise (Alonso et al. 1985, Bijlsma & van den Brink 2005). While some, usually small, communal roosts are located within individual

diurnal activity centers (the area within which individuals spend their days) or DACs, large communal roosts are commonly found outside of DACs (Caccamise & Morrison 1988). In some cases, individuals will travel over 10 km from their DAC to roost communally overnight before returning in the morning (Caccamise & Morrison 1988, Slager & Rodewald 2015, Falconer et al. 2016). This behaviour, termed disjunct roosting, occurs in many species worldwide (Caccamise & Morrison 1988, Slager & Rodewald 2015, Falconer et al. 2016).

Although communal roosting has been well studied during the winter and migratory periods (Caccamise et al.1997, Stolen & Taylor 2003, Laughlin et al. 2014), there are fewer records of this behaviour during the breeding season. These records show that during the breeding season roosts are often smaller and solely occupied by juveniles and sub-adult birds, compared to roosts at other times of the year that are larger and composed of all age classes (Curnutt 1992, Blanco 1996, Cougill & Marsden 2004, McVey et al. 2008). These observations have led to the hypothesis that many active breeders are unable to join communal roosts because of the costs of leaving eggs or young unattended during the night (Curnutt 1992, Blanco 1996, Cougill & Marsden 2004, McVey et al. 2008). However, in studies that directly examined the roosting behaviour of breeding birds, active breeders did occasionally join communal roosts, suggesting that this might not always be the case (Chandler et al. 1995, Hill & Cresswell 1997). For example, Chandler et al. (1995) tracked 11 breeding male Dark-eyed Juncos (*Junco hyemalis*) for five days and found them roosting communally on cold nights. In another study, five (three males and two females) tagged Blackbirds (*Turdus merula*) were tracked during the breeding season and both members of a pair began roosting away

44

from the nest once their young were 11 days old (Hill et al.1997). Therefore, while some breeding birds roost communally during part of the breeding season, this behaviour appears to be restricted by factors such as chick age, sex and weather conditions.

During the winter and migratory periods, similar factors also appear to affect communal roosting behaviour. In previous studies, intrinsic factors such as age, sex, size and breeding stage, affected individual position within roosts, roost site selection, roost composition and roost occupancy (Summers et al. 1986, Curnutt 1992, Blanco 1996, Blanco & Tella 1999, Cougill & Marsden 2004, McVey et al. 2008). Moreover, extrinsic factors such as weather conditions and the distance between DACs and roosts also affected roost occupancy over time (Anthony et al. 1981, Alonso et al. 1985, Obrecht & Dinsmore 2008, Lambertucci & Rulgierrro 2013). Understanding how these factors affect roosting behaviour can help identify individual costs and benefits associated with communal roosting, and therefore can help determined the main evolutionary drivers for this behaviour.

The Bank Swallow (*Riparia riparia*) provides an excellent model for understanding communal roosting behaviour during the breeding season and how both intrinsic and extrinsic factors affect this behaviour. Although Bank Swallows have long been known to roost communally during the winter and migratory periods (Russell et al. 1998, Garrison 1999, Winkler 2006), evidence of this behaviour during the breeding period was scarce until a recent study by Falconer et al. (2016). In this study, both male and female breeding Bank Swallows left their nests and appeared to be roosting communally in cattail wetlands over 35 km away from the breeding colony (Falconer et al. 2016). Although the roost locations were never observed, this study identified some

intriguing patterns that suggested that males were more likely to roost communally than females, especially when the nest contained eggs and young chicks. This suggests that, like other species that roost communally during the breeding season, communal roosting in breeding Bank Swallows may be constrained by factors such as sex and chick age (Falconer et al. 2016).

Although the study of communal roosting during the breeding season is important in its own regard, it can also play a role in species conservation. In Canada, Bank Swallows have declined by 98% since 1971, and have been recommended for listing as Threatened under Canada's Species at Risk Act (SARA). If listed, critical habitat must be identified. Communal roosts for many species often occur outside of individual daily activity centers (either breeding territories or foraging area depending on the season) and so identifying them is necessary to understand the complete habitat requirements for species, including Bank Swallows (Slager & Rodewald 2015). Consequently, identifying the intrinsic (e.g. sex, chick age, active/inactive nest) and extrinsic factors (e.g. weather, distance to a roost site) that affect Bank Swallow communal roosting will not only increase our understanding of communal roosting as a whole, but also inform the designation of critical habitat and the conservation of this species.

The goal of my study, therefore, was to identify Bank Swallow communal roosts during the breeding season and to measure how intrinsic, and extrinsic factors affect the frequency, timing, and the duration of trips to communal roosts and the distribution of Bank Swallows among major (used over 50% of the time) and minor (used under 50% of the time) roost sites. More specifically, using radio tagged birds, I first studied how adult sex, nest occupancy (act/inactive nests), weather and light conditions affected the

likelihood of roosting communally on a given night. Secondly, I measured how these same variables affected the timing and duration of the commute to and from the roost sites and the decision to roost at a major or minor roost site. Finally, I also conducted roost counts at known roosting locations to identify how both tagged and untagged individuals from unidentified breeding colonies were distributed among the roost sites.

3.2 Methods

For information on nest monitoring, trapping, tagging, the study site, the automatic telemetry array, and the measure of intrinsic factors such as sex, chick age, and nest survival, see general methods (Chapter 1).

3.2.1 Extrinsic Factors

To determine how extrinsic factors affected roosting behaviour, I used temperature (°C), relative humidity (%), wind speed (km/h) and cloud cover (categorized as 1 to 4 with 1 being clear and 4 being overcast) data recorded at 20:00 and 06:00 local time to coincide with the approximate timing of departure to and return from roost sites. In addition, I collected the daily moon phase (%) and used it to create the variable "light" that estimated the amount of ambient light available at night. I multiplied moon phase by 1 when the cloud cover was 1, 0.75 when cloud cover was 2, 0.5 when cloud cover was 3 and 0.25 when cloud cover was 4. All variables except cloud cover were recorded by the Nappan (auto) weather station situated 17 km from the colonies and cloud cover was recorded at the Moncton Airport weather station situated 36 km from the colonies.

3.2.2 Identification of Potential Roosts

I assumed that all wet areas including large marshes, shrub thicket and other dense vegetation over water (Alves & Johnstone 1994, Garrison 1999, Winkler 2006, Falconer et al. 2016) within 35 km of the colonies (Falconer et al. 2016) were potential roost sites. I identified eight of these sites using a combination of ground truthing and satellite imagery. I then tested whether these roosts were active or not using a combination of automated telemetry and roost counts (see below).

3.2.3 Bank Swallow Roosting Location

To find Bank Swallow roosting locations, I monitored the tagged birds with an array of 11, 6 m high automated telemetry towers (see Chapter 1 general methods).

In both years, the data collected on Bank Swallow positions were limited by the placement of the towers, the direction of the antennas and their detection range. Tower placements and antenna directions were chosen to maximise the number of detections as a tagged bird moved to and from roosts. However, the location of tagged birds was only recorded when birds were within the detection range of an antenna, leaving gaps where the position of tagged birds was unknown. Moreover, the detection range of radio antennas can be reduced by the presence of boundaries such as topography, vegetation and housing, poor weather conditions and radio "noise" created by other machinery (Kays et al. 2011). Fortunately, because of the high density of towers, the direction of bird movements could often be identified by the sequential detections from different towers or antennas within the array. Nonetheless, the data contain several larger gaps where the position of the bird is uncertain, notably when spending the night in their

burrow or in dense vegetation. Therefore, certain assumptions had to be made to classify the location of the birds at these times.

To identify the location of tagged birds during these gaps, I made the following assumptions:

1) Birds did not move between the colony and roosts or from roost to roost during the night (here defined as the time between 60 minutes after sunset and 30 minutes before sunrise and based on the timing of other roosting swallows (Russell & Gauthreaux 1999, Bijlsma & van den Brink 2005) without being detected. Therefore, if a bird went undetected at night and the location of its last detection in the evening and first detection in the morning were the same, then I assumed it remained at this location throughout the night, be it the colony or a roost site. This assumption is justified because the signal output of the tags becomes diluted when birds roosted in dense vegetation or the nesting burrows, making it possible that the signal was undetected (Kays et al. 2011).

2) If a bird was detected at more than one tower at once, I assumed it was located at the tower where the signal intensity of the detection was the highest.

3) If a bird was undetected at night and the location of the last detection before sunset and the first detection after sunrise were not the same, but both detections were in the same direction from the colony, the latest detection was considered the roosting location

4) If a bird was not detected at night and the last detections before and after sunset did not match and were not the same direction, I assumed that the bird was roosting away from the colony but that I did not know its roosting site.

3.2.4 Timing and Duration of Commutes Between the Colony and Roost

To measure the timing and duration of commutes between the colonies and roosts, I limited my dataset to birds that were at the colony within one hour of sunset, left for a known roost location and returned to the colony within one hour of sunrise in 2015. I calculated the time of departure and return relative to sunset and sunrise respectively. Furthermore, to determine the duration of commutes to and from the roosts, I subtracted the time of the last detection at the colony from the time of the first detection at the roost in the evening and the time of the last detection at the roost from the time of the first detection at the colony in the morning.

Furthermore, I calculated the distance between the colonies and the closest point of each roost using a combination of ground truthing, satellite imagery and Quantum GIS. This allowed me to measure whether distance affected the timing and duration of the commutes to and from roost sites (see analysis).

3.2.5 Roost Counts

To determine if and to what extent the eight cattail marshes identified as potential roost sites (see above) were used by local swallow populations (including tagged birds from my study sites and untagged birds from both my colonies and other unidentified colonies) I conducted 9 to 11 roost counts at each site between 17 July and 26 August 2015.

Some of the marshes were extremely large, which made it difficult to keep track of the birds. For example, MISSA and TINTA were over 19 and 9 km^2, respectively. Therefore, when these marshes had multiple access points onto distinct impoundments, I stationed observers at each point. This resulted in EDDY and AMPNT having two

observers, TINTA having four and all others having one, adding up to a total of 13 roost

count observation points within the eight roosts.

Observations began 20 minutes before sunset and continued for a 40-minute period.

During each session, observers counted (if < 50) or estimated (if > 50) the number of Bank

Swallows that were circling above or entering the roost every 5 minutes. In some cases,

due to the large expanse of some of the marshes, observers did not see birds entering the

marsh. However, because 100% of the Bank Swallows that were directly observed entering

the marsh first joined circling flocks above the marsh before descending into the cattails, I

assumed that any flock exhibiting this behaviour was roosting at this site. Furthermore, if

an observer lost sight of a circling flock that then re-appeared within the session, the flock

was assumed to be the same unless it differed in size from the previously observed flock.

3.2.6 Analysis

To control for large differences in the magnitude of the numerical variables in my

dataset, I re-scaled and centered these variables (Zurr et al. 2013). Therefore, coefficients

are expressed in Z scores, which have a distribution with a mean of 0 and a standard

deviation of 1.

To determine if the likelihood of roosting communally was affected by intrinsic

and extrinsic variables, I fit Generalized Additive Mixed Binomial Models (GAMM)

with the response variable "roosting communally (1) or remaining at the colony (0)", the

random effect "individual ID" and a smoothed relationship selected via Laplace

Approximation between chick age and sex. To select the best fit model, I first created a

full model with the intrinsic factors sex, chick age and nest occupancy and the extrinsic

factors light, wind speed, temperature and relative humidity. I also included the

interaction terms between weather variables and chick age and nest occupancy because

these were hypothesized to affect the thermoregulation costs of roosting communally.

Then, to select the most parsimonious model I compared all possible subsets of this full

model using AICc (Akaike's information criterion corrected for small sample size,

MuMIn package; Aho 2014).

To examine if the relative departure time from the colony in the evening and the

arrival time at the colony in the morning was affected by intrinsic and extrinsic variables,

I fit two series of Generalized Linear Mixed Models (GLMM) with the random effect

"individual ID". In the first series, I modelled the difference between departure time and

sunset and in the second, I modelled the difference between arrival time and sunrise. I

then created a full model for each series, in which I included the intrinsic factors sex,

chick age and nest occupancy and the extrinsic factors light, wind speed, temperature,

relative humidity, distance between the colony and the roost and interactions between

distance and the weather variables. I included the interaction between distance and the

weather variables because poor weather conditions can impede sustained flight

(Richardson 1978). Finally, to select the most parsimonious models for each of the

response variables I compared all possible subsets of these full models using AICc (Aho

2014).

To determine if the likelihood of roosting at a major or a minor roost was affected

by intrinsic or extrinsic factors, I fit Generalized Linear Mixed Binomial Models with the

random effect "individual ID" and the response variable whether a bird was at a major (0)

or minor roost (1) on a given night. I then created a full model with the factors sex, chick

age, nest occupancy, light, wind speed, temperature and relative humidity and compared all subsets of this model using AICc to find the most parsimonious model (Aho 2014).

In all model comparisons, if the AICc statistics of multiple models differed by less than two, the most parsimonious model was selected because this does not suggest substantial differences between the models (Burnham & Anderson 2002).

Mixed-models were run using package lme4 (Bates et al. 2012), glmADMB (Fournier et al. 2012) and gamm4 (Wood 2015) in R (version 2.14.2; R Development Core Team 2012). The fit of each model was assessed visually using residual plots and by inspection of parameter estimates.

3.3 Results

3.3.1 General Results

No tagging effects were observed (see Chapter 2). Tags were recorded for a mean of 26 ± 11 days. One tag fell off less than 24 hours after attachment and therefore data from this tag were not used in the analysis.

All but one of the 67 tagged birds in the analysis roosted away from the colony at least once throughout the study. In total, birds were either known to have either remained at the nest or roosted communally on 1439 occasions (685 in 2014 and 754 in 2015). Of these nights, the mean proportion of nights away from the colony was 63%, with two birds roosting away every night throughout the study. Overall, the mean proportion of nights females spent roosting 0.63 (SD $\pm$ 0.26) was lower than males 0.71 (SD $\pm$ 0.27), although this difference was non-significant ($\beta = 0.08$, 95% CI =-0.05, 0.21). However,

larger differences occur between the sexes when its broken down by breeding stage

(Figure 3.1)
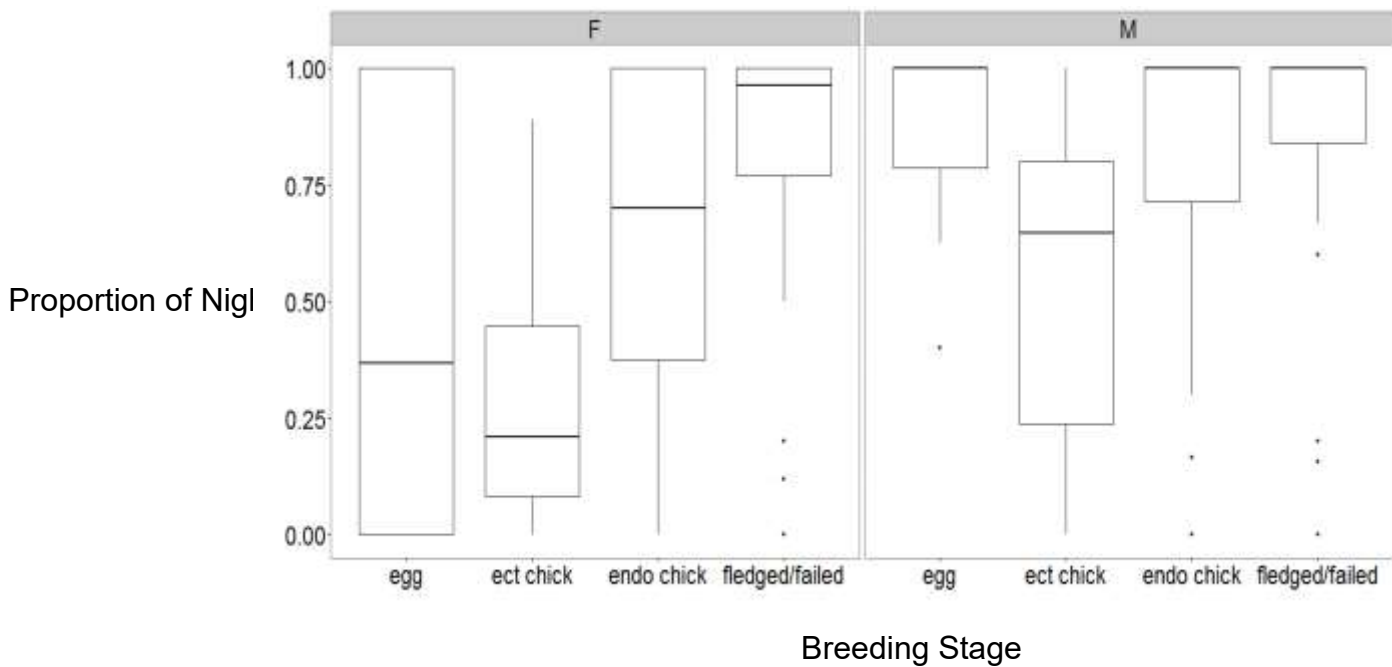
Figure 3.1 Proportion of nights female (F) and male (M) Bank Swallows roosted communally during four breeding stages (egg, ectothermic chicks, endothermic chicks, fledged/failed nest)

Because of the tower set up in 2014, the specific location of communally roosting individuals was rarely known. In contrast, in 2015, the roosting location was known on 94% of the nights where birds roosted communally.

Of the ten pairs tagged at TN, one pair did not have useable data because the male of the pair lost its tag prematurely. Of the nine pairs with useable data, six pairs roosted communally on the same night at least once. Two of these pairs had failed nests and four produced fledglings. Both partners of the four successful pairs began roosting away from their nests when chicks were -18, 6, 8, and 12 days old. None of the pairs roosted away from their young when they were 0 to 5 days old.

3.3.1 Effect of Intrinsic and Extrinsic Factors on the Likelihood of Roosting Communally

The probability of Bank Swallows roosting communally was influenced by both intrinsic and extrinsic factors. The best fit model was an additive mixed model with a smoothed relationship with chick aged which differed between the sexes as well as the coefficients light, temperature and relative humidity (Table 3.1). For males, the likelihood of roosting was lowest when the young reached four to five days old (Figure 3.2). In females, this likelihood was lowest near hatching (age 0) (Figure 3.3). Moreover, both males and females were more likely to roost communally when light was low (β = -0.02, 95% CI = -0.03, -0.01), temperatures were high (β = 0.09, 95% CI = -0.01, 0.20) and relative humidity was low (β = -0.04, 95% CI = -0.06, -0.03).

Table 3.1 Model comparison for the likelihood of Bank Swallows roosting communally. All models within 95% cumulative weight. Model selection is shown in bold.

Model	Parameters	df	logLik	AICc	Δ	weight
R1	s(chick age , by = sex) + sex + light + relative humidity + temperature + (1| tag)	10	-529.2	1078.7	0.0	0.28
R2	**s(chick age, by = sex) + light + relative humidity + temperature (1| tag)**	**9**	**-530.6**	**1079.4**	**0.8**	**0.19**
R3	s(chick age, by = sex) + sex + light + relative humidity	9	-530.7	1079.5	0.8	0.18
R4	s(chick age, by = sex) + sex + light + relative humidity + temperature + act/inactive nest + temperature * act/inactive nest	12	-527.9	1080.1	1.5	0.13
R5	s(chick age, by = sex) + light + relative humidity + (1| tag)	8	-532.1	1080.3	1.7	0.12
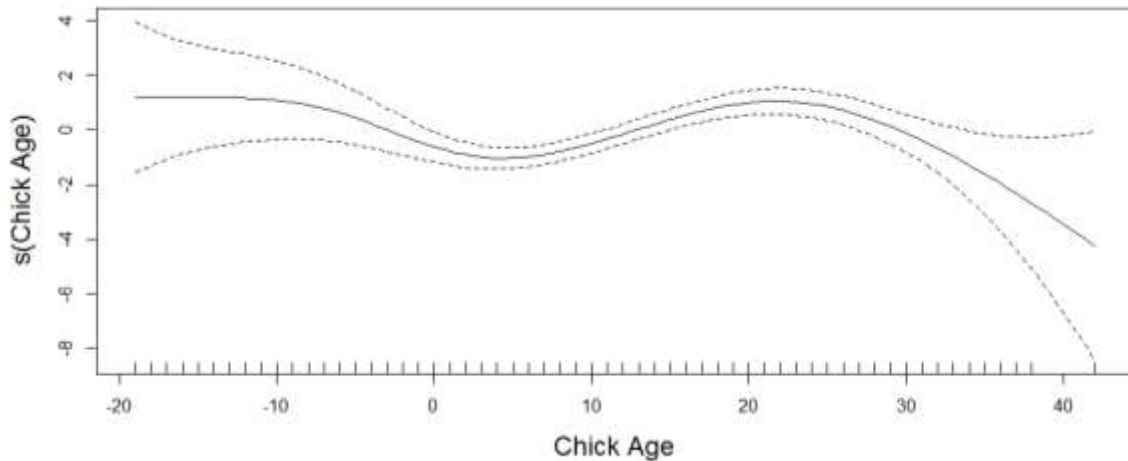
Figure 3.2 Model smoother showing the effect of chick age on the probability of male Bank Swallows roosting.
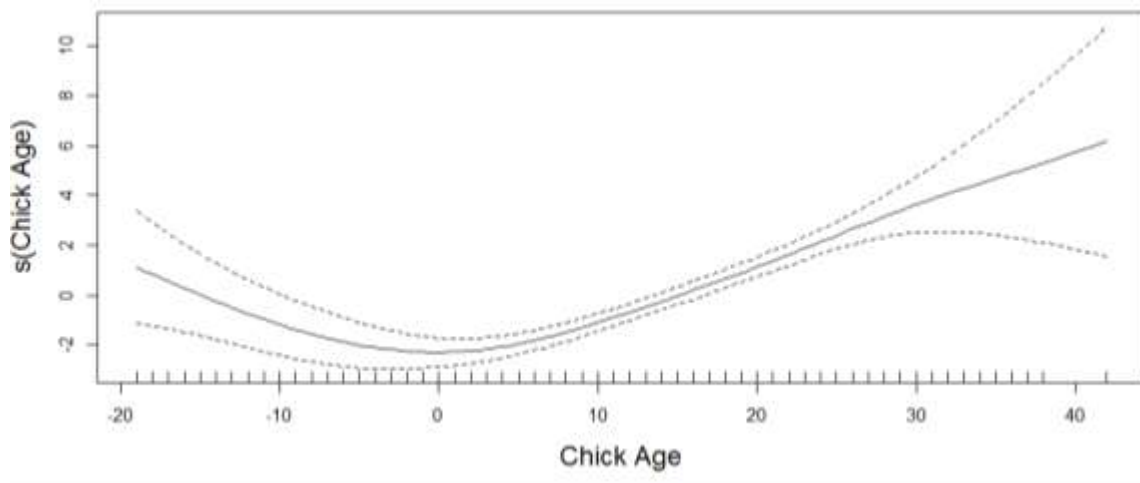
Figure 3.3 Model smoother showing the effect of chick age on the probability of female Bank Swallows roosting.

3.3.2 Effect of Intrinsic Factors on the Timing and Duration of Roosting Commutes

The mean relative departure time from the colony in the evening and arrival time at the colony in the morning was 17.48 minutes before sunset (SD: ± 18.33) and 16.66 minutes after sunrise (SD: ± 16.23), respectively. The best fit model for the effects of intrinsic and extrinsic factors on the evening departure time to the roost (Table 3.2),

included a negative relationship with distance (β = -0.27, 95% CI = -0.35, -0.19) and

chick age (β = -0.32, 95% CI = -0.41, -0.23) and a positive relationship with light (β =

0.08, 95% CI = -0.00, 0.16). Therefore, Bank Swallows depart from the colony earlier in

the evening when they travel to more distant roosts and as their chicks age and depart

later in the evening when the ambient light is high. The best fit model for the effects of

intrinsic and extrinsic factors on the relative morning arrival time at the colony (Table

3.3), included a negative relationship with distance (β = -0.19, 95% CI = -0.11, -0.28) and

chick age (β = -0.22, 95% CI =-0.14, -0.31) and a positive relationship with temperature

(β = 0.23, 95% CI = 0.15, 0.31) and wind speed (β = 0.14, 95% CI = 0.06, 0.22).

Therefore, Bank Swallows leave the roost later when they farther from the colony and as

their chicks age and leave the roost earlier when the temperature and wind speeds are

high.

Overall, the mean duration of the evening commute from the colonies to roosts

was 5.13 ± 3.23 minutes and the morning commute from the roost to colonies was 7.05 ±

2.98 minutes.

Table 3.2 Model comparison for the effects of intrinsic and extrinsic factors on the
relative departure time for Bank Swallows moving from the colony to the roosts in the
evening. Showing all models within 95% cumulative weight. Model selection shown in
bold.

Model	Parameters	df	logLik	AICc	Δ	weight
SS 1	distance + light + chick age + act/inactive nest+ (1 | tag)	7	-680.42	1375.1	0.00	0.517
SS 2	**distance + light +chick age + (1|tag)**	**6**	**-681.77**	**1375.7**	**0.65**	**0.374**
SS 3	distance + light + relative humidity +chick age + act/inactive nest+ (1 | tag)	8	-681.45	1379.2	4.13	0.103
SS 4	distance + light + relative humidity + chick age + (1 | tag)	7	-682.89	1380.0	4.94	0.068

Table 3.3 Model comparison for the effects of intrinsic and extrinsic factors on the arrival time for Bank Swallows moving from the roost to the colony in the morning. Showing all models within 95% cumulative weight. Model selection shown in bold.

Model	Parameters	df	logLik	AICc	Δ	weight
SR 1	**distance + temperature+ wind speed + chick age + (1 | tag)**	**7**	**-690.00**	**1394.2**	**0.00**	**0.537**
SR 2	distance + temperature+ wind speed + chick age + act/inactive nest+ (1 | tag)	8	-689.20	1394.7	0.46	0.426

3.3.3 Effect of Intrinsic and Extrinsic Factors on the Likelihood of Roosting at Major or Minor Roosts

In 2015, I identified eight roosts within 30 km of the colony. Of the 683 occasions when the roosting location of an individual was known, 85% were at the roost site TINTA (Table 3.4). All but two tagged individuals roosted at least once at this site suggesting that TINTA was a major roost site. Despite the overall preference for TINTA, a considerable amount of roost switching was observed throughout the breeding season and on average, individual Bank Swallows used 3.36 roosts (range: 1 - 6).

Table 3.4 Number of Bank Swallow detections at each roost monitored with automated telemetry.

Roost	Detections
AMMAR	13
AMPNT	22
BBSSN	4
EDDY	6
JOGGINS	1
MISSA	10
SCHOOL	34
TINTA	578
UPTAN	12
WCOCK	4

The best fit model for how intrinsic and extrinsic factors affected the likelihood of roosting at the major roost site TINTA or at minor roost sites (all others; Table 3.5), included a negative relationship with chick age (β = -0.49, 95% CI = -0.88, -0.09) and relative humidity (β = -0.70, 95% CI = -1.08, -0.33) and a positive relationship with light (β = 0.27, 95% CI = -0.06, 0.60). Therefore, Bank Swallows were more likely to roost at the major roost TINTA when their chicks aged, relative humidity was high and ambient light was low.

Table 3.5 Model comparison for the effects of intrinsic and extrinsic factors on the probability of Bank Swallows roosting at the major roost TINTA (0) or and other minor roosts (1). Showing all models within 95% cumulative weight. Model selection shown in bold.

Model	Parameters	df	logLik	AICc	Δ	weight
M8	**chick age + light + relative humidity + (1 | tag)**	**5**	**-129.52**	**269.16**	**0.00**	**0.995**
M4	chick age + (1 | tag)	3	-137.77	281.58	12.42	0.002
M9	chick age + light + (1 | tag)	4	-136.81	281.69	12.54	0.002

3.3.4 Roost Counts

Although most tagged birds were recorded roosting at TINTA, AMPNT had the highest and most consistent roost counts (counts of tagged and untagged birds) throughout the breeding season (Table 3.6). The highest number of roosting Bank Swallows recorded during roost counts on a given night was 919. This provides an estimate of the minimum roosting population to use this area.

Table 3.6 Number of Bank Swallow detected at each roosts using automated telemetry compared to the total number of birds counted during the roost counts at each roost.

Roost	Radio Telemetry	Roost Count
AMMAR	13	1485
AMPNT	22	5440
BBSSN	4	14
EDDY	6	73
JOGGINS	1	-
MISSA	10	12
SCHOOL	34	100
TINTA	578	1809
UPTAN	12	7
WCOCK	4	-

3.4 Discussion

I investigated the influence of intrinsic and extrinsic factors on three aspects of Bank Swallow roosting behaviour during the breeding season 1) the likelihood of tagged individuals roosting communally or remaining at the breeding colony over night, 2) the timing and the duration of the commute to the roost sites and 3) the probability of using a major or minor roost site.

Overall, breeding Bank Swallows roosted communally on most nights during the breeding season (63%). However, there was a high degree of variability among individuals. Notably, two tagged males roosted every night, while one female remained at its nest throughout the entire breeding period.

Despite this variability, I found that the likelihood of roosting communally on a given night was affected by both intrinsic and extrinsic factors.

I found that the likelihood of roosting communally was affected differently by chick age for each sex. For males, the likelihood of roosting reached its lowest point when chicks were 4-5 days old, while in females, it reached its lowest point at hatch. These results are consistent with previous work showing that the probability of roosting communally is related to sex and chick age in Bank Swallows and other species (Chandler et al.1995, Hill et al. 1997, Falconer et al. 2016). These effects can be explained by the amount of parental care provided by each sex as well as the needs of the chicks at different life stages. Although both male and female Bank Swallows provide parental care, females spend more time incubating the eggs and brooding the chicks than males (Peterson et al. 1955). This is consistent with my finding that females remained at the colony more often than males, especially during the periods of incubation and brooding. Furthermore, Bank Swallow chicks remain partially ectothermic until they reach 14 g or between 7 and 10 days post hatch (Marsh 1978, Marsh & Wickler 1982) and require frequent brooding to develop during this stage (Peterson et al. 1955). This is consistent with the period of reduced communal roosting in both male and female Bank Swallows, suggesting that one or both members of a pair may need to remain at the nest to brood their young during this time.

However, even during this period when young are most exposed to thermoregulatory stress (Marsh & Wickler 1982), several (mostly male) Bank Swallows still left their nest to roost communally. In one case, both partners of a tagged pair started to roost communally when chicks were as young as 6 days old, and yet managed to successfully fledge young. This suggests that benefits of communal roosting for Bank

Swallows can sometimes outweigh the costs associated with leaving young unattended during this vulnerable stage.

Bank Swallows may also roost communally as chicks age to avoid respiratory stress. Bank Swallow burrows contain a significantly higher ratio of carbon dioxide to oxygen than normal atmospheric levels and this ratio increases with the number and size of the occupants (Birchard et al. 1984). Therefore, adults my chose to roost communally to avoid the accumulation of carbon dioxide in their burrows.

I also found that the likelihood of roosting communally increased in warm, dry weather. There are three possible explanations for this finding. First, nesting burrows may provide more thermoregulatory protection than the habitat at communal roosts. If this were the case, remaining at the nest during bouts of poor weather and leaving during warm weather may be preferred. Nesting burrows in general are effective at protecting developing young from climate extremes (White et al. 1978, Ellis 1982, Lill & Fell 2007), therefore may also be advantageous to adults during periods of inclement weather. In one study, Bank Swallow cavity temperatures ranged from 15.0°C to 24.9°C while temperatures outside ranges from 2.4 °C to 46.7°C, suggesting high thermoregulatory protection (Ellis 1982). Furthermore, Bank Swallows may be roosting communally on warm nights to prevent overheating in their burrows, especially as the chicks age. Bank Swallow burrow temperatures increase with the number of occupants, suggesting that overheating is a potential risk (Birchard et al. 1984). A comparative study on the thermoregulation benefits of remaining at the nest or roosting communally could shed more light on this topic.

Second, Bank Swallows may avoid communal roosting in poor weather because of the cost of travel in these conditions. In this study, Bank Swallows travelled up to 14 km from their nesting colonies to reach communal roost, and colonies in Ontario travelled further (Falconer et al. 2016). Although these movements presumably come with energetic costs in all cases, poor weather conditions may further increase the cost of travelling, making it no longer favourable to roost. Many studies have found that birds avoid travelling in poor weather conditions for both foraging and migration (Evans & Bouwman 2000, Erni et al. 2002). Therefore, Bank Swallows may have remained at the colony during humid cold nights to avoid the costs associated with the commute to roosts.

Finally, Bank Swallows may have remained in their nest during poor weather conditions to protect their offspring from the increased thermoregulation costs. Nestling growth and survival decreases in poor weather conditions and parents often compensate with increased incubation and brooding during these periods (Coe et al. 2015). Therefore, breeding Bank Swallows may also have remained at the colony in poor weather because of the increased thermoregulatory needs of their offspring. These three hypothesis are not mutually exclusive, and all may influence this behaviour.

I also found that the likelihood of roosting communally decreased with increasing ambient light. Bank Swallows may be avoiding roosts during bright nights to avoid predation. Some species with nocturnal predators are known reduce their activity on bright nights (Brooke 1991, Lang et al. 2006). However, further knowledge on the relative predation pressures at the colonies and at the roost is required to measure this effect.

Although the observed effects of intrinsic and extrinsic factors on the likelihood of roosting suggest reasons why individuals stayed at or left the colony at night, the benefits of roosting communally in Bank Swallows remain to be determined. In other bird species, the main benefits for communal roosting are considered to be reduced predation and the transfer of information between individuals (Hoogland & Sherman 1976, Richner and Heebs 1996).

Communal roosting can reduce predation risk in two ways. First, by roosting communally, Bank Swallows may avoid nocturnal predators such as raccoons which commonly depredate nests (Garrison 1999). Second, communal roosts, like other large animal aggregation, can reduce predation risk through safety in numbers (Lack 1968, Hoogland and Sherman 1976). However, to measure whether predator avoidance is an evolutionary driver for this behaviour, predation levels at both the colony and the roost must first be quantified.

Communal roosting can also be attributed to the benefits of information transfer between individuals. The Information Center Hypothesis and later modifications of this hypothesis (e.g., recruitment hypothesis; Richner and Heebs 1996) suggest that communal roosting developed because individuals increased their fitness by sharing information on foraging or breeding success. Although this hypothesis has gained a lot of attention, the empirical evidence to support it is scarce (Bijleveld et al. 2010). While some evidence suggests that communal roosts can act as information centers in several species (Siegfried 1971; Zahavi 1971, Marzluff et al. 1996, Wright et al. 2003), evidence for this in swallows is lacking. However, because Bank Swallows are highly social

species, social interactions such as information transfers may have important implications for their ecology.

Bank Swallows synchronize their roosting movements within approximately 30 minutes of sunset and sunrise. The timing of these movements was similar to previously reported departures and arrival times for roosting swallows during winter and migration (between 10 and 35 minutes of sunset and sunrise (Russell & Gauthreaux 1999, Bijlsma & van den Brink 2005, Smiddy et al. 2009).

Intrinsic and extrinsic factors also affected the timing of Bank Swallow commutes to and from roosts. Swallows departed from the colony earlier and returned later when they travelled to more distant roosts, ambient light (departure only), temperature (return only) and wind speeds (return only) were low and as chicks aged. The fact that Bank Swallows departed earlier and returned later when they travelled to more distant roost suggests that they select roost sites before departing the colony and that they anticipated and correct for longer commutes. This is unlike other species who join pre-roost gatherings (Summers 1989) and further observational studies are needed to confirm this finding. Moreover, because Bank Swallows departed later from the colony when it was brighter, light may be a trigger for roosting movements (Smiddy et al. 2009). This result is consistent with Russell and Gauthreaux's (1999) findings that Purple Martins (*Progne subis*) arrive at the roost earlier and depart later when cloud cover was high. Furthermore, the fact that Bank Swallows returned to the colony earlier on cold days can be explained by the increased thermoregulation requirements of their young (Coe et al. 2015). The positive relationship with wind speed may be explained by increased flight speed in concurrent wind. A closely related species, the Purple Martin, was also found to

return earlier from the roost when wind speeds were high (Russell & Gauthreaux 1999). Wind speed can significantly affect the energy required for flight and birds select favourable winds to reduce travel time and effort (Russell & Gautrheaux 1999, Akesson 2016). Finally, Bank Swallows may have left the colony earlier and returned later as the chicks aged either because of reduced parental care required by older chicks or, indirectly because of the correlation between changes in civil twilight and chick age. Like many other species, Bank Swallows required less parental care as the chicks age and may therefore spend longer bouts away from the nest (Garrison 1999). Alternatively, as chicks aged, the season progressed and the period of civil twilight increased, resulting in longer periods of high ambient light after sunset and before sunrise (Smiddy et al. 2009). Since departure and arrival times were measured in relation of sunrise and sunset, this may also have influenced the results. These effects of both intrinsic and extrinsic factors on the timing of Bank Swallow movements highlight some of the potential triggers and limitations of communal roosting, although future research is needed to fully understand the mechanisms of this behaviour.

In 2015, tagged Bank Swallows from both TN and SE spent 85% of their nights roosting at the major roost site TINTA. On the remaining nights, Bank Swallows switched between seven other minor roost and individuals switched roosts up to six times throughout the breeding season. The use of both major and minor roosts has also been described in European Starlings (Morrison & Caccamise 1985). Starlings have a high degree of variability in roost site fidelity overall with some individuals remaining at one major roost site while others switch frequently between a combination of major and minor roost sites (Morrison & Caccamise 1985). This is similar to what was observed in

my study, as some Bank Swallows remained at TINTA throughout the breeding season or switched between TINTA and other, minor roost.

There are several possible advantages of roost switching including predator avoidance, increased information transfer and direct benefits derived from particular roosts. Roost switching may be a strategy to avoid predators learning the patterns of where and when individuals roost. Large animal aggregations are highly conspicuous to predators (Beauchamp 1999) and a study on avian predation at roosts found that predators became accustomed repeated roosting events and would anticipate the arrival of roosting birds (Bijlsma & van den Brink 2005). Therefore, by switching roosts, Bank Swallows may prevent predators from learning when and where they roost. Furthermore, switching roosts may increase the total amount of information gained through information centers and public information (i.e. reproductive fitness or success) (Brown 1988, Boulinier et al. 2008). Information such as the location of high density insect patches or individual reproductive fitness and success may be directly or indirectly transferred between individuals at roost sites. Although there is no empirical evidence supporting shared foraging information in Bank Swallows (Stutchbury 1988), Brown et al. (2000) showed that Cliff Swallows prospect conspecific reproductive success towards the end of the nesting period and that colony sizes increased in subsequent years at sites with highest reproductive success. Therefore, Bank Swallows may have been switching roosts to maximizing their knowledge of conspecific reproductive success. Finally, individual roost site characteristics such as distance, area and water levels, may promote roost switching, if some roosts become more favourable than others at different times of the year. Future studies on predation at the roost, the transfer of foraging and social

information as well as specific site characteristic are needed to fully understand the role of this behaviour.

Although this study does not clearly identify a single driving force behind communal roosting, the influence of both intrinsic and extrinsic factors on this behaviour highlights both the numerous benefits and costs associated with this behaviour. Furthermore, the study of this behaviour raises interesting questions about communal roosting as a whole and how the costs and benefits of this behaviour may change between the breeding, wintering and pre-migratory periods. Finally, this study also underlines the need to maintain wetland habitats, well beyond the DAC of this species. In light of this species' current population declines (COSEWIC 2013), identifying and protecting habitat throughout the breeding season will be necessary for the recovery of this species.

CHAPTER 4: GENERAL DISCUSSION

4.1 Summary

The purpose of my study was to identify the foraging (Chapter 2) and roosting (Chapter 3) habitat of breeding Bank Swallows and to determine how both intrinsic and extrinsic factors affect this species' habitat use throughout the breeding season. To do this, I used a combination of automated and manual radio telemetry to track the movements of 68 breeding Bank Swallows from three colonies in Sackville, NB throughout the breeding season.

In Chapter 2, I showed that Bank Swallows foraged further from the colony than previously observed, with most foraging trips occurring within 2 km and some occurring up to 15 km from the nest. Despite the use of this larger foraging range, I also found that the numbers of Bank Swallows foraging decreased with distance from the colony. Additionally, I found that all three colonies selectively foraged in salt marshes. Other habitat types such as wet grassland, urban areas, crop and river as well as habitat heterogeneity also influenced foraging habitat use, although not consistently among the colonies. In addition, my study suggests that foraging habitat changes throughout the breeding season, as indicated by increased foraging distance with cold and windy weather, as chicks age and when the nests were inactive.

In Chapter 3, I identified 8 Bank Swallow communal roosts in cattail marshes and measured whether the likelihood of roosting communally, the timing and duration of the commute to and from roosts and whether individuals roosted in major or minor roosts were affected by intrinsic and extrinsic factors. I found that males were more likely to roost than females and that the likelihood of roosting for both sexes was higher as chicks

aged, in dry weather and on bright nights. The relative departure time to and from the roost were 17.48 minutes before sunset (SD: ± 18.33) and 16.66 minutes after sunrise (SD: ± 16.23), and both were affected by distance, chick age and weather conditions. The commutes to and from the roost were of similar durations (5.13 ± 3.23 and 7.05 ± 2.98, respectively). Bank Swallows roosted at major roosts more often as the chicks aged, and on nights with low ambient light and high humidity.

4.2 Study Limitations

Although the use of automated telemetry had many benefits, this method cannot identify the exact position of the birds due to the extreme variability in the antenna ranges. Consequently, I had to make assumptions about the exact location of birds between detections, especially at roosting sites where antenna ranges were reduced by the vegetation cover. This also means that some Bank Swallows were not accounted for at either colonies or roosts. In addition, some tags fell off prematurely causing an early stop to tracking. With the advancement of tagging technology and automated telemetry these limitations might become negligible in the near future.

For measuring Bank Swallow foraging habitat use, I was also limited by the 300m detection range of the manual tracking receiver and therefore could not examine Bank Swallow foraging habitat use on more broad or fine scales.

4.3 Implications and Future Work

My study not only aimed to improve the scientific knowledge on foraging and roosting dynamics in general but also to fill important knowledge gaps on the habitat use of Bank Swallows during a critical time in their life cycle. In the past 40 years, Bank

Swallows have suffered steep population declines across North America. Although the cause for this decline remains unclear, habitat loss and degradation by agricultural intensification is hypothesized to be one of the main causes, making the study of these dynamics critical for the protection of this species. Furthermore, as a consequence of these declines, this species was assessed as Threatened by the Committee on the Status of Endangered wildlife in Canada in 2013 and formal protection is currently being considered. If this species is listed under the Species At Risk Act, its critical habitat will need to be identified and protected by law. Therefore, by identifying how intrinsic and extrinsic factors affect Bank Swallow foraging and roosting habitat use, I hope to inform future management decisions such as the designation of critical habitat for this species. I hope that my thesis will both aid the conservation of Bank Swallows and generally improve the understanding of foraging and roosting behaviour.

Future studies on communal roosting may investigate if roosting during the breeding season also occurs in related birds, such as Barn Swallows and Tree Swallows, which were observed roosting among Bank Swallows during several of the roost counts. In addition, the factors favouring roosting behaviour still remain unclear and studies on the importance of thermoregulation, predation, and the sharing of information may shed light on this behaviour.

Future studies on foraging habitat use of Bank Swallows may investigate if the observed predictors for foraging are more universal and also true for other swallow colonies. Since habitat use is inherently limited by the available habitat composition, future studies may investigate if the observed relationships hold true in areas with different habitat compositions or at different scales of habitat use.

REFERENCES

Adams, J. S., Knight, R. L., McEwen, L. C. and George, T. L., 1994. Survival and growth of nestling Vesper Sparrows exposed to experimental food reductions. *The Condor* 96 (3): 739-748.

Aho, K. A., 2014. *Foundational and applied statistics for biologists using R*. CRC Group: Florida.

Akesson, S., 2016. Flying with the winds: differential migration strategies in relation to winds in moth and songbirds. *Journal of Animal Ecology* 85 (1):1-4

Allee, W. C., 1931. Co-operation among animals. *American Journal of Sociology* 37 (3): 386-398.

Alonso, J. A., Alonso, J. C. and Veiga, J. P., 1985. The influence of moonlight on the timing of roosting flights in Common Cranes *Grus grus*. *Ornis Scandinavica* 16 (4): 314-318.

Altieri, M. A., 1999. The ecological role of biodiversity in agroecosystems. *Agriculture, Ecosystems & Environment* 74 (1): 19-31.

Alves, M. A. S. and Johnstone, I. G., 1994. Radio-tracking small aerial foraging birds: a preliminary study of the sand martin *Riparia riparia*. *Avocetta* 18 (1): 13-20.

Andren, H., 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71 (3): 355-366.

Anthony, E. L. P., Stack, M. H. and Kunz, T. H., 1981. Night roosting and the nocturnal time budget of the little brown bat, *Myotis lucifugus*: effects of reproductive status, prey density, and environmental conditions. *Oecologia* 51 (2): 151-156.

Asbirk, S., 1976. Studies on the breeding biology of the Sand Martin *Riparia riparia* (L.)(Aves) in artificial nest sites. *Videnskabelige Meddelelser fra Dansk Naturhistorik Forening* 139 (1): 147-177.

Attwood, S. J., Maron, M., House, A. P. N. and Zammit, C., 2008. Do arthropod assemblages display globally consistent responses to intensified agricultural land use and management?. *Global Ecology and Biogeography* 17 (5): 585-599.

Baines, D., Redpath, S., Richardson, M. and Thirgood, S., 2008. The direct and indirect effects of predation by Hen Harriers *Circus cyaneus* on trends in breeding birds on a Scottish grouse moor. *Ibis* 150 (s1): 27-36.

Bates, D., Maechler, M., Bolker, B. and Walker, S., 2015. Fitting linear mixed effect models using lme4. *Journal of Statistical Software* 67 (1): 1-48.

Beauchamp, G., 1999. The evolution of communal roosting in birds: origin and secondary losses. *Behavioral Ecology* 10 (6): 675-687.

Benton, T. G., Bryant, D. M., Cole, L. and Crick, H. Q., 2002. Linking agricultural practice to insect and bird populations: a historical study over three decades. *Journal of Applied Ecology* 39 (4): 673-687.

Benton, T. G., Vickery, J. A. and Wilson, J. D., 2003. Farmland biodiversity: is habitat heterogeneity the key?. *Trends in Ecology & Evolution* 18 (4): 182-188.

Bijlsma, R. G. and van den Brink, B., 2005. A Barn Swallow *Hirundo rustica* roost under attack: timing and risks in the presence of African Hobbies *Falco cuvieri*. *Ardea* 93 (1): 37-48.

Birchard, G. F., Kilgore Jr, D. L. and Boggs, D. F., 1984. Respiratory gas concentrations and temperatures within the burrows of three species of burrow-nesting birds. *The Wilson Bulletin 96* (3): 451-456.

Blancher, P. J., Phoenix, R. D., Badzinski, D. S., Cadman, M. D., Crewe, T. L., Downes, C. M., Fillman, D., Francis, C. M., Hughes, J., Hussell, D. J. and Lepage, D.,

2009. Population trend status of Ontario's forest birds. *The Forestry Chronicle* 85 (2): 184-201.

Blanco, G., 1996. Population dynamics and communal roosting of White Storks foraging at a Spanish refuse dump. *Colonial Waterbirds* 9 (2): 273-276.

Blanco, G., Tella, J. L., 1999. Temporal, spatial and social segregation of red-billed choughs between two types of communal roost: a role for mating and territory acquisition. *Animal Behaviour* 57 (6): 1219-1227.

Boatman, N. D., Brickle, N. W., Hart, J. D., Milsom, T. P., Morris, A. J., Murray, A. W., Murray, K. A. and Robertson, P. A., 2004. Evidence for the indirect effects of pesticides on farmland birds. *Ibis* 146 (s2): 131-143.

Bonduriansky, R. and Brooks, R. J., 1999. Why do male Antler Flies (*Protopiophila litigata*) fight? The role of male combat in the structure of mating aggregations on moose antlers. *Ethology Ecology & Evolution*, 11 (3): 287-301.

Bontadina, F., Schofield, H. and Naef-Daenzer, B., 2002. Radio-tracking reveals that Lesser Horseshoe Bats (*Rhinolophus hipposideros*) forage in woodland. *Journal of Zoology*, 258 (3): 281-290.

Boulinier, T., McCoy, K.D., Yoccoz, N.G., Gasparini, J. and Tveraa, T., 2008. Public information affects breeding dispersal in a colonial bird: Kittiwakes cue on neighbours. *Biology Letters* 4 (5): 538-540.

Bowman, J., Wallace, M. C., Ballard, W. B., Brunjes IV, J. H., Miller, M. S. and Hellman, J. M., 2002. Evaluation of two techniques for attaching radio transmitters to turkey poults. *Journal of Field Ornithology* 73 (3): 276-280.

Brawley, A. H., 1995. *Birds of Connecticut's tidal wetlands: Relating patterns of use to environmental conditions*. MSc, Connecticut College.

Bridge, E. S., Thorup, K., Bowlin, M. S., Chilson, P. B., Diehl, R. H., Fléron, R. W., Hartl, P., Kays, R., Kelly, J. F., Robinson, W. D. and Wikelski, M., 2011. Technology on the move: recent and forthcoming innovations for tracking migratory birds. *Bioscience* 61 (9): 689-698.

Brooke, M. D. L. and Prince, P. A., 1991. Nocturnality in seabirds. *Proceedings of the International Ornithological Congress* 20 (1): 1113-1121.

Brown, C. R. and Brown, M. B., 1999. Fitness components associated with laying date in the Cliff Swallow. *Condor* 101 (12): 230-245.

Brown, C. R. and Brown, M. B., 2000. Weather-mediated natural selection on arrival time in Cliff Swallows (*Petrochelidon pyrrhonota*). *Behavioural Ecology and Sociobiology* 47 (5): 339-345.

Brown, C. R., 1988. Enhanced foraging efficiency through information centers: a benefit of coloniality in Cliff Swallows. *Ecology* 69 (3): 602-613.

Brown, C. R., Brown, M. B. and Ives, A. R., 1992. Nest placement relative to food and its influence on the evolution of avian coloniality. American Naturalist 139 (1): 205–217.

Bryant, D. M. and Turner, A. K., 1982. Central place foraging by swallows (Hirundinidae): the question of load size. *Animal Behaviour* 30 (3): 845-856.

Burger, A. E. and Shaffer, S. A., 2008. Perspectives in ornithology application of tracking and data-logging technology in research and conservation of seabirds. *The Auk* 125 (2): 253-264.

Burnham, K. P., and D. R. Anderson., 2002. *Model selection and multimodel inference: a practical information-theoretic approach, 2nd edition*. Springer-Verlag: New York.

Caccamise, D. F. and Morisson, D. W., 1988. Avian communal roosting: a test of the "patch-sitting" hypothesis. *The Condor* 90 (2): 453-458.

Caccamise, D. F., Reed, G. and Stouffer, P. C., 1996. Roosting behaviour and group territoriality in American Crows. *The Auk* 114 (4): 628-637.

Chamberlain, D. E., Wilson, J. D. and Fuller, R. J., 1999. A comparison of bird populations on organic and conventional farm systems in southern Britain. *Biological conservation* 88 (3): 307-320.

Chan, K. H. and Blake, R. W., 2006. Flight speeds of seven bird species during chick rearing. *Canadian journal of zoology* 84 (7): 1047-1052.

Chandler, C. R., Ketterson, E. D. and Nolan, V., 1995. Spatial aspects of roost-site selection in breeding male dark-eyed juncos. *The Condor* 97 (1): 279-282.

Clarke, J. A., Harrington, B.A., Hruby, T. and Wasserman F. E., 1984. The effects of ditching for mosquito control on salt marsh use by birds in Rowley, Massachusetts. *Journal of Field Ornithology* 55 (2):160-180.

Coe, B. H., Beck, M. L., Chin, S. Y., Jachowski, C. and Hopkins, W.A., 2015. Local variation in weather conditions influences incubation behavior and temperature in a passerine bird. *Journal of Avian Biology* 46 (4): 385-394.

Coleman, J. L. and Barclay, R. M. R., 2013. Prey availability and foraging activity of grassland bats in relation to urbanization. *Journal of Mammalogy* 94 (5):1111–1122.

COSEWIC. 2013. *COSEWIC assessment and status report on the Bank Swallow Riparia riparia in Canada*. Committee on the Status of Endangered Wildlife in Canada: Ottawa.

Cougill, S. and Marsden, S. J., 2004. Variability in roost size in an Amazona Parrot: implications for roost monitoring. *Journal of Field Ornithology* 75 (1): 67-73.

Crysler, Z. J., Ronconi, R. A. and Taylor, P. D., 2016. Differential fall migratory routes of adult and juvenile Ipswich Sparrows (*Passerculus sandwichensis princeps*). *Movement ecology* 4 (1): 3.

Curnutt, J. L., 1992. Dynamics of a year-round communal roost of Bald Eagles. *The Wilson Bulletin* 104 (3): 536-540.

Dionne, M., Maurice, C., Gauthier, J. and Shaffer, F., 2008. Impact of Hurricane Wilma on migrating birds: the case of the Chimney Swift. *Wilson Journal of Ornithology* 120 (4): 784-792.

Donald, P. F., Green, R. E. and Heath, M. F., 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. *Proceedings of the Royal Society of London B: Biological Sciences* 268 (1462): 25-29.

Donald, P. F., Sanderson, F. J., Burfield, I. J. and Van Bommel, F. P., 2006. Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990–2000. *Agriculture, Ecosystems & Environment* 116 (3): 189-196.

Dossman, B. C., Mitchell, G. W., Norris, D. R., Taylor, P. D., Guglielmo, C. G., Matthews, S. N. and Rodewald, P. G., 2016. The effects of wind and fuel stores on stopover departure behavior across a migratory barrier. *Behavioral Ecology* 27 (2): 567-574.

Dunn, P. O. and Whittingham, L. A., 2005. Radio-tracking of female tree swallows prior to egg-laying. *Journal of Field Ornithology* 76 (3): 259-263.

Dunn, P. O., Winkler, D. W., Whittingham, L. A., Hannon, S. J. and Robertson, R. J., 2011. A test of the mismatch hypothesis: How is timing of reproduction related to food abundance in an aerial insectivore?. *Ecology* 92 (2): 450-461.

Ellis, J. H., 1982. The thermal nest environment and parental behavior of a burrowing bird, the Bank Swallow. *The Condor*, 84(4): 441-443.

Emlen, S. T. and Demong, N. J., 1975. Adaptive significance of synchronized breeding in a colonial bird: a new hypothesis. *Science* 188 (4192): 1029-1031.

Erni, B., Liechti, F., Underhill, L. G. and Bruderer, B., 2002. Wind and rain govern the intensity of nocturnal bird migration in central Europe-a log-linear regression analysis. *Ardea* 90 (1): 155-166.

Evans, K. L., Bradbury, R. B. and Wilson, J. D., 2003. Selection of hedgerows by Swallows *Hirundo rustica* foraging on farmland: the influence of local habitat and weather. *Bird Study* 50 (1): 8-14.

Evans, K. L., Wilson, J. D. and Bradbury, R. B., 2007. Effects of crop type and aerial invertebrate abundance on foraging Barn Swallows *Hirundo rustica*. *Agriculture, ecosystems & environment* 122 (2): 267-273.

Evans, S. W. and Bouwman, H., 2000. The influence of mist and rain on the reproductive success of the Blue Swallow *Hirundo atrocaerulea*. *Ostrich* 71 (1-2): 83-86.

Fahrig, L., 1997. Relative effects of habitat loss and fragmentation on population extinction. The *Journal of Wildlife Management*: 61 (3): 603-610.

Falconer, C. M., Mallory, M. L. and Nol, E., 2008. Breeding biology and provisioning of nestling Snow Buntings in the Canadian High Arctic. *Polar Biology* 31(4): 483-489.

Falconer, C. M., Mitchell, G. W., Taylor, P. D. and Tozer, D. C., 2016. Prevalence of disjunct roosting in nesting Bank Swallows (*Riparia riparia*). *The Wilson Journal of Ornithology* 128 (2): 429-434.

Fischer, J. and Lindenmayer, D. B., 2007. Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography* 16 (3): 265-280.

Flohre, A., Fischer, C., Aavik, T., Bengtsson, J., Berendse, F., Bommarco, R., Ceryngier, P., Clement, L. W., Dennis, C., Eggers, S. and Emmerson, M., 2011. Agricultural intensification and biodiversity partitioning in European landscapes comparing plants, carabids, and birds. *Ecological Applications* 21 (5): 1772-1781.

Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., Chapin, F. S., Coe, M. T., Daily, G. C., Gibbs, H. K. and Helkowski, J. H., 2005. Global consequences of land use. *Science* 309 (5734): 570-574.

Fournier, D. A., Skaug, H. J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M., Nielsen, A. and Sibert, J., (2012). AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optimization Methods and Software* 27 (2): 233-249.

Freer, V. M. 1977. *Colony structure and function in the Bank Swallow, Riparia riparia L*. Ph.D. State University of New York.

Freer, V. M., 1979. Factors affecting site tenacity in New York Bank Swallows. *Bird-Banding* 50 (4): 349-357.

Fuller, R. J., Gregory, R. D., Gibbons, D. W., Marchant, J. H., Wilson, J. D., Baillie, S. R. and Carter, N., 1995. Population declines and range contractions among lowland farmland birds in Britain. *Conservation Biology* 9 (6): 1425-1441.

Garrison, B. A., 1999. Bank Swallow (*Riparia riparia*), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; retrieved from the Birds of North America Online. doi:10.2173/bna.414 [website accessed November 2015].

Ghilain, A. and Belisle, M., 2008. Breeding success of Tree Swallows along a gradient of agricultural intensification. *Ecological Applications* 18 (5): 1140-1154.

Goulson, D., 2014. Ecology: Pesticides linked to bird declines. *Nature* 511 (7509): 295-296.

Green, M., 2004. Flying with the wind - Spring migration of Arctic-breeding waders and geese over South Sweden. *Ardea* 92 (2): 149-159.

Grüebler, M. U., Schuler, H., Müller, M., Spaar, R., Horch, P. and Naef-Daenzer, B., 2008. Female biased mortality caused by anthropogenic nest loss contributes to population decline and adult sex ratio of a meadow bird. *Biological Conservation* 141 (12): 3040-3049.

Hagen, A. N. and Hodges, K. E., 2006. Resolving critical habitat designation failures: reconciling law, policy, and biology. *Conservation Biology* 20 (2): 399-407.

Haila, Y., 2002. A conceptual genealogy of fragmentation research: from island biogeography to landscape ecology. *Ecological applications* 12 (2): 321-334.

Hansbauer, M. M. and Pimentel, R. G., 2008. A comparison of five techniques for attaching radio-transmitters to tropical passerine birds. *Revista Brasiliera de Ornitologia* 16 (2): 131-136.

Heneberg, P., 2009. Soil penetrability as a key factor affecting the nesting of burrowing birds. *Ecological Research* 24 (2): 453-459.

Hickman, G.R. 1979. *Nesting ecology of Bank Swallows in interior Alaska*. MSc. University of Alaska.

Hill, I. F. and Cresswell, B., 1997. The use of a communal summer roost by radio-tagged Blackbirds *Turdus merula*. *Bird Study* 44 (1): 114-116.

Hobbs, R. J. and Yates, C. J., 2003. Impacts of ecosystem fragmentation on plant populations: generalising the idiosyncratic. *Australian Journal of Botany* 51 (5): 471-488.

Hoogland, J. L. and Sherman, P. W., 1976. Advantages and disadvantages of Bank Swallow (*Riparia riparia*) coloniality. *Ecological Monographs* 46 (1): 33-58.

Horn, H. S., 1968. The adaptive significance of colonial nesting in the Brewer's blackbird. *Ecology* 49 (4): 682-694.

Jacobson, S. L., Kelly, J. P. and Base, D. L., 1983. 46th breeding bird census: Restored coastal salt marsh. *American Birds* 37 (1):102-103.

Jeliazkov, A., Mimet, A., Chargé, R., Jiguet, F., Devictor, V. and Chiron, F., 2016. Impacts of agricultural intensification on bird communities: new insights from a multi-level and multi-facet approach of biodiversity. *Agriculture, Ecosystems & Environment* 216 (1): 9-22.

Johnson, G. D., Pebworth, J. L. and Krueger, H. O., 1991. Retention of Transmitters Attached to Passerines Using a Glue-on Technique (Retención de transmisores en Passeriformes utilizando la técnica de pegamentos). *Journal of Field Ornithology* 64 (2): 486-491.

Johst, K., Brandl, R. and Pfeifer, R., 2001. Foraging in a patchy and dynamic landscape: human land use and the White Stork. *Ecological Applications* 11 (1): 60-69.

Kacelnik, A., 1984. Central place foraging in Starlings (*Sturnus vulgaris*). I. Patch residence time. *The Journal of Animal Ecology* 53 (1): 283-299.

Kang, S. R. and Kaller, M. D., 2013. Foraging habitat use of breeding Barn Swallow (*Hirundo rustica*) in farmland, estuary, and island. *Open Journal of Ecology* 3 (1): 30-33.

Karg, J., 1994. Insect community response to the shelterbelt-field ecotone. In: Ryszkowski L., Bałazy S. (eds). Functional Appraisal of Agricultural Landscape in Europe. Research Center for Agricultural and Forest Environment, Bulletin of the Polish Academy of Sciences., Poznań. Lorek G., Stankowski

Kays, R., Tilak, S., Crofoot, M., Fountain, T., Obando, D., Ortega, A., Kueemeth, F., Mandel, J., Swenson, G., Lambert, T., Hirsch, B. and Wikelski, M., 2011. Tracking animal location and activity with an automated radio telemetry system in a tropical forest. *The Computer Journal* 54 (12): 1–18.

Krause, J. and Ruxton, G. D., 2002. *Living in groups*. Oxford University Press.

Krebs, J. R., Wilson, J. D., Bradbury, R. B. and Siriwardena, G. M., 1999. The second silent spring?. *Nature* 400 (6745): 611-612.

Kuhnen, K., 1985. On pair-formation in the Sand Martin *Riparia riparia*. *Journal fur Ornithologie* 126 (1): 1-13.

Lack D (1968) *Ecological adaptations for breeding in* birds, 1st ed. Chapman & Hall: London

Lambertucci, S. A. and Ruggiero, A., 2013. Cliffs used as communal roosts by Andean Condors protect the birds from weather and predators. *PloS one* 8 (6): e67304.

Lang, A. B., Kalko, E. K. V., Romer H., Bockholdt, C. and Dechmann, D. K. N., 2006. Activity levels of bats and katydids in relation to the lunar cycle. *Oecologia* 146:659–666.

Laughlin, A. J., Sheldon, D. R., Winkler, D. W. and Taylor, C. M., 2014. Behavioral drivers of communal roosting in a songbird: a combined theoretical and empirical approach. *Behavioral Ecology* 25 (4): 734-743.

Lewis, C. and Casagrande, D. G., 1997. Using avian communities to evaluate salt marsh restoration. *Restoration of an Urban Salt Marsh* 100 (1): 204-236.

Lill, A. and Fell, P. J., 2007. Microclimate of nesting burrows of the Rainbow Bee-eater. *Emu* 107 (2):108-114.

MacBriar, Jr., W. N., and Stevenson, D. E., 1976. Dispersal and survival in the Bank Swallow (*Riparia riparia*) in southeastern Wisconsin. *Milwaukee Public Museum Contributions in Biology and Geology* 10 (1): 1-14.

MacHunter, J., Wright, W., Loyn, R. and Rayment, P., 2006. Bird declines over 22 years in forest remnants in southeastern Australia: Evidence of faunal relaxation?. *Canadian Journal of Forest Research* 36 (11): 2756-2768.

Marsh, R. L. and Wickler, S. J., 1982. The role of muscle development in the transition to endothermy in nestling Bank Swallows, *Riparia riparia*. *Journal of comparative physiology*, 149 (1): 99-105.

Marsh, R., 1978. Development of endothermy in nestling Bank Swallows (*Riparia riparia*). *Physiological Zoology* 52 (3): 340-353.

Marzluff, J. M., Heinrich, B. and Marzluff, C., 1996. Raven roosts are mobile information centres. *Animal Behaviour* 51 (1): 89-103.

Matson, P. A., Parton, W. J., Power, A. G. and Swift, M. J., 1997. Agricultural intensification and ecosystem properties. *Science* 277 (5325): 504-509.

McCarty, J. P. and Winkler, D. W., 1999a. Foraging ecology and diet selectivity of Tree Swallows feeding nestlings. *Condor* 101 (2): 246-254.

McCarty, J. P. and Winkler, D. W., 1999b. Relative importance off environmental variables in determining the growth off nestling Tree Swallows *Tachycineta bicolor*. *Ibis* 141 (2): 286-296.

McVey, K. J., Skrade, P. D. and Sordahl, T. A., 2008. Use of a communal roost by Turkey Vultures in northeastern Iowa. *Journal of Field Ornithology*, 79 (2): 170-175.

Meyer, W. B. and Turner, B. L., 1992. Human population growth and global land-use/cover change. *Annual review of ecology and systematics* 23 (1): 39-61.

Moffatt, K. C., Crone, E. E., Holl, K. D., Schlorff, R. W. and Garrison, B. A., 2005. Importance of hydrologic and landscape heterogeneity for restoring Bank Swallow (*Riparia riparia*) colonies along the Sacramento River, California. *Restoration Ecology* 13 (2): 391-402.

Møller, A. P., 1987. Advantages and disadvantages of coloniality in the swallow, *Hirundo rustica*. *Animal Behaviour* 35 (3): 819-832.

Møller, A. P., 2001. The effect of dairy farming on Barn Swallow *Hirundo rustica* abundance, distribution and reproduction. *Journal of Applied Ecology* 38 (2): 378-389.

Mong, T. W. and Sandercock, B. K., 2007. Optimizing radio retention and minimizing radio impacts in a field study of upland sandpipers. *The Journal of wildlife management* 71 (3): 971-980.

Morrison, D. W. and Caccamise, D. F., 1985. Ephemeral roosts and stable patches? A radio telemetry study of communally roosting starlings. *The Auk* 102 (4): 793-804.

Murphy, M. T., 2003. Avian population trends within the evolving agricultural landscape of eastern and central United States. *The Auk* 120 (1): 20-34.

Mysterud, A. and Ims, R. A., 1998. Functional responses in habitat use: availability influences relative use in trade-off situations. *Ecology* 79 (4): 1435-1441.

Naef-Daenzer, B., Widmer, F. and Nuber, M., 2001. A test for effects of radio-tagging on survival and movements of small birds. *Avian Science* 1 (1): 15-23.

Nakano, D., Akasaka, T., Kohzu, A. and Nakamura, F., 2007. Food sources of Sand Martins *Riparia riparia* during their breeding season: insights from stable-isotope analysis. *Bird Study* 54 (1): 142-144.

Nebel, S., Mills, A., McCracken, J. D. and Taylor, P. D., 2010. Declines of aerial insectivores in North America follow a geographic gradient présence d'un gradient géographique dans le déclin des insectivores aériens. *Avian Conservation and Ecology* 5 (2): 1.

Obrecht, J. D. and Dinsmore, S. J., 2008. Weather factors influencing winter roosts of American Crows in central Iowa. *Journal of the Iowa Academy of Science* 114 (1-2): 35.

Owens, I. P. and Bennett, P. M., 2000. Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. *Proceedings of the National Academy of Sciences* 97 (22): 12144-12148.

Paquette, S. R., Garant, D., Pelletier, F. and Bélisle, M., 2013. Seasonal patterns in tree swallow prey (Diptera) abundance are affected by agricultural intensification. *Ecological Applications* 23 (1): 122-133.

Peck, G. K. and James, R. D., 1987. *Breeding birds of Ontario: nidiology and distribution (Vol. 2)*. Royal Ontario Museum: Ontario.

Perlut, N. G., Strong, A. M. and Alexander, T. J., 2011. A model for integrating wildlife science and agri-environmental policy in the conservation of declining species. *The Journal of Wildlife Management* 75 (7): 1657-1663.

Petersen, A. J., 1955. The breeding cycle in the Bank Swallow. *The Wilson Bulletin* 67 (4): 235-286.

Petersen, P. C. and Mueller, A. J., 1979. Longevity and colony loyalty in Bank Swallows. *Bird-Banding* 50 (1): 69-70.

Phillips, R. A., Xavier, J. C. and Croxall, J. P., 2003. Effects of satellite transmitters on albatrosses and petrels. *The Auk* 120 (4): 1082-1090.

Pyle, P., Howell, S. N. and David, F. Y., 1997. Identification guide to North American birds. State Creek Press: California.

Raim, A., 1978. A radio transmitter attachment for small passerine birds. *Bird-Banding* 49 (4): 326-332.

Richardson, W. J., 1978. Timing and amount of bird migration in relation to weather. *Oikos* 30 (2): 224–272

Richner, H. and Heeb, P., 1996. Communal life: honest signaling and the recruitment center hypothesis. *Behavioral Ecology* 7 (1):115-119.

Robinson, S. K., Thompson III, F. R., Donovan, T. M., Whitehead, D. R. and Faaborg, J., 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* 267 (1): 1987-1990.

Russell, K. R. and Gauthreaux Jr, S. A., 1999. Spatial and temporal dynamics of a Purple Martin pre-migratory roost. *The Wilson Bulletin* 111 (3): 354-362.

Russell, K. R., Mizrahi, D. S. and Gauthreaux Jr, S. A., 1998. Large-scale mapping of Purple Martin pre-migratory roosts using WSR-88D weather surveillance radar (Mapas a larga escala de los dormideros pre-migratorios de *Progne subis* utilizando radares WSR-88D para el monitoreo del clima). *Journal of Field Ornithology* 69 (2): 316-325.

Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A. and Leemans, R., 2000. Global biodiversity scenarios for the year 2100. *Science* 287 (5459): 1770-1774.

Sauer, J. R., Hines, J. E., Fallon, J. E., Pardieck, K. L., Ziolkowski Jr, D. J. and Link, W. A., 2012. The North American Breeding Bird Survey, Results and Analysis 1966–2011. Version 07.03. 2013USGS.

Sauer, J. R., Pendleton, G. W. and Peterjohn, B. G., 1996. Evaluating causes of population change in North American insectivorous songbirds. *Conservation Biology* 10 (2): 465-478.

Schulz, J. H., Bermudez, A. J., Tomlinson, J. L., Firman, J. D. and He, Z., 2001. Comparison of radiotransmitter attachment techniques using captive Mourning Doves. *Wildlife Society Bulletin* 29 (3): 771-782.

Sieber, O., 1980. Casual and functional aspects of brood distribution in Sand Martins (*Ripari ripari L.*). *Journal of Comparative Ethology*, 52 (1): 19-56.

Siegfired, W. R., 1971. Communal roosting of the Cattle Egret. *Transactions of the Royal Society of South Africa* 39 (4): 419-443.

Silver, M. and Griffin, C. R., 2009. Nesting habitat characteristics of Bank Swallows and Belted Kingfishers on the Connecticut River. *Northeastern Naturalist* 16 (4): 519-534.

Slager, D. L. and Rodewald, P. G., 2015. Disjunct nocturnal roosting by a Yellow-rumped Warbler (*Setophaga coronata*) during migratory stopover. *The Wilson Journal of Ornithology* 127 (1): 109-114.

Smiddy, P., Cullen, C. and O'Halloran, J., 2007. Time of roosting of Barn Swallows *Hirundo rustica* at an Irish reedbed during autumn migration. *Ringing & Migration* 23 (4): 228-230.

Sokolov, V., Lecomte, N., Sokolov, A., Rahman, M. L. and Dixon, A., 2014. Site fidelity and home range variation during the breeding season of Peregrine Falcons (*Falco peregrinus*) in Yamal, Russia. *Polar Biology* 37 (11): 1621-1631.

Sotherton, N. and Holland, J., 2002. Indirect effects of pesticides on farmland wildlife. In: Lewis, P. ed. *Handbook of ecotoxicology*. Lewis Publishers: Florida.

Stanton, R., 2015. *Indirect effects of agricultural intensification on tree swallow (Tachycineta bicolor) foraging behaviour, body condition, and physiology*. MSc. University of Saskatchewan.

Stokke, B. G., Møller, A. P., Sæther, B. E., Rheinwald, G. and Gutscher, H., 2005. Weather in the breeding area and during migration affects the demography of a small long-distance passerine migrant. *The Auk* 122 (2): 637-647.

Stolen, E. D. and Taylor, W. K., 2003. Movements of Black Vultures between communal roosts in Florida. *The Wilson Bulletin* 115 (3): 316-320.

Stutchbury, B. J., 1988. Evidence that Bank Swallow colonies do not function as information centers. *The Condo*r, 90(4): 953-955.

Summers, R. W., Westlake, G. E. and Feare, C. J., 1987. Differences in the ages, sexes and physical condition of Starlings *Sturnus vulgaris* at the centre and periphery of roosts. *Ibis* 129 (1): 96-102.

Sykes, P. W., Carpenter, J. W., Holzman, S. and Geissler, P. H., 1990. Evaluation of three miniature radio transmitter attachment methods for small passerines. *Wildlife Society Bulletin* 18 (1): 41-48.

Szabó, Z. D. and Szép, T., 2010. Breeding dispersal patterns within a large Sand Martin (*Riparia riparia*) colony. *Journal of Ornithology* 151 (1): 185-191.

Szép, T., 1990. Estimation of abundance and survival rate from capture-recapture data of Sand Martin (*Riparia riparia*) ringing. *The Ring* 13 (101): 204-214.

Taylor, L. R., 1963. Analysis of the effect of temperature on insects in flight. *The Journal of Animal Ecology* 32 (1): 99-117.

Taylor, P. D., Mackenzie, S. A., Thurber, B. G., Calvert, A. M., Mills, A. M., McGuire, L. P. and Guglielmo, C. G., 2011. Landscape movements of migratory birds and bats reveal an expanded scale of stopover. *PLoS One* 6 (11): e27054.

Tilman, D., Balzer, C., Hill, J. and Befort, B. L., 2011. Global food demand and the sustainable intensification of agriculture. *Proceedings of the National Academy of Sciences* 108 (50): 20260-20264.

Turner, A. 1980. *The use of time and energy by aerial feeding birds*. Ph.D. University of Stirling

Turner, A. and Rose, C., 1989. *Swallows and martins: an identification guide and handbook*. Houghton Mifflin Co: Boston.

Vickery, P. D. and Herkert, J. R., 2001. Recent advances in grassland bird research: Where do we go from here?. *The Auk* 118 (1): 11-15.

Ward, P. and Zahavi, A., 1973. The importance of certain assemblages of birds as "information-centres" for food-finding. *Ibis* 115 (4): 517-534

White, F. N., Bartholomwan, D. J. and Kinny, D. L, 1978 Physiological and ecological correlates of tunnel nesting in the European Bee-eater Merops apiuster. *Physiological Zoology* 5 (1): 140-154.

Winkler, D. W., 2006. Roosts and migrations of swallows. *El hornero* 21 (2): 085-097.

Wood, S. and Scheipl, F., 2013. Package "gamm4". R package version 0.2-2. URL: http://cran.r-project.org/web/packages/gamm4/index.html/.

Wright, J., Stone, R. E. and Brown, N., Communal roosts as structured information centres in the raven, Corvus corax. *Journal of Animal Ecology* 72 (6):1003-1014.

Wuczyński, A., Kujawa, K., Dajdok, Z. and Grzesiak, W., 2011. Species richness and composition of bird communities in various field margins of Poland. *Agriculture, ecosystems & environment* 141 (1): 202-209.

Ydenberg, R. C., Butler, R. W., Lank, D. B., Smith, B. D. and Ireland, J., 2004. Western Sandpipers have altered migration tactics as Peregrine Falcon populations have recovered. *Proceedings of the Royal Society of London, Series B: Biological Sciences* 271 (1545): 1263-1269.

Yom-Tov, Y., 1979. The disadvantages of low positions in colonial roosts: an experiment to test the effects of droppings on plumage quality. *Ibis* 121 (3): 331-333.

Zahavi, A., 1971. The function of pre-roost gatherings and communal roosts. *Ibis* 113 (1): 106-109.

Zuur, A. F., Hilbe, J. M. and Ieno, E. N., 2013. *A beginner's guide to GLM and GLMM with R*. Highland Statistics Ltd.: United Kingdom