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The post-fledging survival and movements of juvenile Barn Swallows (Hirundo rustica): an automated telemetry approach

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Abstract

For migratory songbirds, population dynamics are primarily influenced by juvenile or first year survival, but survival between fledging and fall migration is particularly important. Unfortunately, our knowledge of this post-fledging period is largely limited due to the difficulty of tracking juveniles outside the nest. For this thesis, I used automated radio telemetry to track the survival and post-fledging movements of 216 juvenile Barn Swallows (*Hirundo rustica*) from fledging up until departure for autumn migration in 2016-2017. Average apparent survival was 42% for both broods and nestlings in better body condition had higher survival. Nestlings from second broods migrated 21 days younger and moved less overall during the post-fledging period but had significantly higher daily post-fledging movements suggesting they might be trying to compensate for their shorter time near the breeding grounds. My results suggest that the post-fledging period is a critical period of survival and exploration for juvenile Barn Swallows.

Keywords: post-fledging survival, post-fledging movement, Barn Swallow, automated radio telemetry

Co-Authorship Statement

This thesis was conceived and designed by Dean R. Evans with the help of Keith A. Hobson from Western University and Greg W. Mitchell from Environment and Climate Change Canada. The fieldwork was primarily conducted by Dean R. Evans with the help of Jackson W. Kusack, Greg W. Mitchell, and Michael D. Cadman of the Canadian Wildlife Service. All analysis and writing were conducted by Dean R. Evans. Keith A. Hobson and Greg W. Mitchell both helped with editing and feedback on writing. Any resulting publications will be published with Keith A. Hobson, Greg W. Mitchell, Jackson W. Kusack, and Mike Cadman.

Dedication

This thesis is dedicated to my mother,

Brenda McLean,

Whose love, strength, and determination will always inspire my existence and success.

"We're here for a good time not a long time"

-   Trooper

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This thesis was largely a collaborative project that could have not been completed without the help and support of many people. First and foremost, I would like to thank Keith A. Hobson and Greg W. Mitchell for their continued guidance and supervision throughout the duration of this thesis. Both of you have provided me with a wealth of knowledge that I will be forever grateful for. You both have made this thesis a very enjoyable experience.

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A very special thank you to my family. Dad and Brittney thank you for your continued love and support. Andrew thank you for being by my side through many stressful days, all of this would have been impossible without you, your love, and your patience.

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Chapter 1

General Introduction

Declines of many migratory songbird populations in North America during and since the latter half of the 20th century (Robbins et al. 1989) have prompted extensive study of songbird ecology and demography (Faaborg et al. 2010a). At the core of this research has been the important question of when and how migratory songbird populations are regulated throughout the annual cycle (Holmes 2007; Hostetler et al. 2015). Migratory songbird populations can be limited either on the breeding or wintering grounds or along migration routes and although all portions of the annual cycle cumulatively influence population growth, there has been some speculation as to which portion of the cycle is the most important in determining population dynamics (Holmes 2007). Some studies suggest the breeding period is the most limiting (e.g. Holmes et al. 1996; Rodenhouse et al. 2003; Schmidt 2003; Cox et al. 2014) while others suggest it is the non-breeding period (e.g. Sillett and Holmes 2002; Tarof et al. 2011). Another important factor in understanding migratory songbird demographics is age-specific survival (Reid et al. 2011). Population dynamics and persistence of many songbirds are primarily sensitive to juvenile survival, thus, understanding the factors that influence juvenile survival can be essential to population management (Bonnot et al. 2011; Streby and Andersen 2011; Cox et al. 2014).

TRACKING MIGRATORY SONGBIRDS

Our understanding of the year-round ecology of migratory songbirds remains largely incomplete (Faaborg et al. 2010b; Robinson et al. 2010). This is due to the immense difficulty of tracking migratory songbirds across multiple life history stages that span 100s-

1000s of kilometers (Holmes 2007; Hobson and Wassenaar 2008; Bridge et al. 2011). The primary limitation being the size of tracking technology that can be used on small songbirds often weighing less than 30g (Bridge et al. 2011). Currently, Global Positioning Systems (GPS) and satellite technology are still too large for most migratory songbirds (Webster et al. 2002; Thorup et al. 2014; Taylor et al. 2017). Small passive markers, such as leg bands, have historically been used to track migratory songbirds; however, recapture rates of banded birds are extremely low (<0.5%; Hobson and Wassenaar 2008). The use of light level geolocators has been an important advancement in understanding the ecology of some migratory songbirds (Bridge et al. 2011; McKinnon et al. 2013a). However, geolocators have relatively low accuracy (e.g. within 365 km of latitude and 66 km of longitude) and require tagged individuals to be recaptured, which is challenging (McKinnon et al. 2013a,b). Moreover, having to capture tagged individuals, introduces bias into results, as re-captured individuals may not represent a random sample, if for example, surviving and returning individuals are the most fit and differ in their ecology and life-histories in some important way. Alternatively, radio telemetry is another option for tracking small songbirds that largely overcomes some of the inherent biases mentioned above and has been used to determine stopover sites, travel decisions, and orientation and navigation abilities (Robinson et al. 2010). Unfortunately, radio telemetry has historically required ground tracking of tagged individuals which are often moving at large spatial scales and are limited in battery life which means only a portion of the annual cycle can be investigated (Hobson and Wassenaar 2008; Taylor et al. 2017).

The recent development of a large-scale terrestrial automated radio telemetry array, the Motus Wildlife Tracking System (hereafter 'Motus'), is proving beneficial to our understanding of the ecology of small songbirds (Taylor et al. 2017). Motus is the largest

terrestrial automated telemetry array in the world and allows birds to be tracked at greater

spatial and temporal scales when compared to traditional radio telemetry. Some examples

include evaluation of stopover decisions of American Redstarts (*Setophaga ruticilla*) and

Yellow-rumped Warblers (*Setophaga coronata coronate*) during spring migration (Dossman

et al. 2015), differential post-fledging movements of Blackpoll Warblers (*Setophaga striata*;

Brown and Taylor 2015), influence of fuel loads on the migratory speed of Grey-cheeked

Thrush (*Catharus minimus* Gomez et al. 2017), and the differential migratory departure

decisions of adult and juvenile Ipswich Sparrows (*Passerculus sandwichensis princeps*;

Crysler et al. 2016).

Not only is tracking migratory birds essential to understanding their behaviour, but

also their population demography. Capture-recapture methods are the primary tool used to

obtain information on the population dynamics of wildlife and involves marking and/or

tracking sample individuals from a population throughout time (Lebreton et al. 1992; Ergon

and Gardner 2014). For migratory songbirds, recaptures of banded birds have often been

used to obtain apparent survival estimates (i.e. the product of the probability of true survival

and site fidelity; e.g. Bayne and Hobson 2002; García-Pérez et al. 2014; Marra et al. 2015;

McKellar et al. 2015). True survival estimates are difficult to obtain because mortality can be

confounded with emigration from the study site and, for many species of songbird, site

fidelity for both adults and first year birds between years is unknown (Marshall et al. 2004;

Cox et al. 2014). This method is also spatially limited to areas where researches choose to

recapture banded birds such as major banding stations (Hobson and Wassenaar 2008). An

alternative to tracking banded birds to study population demography is to track individuals

using radio telemetry (e.g. Kershner et al. 2004; Yackel Adams et al. 2006; Dittmar et al.

2016). Using radio telemetry can be advantageous as individuals can be relocated at much

finer temporal scales (e.g. days; Vitz and Rodewald 2011; Grüebler et al. 2014; Jones et al. 2017). Furthermore, using an automated telemetry array offers the additional advantage of being able to track individuals at large spatial scales (e.g. Brown and Taylor 2015; Crysler et al. 2016).

THE POST-FLEDGING PERIOD

The first year of life for a songbird is composed of several key life history stages that can each vary in terms of survival; however, evidence suggests that one of these life history stages, the post-fledging period, should be the primary focus for the management of declining populations (Cox et al. 2014; Naef-Daenzer and Grüebler 2016). The post-fledging period represents the time between when a juvenile leaves the nest for the first time (i.e. fledges) up until their departure for migration (Vitz and Rodewald 2011; Jones et al. 2017). This period can last up to several months and is comprised of two parts; the parental care period between fledging and family breakup, and the independence period between family breakup and autumn migration (Suedkamp Wells et al. 2007; Vitz and Rodewald 2011; Dybala et al. 2013; Jones et al. 2017).

A limited number of studies to date suggest mortality rates for juvenile songbirds during the post-fledging period are high (e.g. Anders et al. 1997; Berkeley et al. 2007; Rush and Stutchbury 2008). Within the post-fledging period, the parental care period is arguably the most crucial in terms of survival for migratory songbirds (Vitz and Rodewald 2011; Cox et al. 2014; Dittmar et al. 2016; Naef-Daenzer and Grüebler 2016). Initially, fledglings are dependent on parental care and remain in family groups with limited mobility (Anders et al. 1997; Berkeley et al. 2007; Vitz and Rodewald 2011). This period lasts up to several weeks, during which time young are vulnerable to predators because of conspicuous foraging and

begging behavior, but also to exposure to the elements because of limited energy reserves (Berkeley et al. 2007; Cox et al. 2014; Jones et al. 2017). Many studies have reported consistently high mortality during the first week of the post-parental care period (upwards of 80%; Rush and Stutchbury 2008) that typically improves with age (e.g. Anders et al. 1997; Yackel Adams et al. 2006; Berkeley et al. 2007; Ausprey and Rodewald 2011). For studies that were able to document the causes of mortality, the major source was predation (Anders et al. 1997; Ausprey and Rodewald 2011). The majority of mortalities due to predation were from raptors and snakes (e.g. Anders et al. 1997; Kershner et al. 2004; Suedkamp Wells et al. 2007; Ausprey and Rodewald 2011; Vitz and Rodewald 2011), but others include small rodents such as squirrels (Anders et al. 1997; Schmidt et al. 2008), and domestic cats (Ausprey and Rodewald 2011; Vitz and Rodewald 2011).

Once juveniles become independent they often leave their natal sites for up to three months prior to departure for autumn migration to engage in behaviours including prospecting and socializing (Betts et al. 2008; Dittmar et al. 2016). Again, mortality risk may be increased during this period because juveniles presumably lack experience navigating, acquiring resources, and evading predators (Cox et al. 2014; Naef-Daenzer and Grüebler 2016). Of the few studies that have estimated survival to independence, only a few have documented a decrease in survival during the post-fledging independence period and typically this is at the onset of independence (Anders et al. 1997; Grüebler and Naef-Daenzer 2010b). For some species, the post-fledging independence period is a time of great mobility, with some studies reporting large landscape and regional-level movements from 10s to 100s of kilometres (Morton 1991; Mitchell et al. 2010; Brown and Taylor 2015). Although the exact function of these movements are unknown, there are three leading hypotheses to explain such movements (Brown and Taylor 2015). The first is the habitat amelioration

hypothesis which explains post fledging movements as a means of acquiring resources (Rappole and Ballard 1987) or evading predators (Rodríguez et al. 2001). The second is the exploration hypothesis, which suggests that broad-scale movements serve to assess habitat and social cues for selection of future breeding sites (Betts et al. 2008) or for providing a mental map to aid in future navigation (Baker 1993; Mitchell et al. 2010). Lastly, the migration hypothesis explains post-fledging movements as initial displacement in the direction of migration without individuals entering a migratory physiological state (Cherry 1985; Rappole and Ballard 1987).

Previous studies have investigated a wide variety of physiological through environmental factors that can influence post-fledging survival (e.g. Suedkamp Wells et al. 2007; Vitz and Rodewald 2011; Haché et al. 2014; Jones et al. 2017). Although equivocal, intrinsic factors at the time of fledging such as body condition, mass, and size have all been demonstrated to be important in predicting post-fledging survival of many songbird species (Vitz and Rodewald 2011; Mitchell et al. 2011; Cox et al. 2014; Jones et al. 2016). Being in better condition is thought to provide fledglings with a buffer from inclement weather as well as provide energy reserves that reduce predation risk by minimizing risk-taking behavior associated with acquiring additional resources (Anders et al. 1997; Maness and Anderson 2013; Jones et al. 2017). Other factors shown to influence post-fledging survival include environmental conditions (e.g. Yackel Adams et al. 2006; Ausprey and Rodewald 2011), habitat (e.g. Ausprey and Rodewald 2011; Vitz and Rodewald 2011), and the timing of breeding (e.g. Naef-Daenzer et al. 2001; Grüebler and Naef-Daenzer 2010a). Few studies have looked at factors that can influence post-fledging movements, however, there is some evidence that body condition is important for small scale post-fledging movements (Vitz and Rodewald 2010).

Despite the importance of the post-fledging period for the success and survival of juvenile songbirds, this period remains the least understood period of avian life history (Kershner et al. 2004; Mitchell et al. 2010). This is largely due to the cryptic and mobile nature of songbirds throughout the post-fledging period (Anders et al. 1997; Rush and Stutchbury 2008). As such, radio telemetry has become a useful tool for investigating both post-fledging survival and post-fledging movements (e.g. Kershner et al. 2004; Berkeley et al. 2007; Haché et al. 2014). However, given recent constraints of transmitter size and battery length (Bridge et al. 2011) many studies have been biased to the beginning of the post-fledging period (Cox et al. 2014; Naef-Daenzer and Grüebler 2016). Furthermore, the mobile nature of songbirds once they become independent makes it extremely difficult to follow individuals resulting in a critical part of the post-fledging period being undocumented (Dittmar et al. 2016). As transmitter battery life improves (e.g. Lotek NTQB-2 transmitters with a 10 second burst interval are warrantied for 52 days) the major hurdle to documenting the post-fledging period is now tracking individuals as they move across the landscape. Like Brown and Taylor (2015), the use of automated radio telemetry provides an opportunity to explore the post-fledging period in its entirety, however, to date no studies have used this approach to look at survival.

STUDY SPECIES

The Barn Swallow (*Hirundo rustica*) is the most widespread and abundant swallow in the world breeding in North America, Europe, and Asia while wintering in Central/South America, Africa, India, and Australia (Brown and Brown 1999). In Canada, Barn Swallows can be found breeding in all provinces and territories, however, they are limited to the southern part of the Yukon and Northwest Territories, sporadic in Nunavut, and absent from the Boreal Shield Ecotone of Ontario (COSEWIC 2011). Barn Swallows have a close

association with human settlement where they often build their nests on man made structures (e.g. barns, garages, and sheds) that provide vertical surfaces for the construction of their mud nests (Zink et al. 2006). Breeding pairs can produce up to two broods per breeding season, however, this is less common in the northern parts of their range (COSEWIC 2011). In Canada, females lay 4-5 eggs per clutch and first clutches are often larger than second clutches (COSEWIC 2011). Incubation starts after the second to last egg is laid and lasts on average of 14 days before the eggs begin to hatch (Brown and Brown 1999). Nestling remain in the nest until they fledge at about 19-20 days old (Brown and Brown 1999; COSEWIC 2011). Newly fledged young remain dependent on parental care for a period up to two week after which juveniles are thought to travel widely before migration (Brown and Brown 1999). Barn Swallows, like most aerial insectivores, have been experiencing serious population declines in Canada (decrease of 76% between 1969 and 2009) yet causes of this decline remain largely unknown (Nebel et al. 2010; COSEWIC 2011). In Europe, Barn Swallows have also been experiencing some decline, although not as extreme as what is observed in North America (Evans and Robinson 2004; Grüebler et al. 2010). The post-fledging survival of Barn Swallows in Europe has also been studied extensively and evidence from Grüebler et al. (2014) suggests that the post-fledging period is the major population bottleneck. Other findings from Europe suggest that the duration of parental care and the timing of breeding are important predictors of juvenile survival (Grüebler and Naef-Daenzer 2008, 2010a; Naef-Daenzer et al. 2011). However, much of the research done in Europe has been limited both temporally (three weeks) and spatially (100 km^2).

OBJECTIVES & HYPOTHESES

The objectives of this thesis were to examine the post-fledging survival and movements of juvenile Barn Swallows in southern Ontario using automated radio telemetry. My thesis was

separated into two data chapters addressing post-fledging survival and movement separately. In my first chapter I set out to apply an analytical framework that, for the first time, could use automated radio telemetry detections from the Motus array to determine accurate estimates of post-fledging apparent survival as well as assess the extent intrinsic factors of age, brood, sex, and relative body condition could influence overall survival. For my second chapter, I set out to quantify the amount of movement juvenile Barn Swallows make prior to migration as well as to what extent extrinsic factors of age, brood, sex, and relative body condition can influence both total and daily movement. Specifically, I hypothesized:

1) That daily apparent survival would be the lowest immediately following fledging due to high predation pressure and exposure to environmental conditions.

2) That daily apparent survival would decrease again a few weeks after fledging when juveniles become independent and more mobile due to their lack of knowledge navigation, foraging, and evading predators.

3) That daily apparent survival would be lowest for juveniles from later broods due to time constraints and the reduction of resources at the end of the breeding season.

4) That daily apparent survival would be similar between juveniles of opposite sexes based on unbiased sex ratios in the adult population.

5) That daily apparent survival would be lower for individuals in poorer condition due to their lack of energy reserves needed to withstand inclement weather and limit exposure to predators

6) That juveniles from second broods would move less than first broods due to time constraints of having to migrate at a younger age.

7) Daily post-fledging movements would be dependent on age where juveniles remain immobile during the beginning of the post-fledging period when they are dependent on parental care followed by increasing mobility once they become independent.

8) Juveniles in better condition would move more during the post-fledging period because they have more resources to do so (i.e. fat).

9) Females would move more than males because of female biased dispersal observed in Barn Swallows and many other species.

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Chapter 2

Post-fledging survival of juvenile Barn Swallows (*Hirundo rustica*): New insights from automated telemetry

INTRODUCTION

Survival is a vital demographic rate that directly influences population growth and decline (Baker et al. 2004; Bromaghin et al. 2015; Bakker et al. 2017). Obtaining reliable estimates of survival and understanding factors that influence survival are fundamental, then, for effective conservation and management of animal populations. Migratory species often move over large distances throughout their annual cycle and are exposed to numerous factors that might influence their survival. However, such factors remain poorly understood (Newton 2004; Holmes 2007) due to the immense challenges of tracking animals across multiple life history stages (Hobson and Wassenaar 2008; Krauel et al. 2018; Torney et al. 2018). With the continual development of new electronic tagging technologies, a better understanding of the behavior and physiology of many free-living animals is now possible (Lennox et al. 2016), yet, many knowledge gaps still exist for smaller migratory species such as songbirds (Bridge et al. 2011). This is concerning given recent and continuous declines observed in many migratory bird populations in North America (NABCI 2016; Sauer et al. 2017) and Europe (Bairlein 2016).

For migratory songbirds, population dynamics and persistence are most sensitive to variation in juvenile survival (Bonnot et al. 2011; Streby and Andersen 2011). Several key life history stages occur within a juvenile songbird's first year that can be limiting; however, the post-fledging period between fledging and autumn migration is likely the most important (Cox et al. 2014; Naef-Daenzer and Grüebler 2016). High post-fledging mortality typically

occurs in the first weeks following fledging when juveniles have limited mobility and remain dependent on parental care, making them conspicuous to predators and vulnerable to environmental conditions (hereafter the 'dependence period' (Anders et al. 1997; Kershner et al. 2004; Ausprey and Rodewald 2011; Vitz and Rodewald 2011)). Once juveniles become independent and increasingly mobile, they must still learn to navigate, acquire resources, and evade predators, which again can result in reduced survival (hereafter the 'independence period' (Anders et al. 1997; Kershner et al. 2004; Mitchell et al. 2010; Dittmar et al. 2016)).

Despite the importance of the post-fledging period, it remains the least understood stage of avian life history (Kershner et al. 2004; Vitz and Rodewald 2011; Naef-Daenzer and Grüebler 2016) due to the furtiveness and mobility of juveniles after leaving the nest (Anders et al. 1997; Rush and Stutchbury 2008; Vitz and Rodewald 2011). To overcome this challenge, most studies have relied on following birds on foot using radio telemetry and documenting known fates (e.g. Kershner et al. 2004; Berkeley et al. 2007; Jones et al. 2017; Vernasco et al. 2017). However, given historical constraints in radio transmitter size and battery life, previous studies largely focused on the first three weeks of the post-fledging period and on relatively large songbird species (Cox et al. 2014; Naef-Daenzer and Grüebler 2016). Such studies have also been limited spatially to when juveniles remain close to their natal area. Once juveniles become independent, they often leave their natal area (Dittmar et al. 2016) and become challenging to follow (e.g. Berkeley et al. 2007; Mitchell et al. 2010; Grüebler et al. 2014; Vernasco et al. 2017), and as a consequence, individuals are either censored in the analysis or are assumed to have survived until migration (Anders et al. 1997; Kershner et al. 2004; Suedkamp Wells et al. 2007). This is problematic given recent evidence that juvenile songbirds can move hundreds of kilometers prior to migration (Brown and Taylor 2015). An alternative is the use of a passive automated telemetry array, such as the

Motus Wildlife Tracking System (hereafter 'Motus'), which allows small birds to be tracked

at broad temporal and spatial scales (months and 100s to 1000s of km; Taylor et al. 2017),

providing a new opportunity to measure survival at previously undocumented spatial and

temporal extents.

The Barn Swallow (*Hirundo rustica erythrogaster*) is a double-brooded aerial

insectivore that has experienced precipitous population declines in Canada (decrease of 76%

between 1969 and 2009) but causes of this decline remain largely unknown (COSEWIC

2011). Post-fledging survival of the European Barn Swallow (*Hirundo rustica rustica*) has

been studied extensively (Grüebler and Naef-Daenzer 2010b,a; Grüebler et al. 2014; Naef-

Daenzer and Grüebler 2016), but at relatively limited spatial and temporal scales. In contrast,

virtually nothing is known about post-fledging survival of North American Barn Swallows.

Here, we investigated post-fledging survival of juvenile Barn Swallows in North America

using the Motus Wildlife Tracking System and provide the first apparent survival estimates

of songbirds at a spatial extent of 1000s of km^2 and an associated temporal extent of

approximately two months. Our objectives were to apply an analytical framework that can

easily incorporate automated telemetry detections to derive accurate estimates of post-

fledging apparent survival and to assess the extent to which intrinsic factors (e.g. age, brood,

sex, and condition prior to fledging) influenced overall survival. We hypothesized that daily

apparent survival will (1) be lowest following fledging as a result of high predation pressure

and exposure to environmental conditions, (2) decrease again a few weeks following fledging

when juveniles become independent and more mobile, (3) be lower for individuals from

second broods due to decreased resources at the end of the season, (4) be similar between the

sexes given an unbiased sex ratio in the adult breeding population, and (5) be lower in

individuals in poorer condition.

(a) Study site and species

We studied post-fledging survival of juvenile Barn Swallows from 33 nesting colonies in 2016 and 15 nesting colonies in 2017 (Figure 2-1). In 2016, 19 of the nesting colonies were in Wellington County, Ontario, Canada (43.55° N, 80.25° W) and the remaining 14 nesting colonies were in Norfolk County, Ontario, Canada (42.58° N, 80.43° W). In 2017, we returned to 15 of the same nesting colonies from Wellington County. We excluded four sites for radio tagging in 2017 owing to logistical constraints. Each site was located on private property and all colonies were located within barns and one garage. Landcover around each of the nesting sites was dominated by agriculture (e.g. row crop, forage, and pasture; average 65% within 1 km) with some small natural areas (e.g. ponds and treed areas; average 27% within 1 km).

(b) Nest monitoring and radio tagging

Data collection and nest monitoring for Wellington County in 2016 and 2017 involved weekly visits starting in late April/early May to determine the onset of laying. Timing of the penultimate egg was used to gauge the timing of hatch given a 14 d incubation period (Brown and Brown 1999). Prior to expected hatch we revisited each nest at least twice weekly to determine hatch day. Hatch day was recorded if there was evidence of hatch (e.g. eggshell present, only partial nest hatch, and nestlings still wet) otherwise nestlings were aged based on feather tract development. This process was repeated mid-July for second broods. Nestlings were revisited at 6-12 d old in 2016 or 8 d old in 2017 for ringing with uniquely numbered US Fish and Wildlife/ Canadian Wildlife Service aluminum rings and to record morphological measurements (wing length and mass in 2016/17 plus tarsus in 2017).

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A subset of nests was visited again when nestlings could be fitted with a radio transmitter (ages 13-21 d old in 2016 and 15 d old in 2017). Morphological measurements were taken and one randomly selected nestling from each nest was fitted with a digitally coded transmitter (model NTQB-2, Lotek, Newmarket, Ontario) using Rappole and Tipton's (1991) two loop leg harness method (n = 86 nestlings in 2016; n = 101 nestlings in 2017). Each harness was made of elastic thread, which allowed for growth, flexibility, and eventual breakdown. Together the harness and transmitter weighed 0.43g (0.08g and 0.35g respectively; approximately 2.3% of average body mass). Each transmitter was programmed with a unique identity which transmitted at a frequency of at 166.380 MHz every 9.7-10.1 seconds resulting in an approximate battery life of 58 d (www.lotek.com). Because mortality can be confounded with tag loss, we examined tag retention of 38 pre-breeding adult Barn Swallows that were radio tagged and recaptured throughout the breeding season as a part of another study. Average minimum tag retention was 63.25 ± 4.70 (SE) days (see Appendix A). Therefore, we are confident that tag retention in our study is close to or at 100%.

In 2017, we sampled blood from radio tagged nestlings for sexing (see Chapter 2: Molecular sexing). For each nest with a radio tagged nestling, we checked for the presence of nestlings during subsequent visits to colonies to determine if the nest had fledged. Dead radio tagged birds were never observed in the nest, however, three tagged individuals were found dead within their nesting barn. We assumed these birds had died after fledging and so were retained in the analysis.

Data collection and nest monitoring for Norfolk county in 2016 included visits to 16 nesting colonies 1-4 times depending on the size of the colony (larger colonies were visited more frequently). Banding and radio tagging occurred at the same time at 36 nests following

the same methods as above. Nests with nestlings old enough to be radio tagged were ringed and morphological measurements recorded. One nestling from each of these nests was fitted with a radio transmitter (n = 36 nestlings). Because of the infrequency of visits, we were unable to age these nestlings based on hatch date. Instead we used a linear model of age controlled by wing length (Age ~ Wing Length) from Wellington County in 2016 to predict the age of the nestlings from Norfolk County (see Appendix B; Figure B1 and Table B1)

(c) Molecular sexing

To extract DNA from dried blood on filter paper, a 6mm circle of blood (~ 10 uL) was cut from the paper and extracted using a modified Chelex protocol (Walsh et al. 1991; Burg and Croxall 2001). Samples were place in a 1.5 ml centrifuge tube with 300 uL extraction buffer (0.1 M Tris pH 8; 0.05 M EDTA; 0.2 M NaCl; 1% SDS) with 5% Chelex w/v, 2.5 uL RNase (10 mg/ml) and 3.0 uL Proteinase K (20 mg/ml) and incubated for 12 hours @ 50°C. From this, 200 uL of solution was transferred to a new 1.5 ml centrifuge tube with 300 uL 1x low TE (10 mM Tris pH 8; 0.1 mM EDTA) with 5% Chelex w/v. Nestling sex was then determined by using PCR and the P8/P2 primer set to amplify the chromo helicase DNA-binding genes of the Z and W sex chromosomes (Griffiths et al. 1998). For Barn Swallows, this reaction produces a 355-base pair product from the Z chromosome (both males and females) and a 390-base pair product from the W chromosome (only in females). DNA extractions were diluted 1:20 for PCR amplification. PCR conditions (per 10 uL reaction) were 2.0 uL ClearFlexi Buffer 5x (Promega), 2.0 mM MgCl$_2$, 200 uM dNTP, 1.0 uM each primer, 0.5 units GoTaq (Promega) and 1 uL 1:20 dilution DNA template. The cycling conditions were as follows: 1 min 30 sec at 94°C, 35 cycles of 30 sec at 94°C, 45 sec at 48°C, 45 sec at 72°C and a final extension of 5 min at 72°C followed by 5 sec at 4°C. PCR products were then run on a 3% agarose gel with a negative control and sex was manually

scored by an observer based on the presence (female) or absence (male) of the W

chromosome (n = 54 females and n = 46 males).

(d) Automated radio telemetry array

We tracked the activity of radio tagged juvenile Barn Swallows using the Motus automated

telemetry array (Taylor et al. 2017; http://motus.org). The Motus array in southern Ontario is

dense and consists of more than 80 radio receiving towers. We specifically added 4 towers in

2016 and 5 towers in 2017 to the Motus array east of Guelph, Ontario to increase the

detectability of our birds. Each of the Motus towers can have 1-4 antenna which are

connected to a SensorGnome receiver which records continuously. With ideal conditions,

each antenna can pick up a radio detection from a distance of 12 – 15 km (Taylor et al.

2017). Every time a tag is detected, its identity is recorded along with the signal strength,

GPS synchronized time, and which antenna the detection was on. Data from all towers are

combined and filtered based on tags unique to a study project. This results in a final data file

that consists of all the tower detections from every tag in a given study across the entire

Motus array.

(e) Mark-recapture

We modeled survival using a multistate closed robust-design (MSCRD) approach. Robust-

design models consist of multiple primary periods and multiple secondary periods within

each primary period which allow for improved accuracy of parameter estimates (Pollock

1982; White et al. 2006). Primary periods were represented by days, while secondary periods

were represented by six 4-hour periods per day. We used a multistate approach to deal with

emigrating juveniles upon departure for migration which can be confounded with mortality.

To analyze our Motus data in a mark-recapture framework, detection data was annotated into encounter histories for each juvenile Barn Swallow. We did this on an individual and daily basis by visually inspecting daily detections across each of the six secondary sampling periods (see Appendix C). A given secondary sampling period was assigned either a '0' when a bird was not detected, an 'L' when a bird was detected within the array, and 'M' when a bird was last detected along the southern edge of the Motus array and moving in a southerly migratory orientation. Preliminary data inspection suggested < 6 tag detections within a sub-sampling period often resulted from random radio interference so we filtered our data to ensure there were a minimum of six tag detections when classifying a bird as being detected. All encounter histories were aligned by age starting at 15 d and continued until an age of 70 d which equates to 56 d (8 weeks) of monitoring (fledge age ranged between 15-24 d). We assigned the last time birds were observed alive in the nest as their first encounter, 'L', to increase our accuracy of estimating mortality for individuals radioed and presumed fledged, but never detected on the Motus array. We excluded individuals from the study that were radioed, not detected on the array, and for which we were not able to confirm fledging by revisiting the nest because we were not able to revisit the colony. This resulted in the exclusion of one individual from Wellington County and five individuals from Norfolk County in 2016. We also excluded one individual from 2017 because we could not obtain a blood sample. This resulted in a total of 116 juveniles from 2016 (n = 85 Wellington County; n = 31 Norfolk County; n = 74 Brood One; n = 42 Brood Two) and 100 juveniles from 2017 (n = 100; n = 51 Brood One; n = 49 Brood Two) for statistical analysis.

(f) Statistical analyses

All statistical analyses were conducted using R 3.4.3 (R Core Team 2017). Survival models were fit using the RMark 2.2.4 package (Laake 2017). We used Huggins closed robust-design multi-state models (HCRDMS) which is a type of MSCRD that does not include abundance as a model parameter (Requena et al. 2012). Parameters estimated from our model included apparent survival (denoted by Φ), the transition probability between states (denoted by ψ), and the probabilities of first capture (denoted by p) and recapture (denoted by c). For each model we fixed the probability of going from the migratory state (M) to the local state (L) to zero because once a juvenile departed for migration they did not return based on our tag detection data. This resulted in just the estimation of the probability of transitioning to the migratory state from the local state (ψ_{LM}) which is ultimately the probability of migrating and its inverse ($\psi_{LL=1-}\psi_{LM}$), the probability of not transitioning. We also fixed the probability of first capture and recapture to equal each other ($p = c$) which results in only one measure of recapture probability (hereafter 'p'). We assumed that these probabilities are equal given that individuals were passively encountered (i.e. no trap response). Lastly, we fixed apparent survival in the migratory state to zero because once an individual enters the migratory state they leave the regional Motus array and are no longer detected. Each year (2016/2017) was modeled independently.

We used a three-stage modeling approach in which we modeled (1) recapture probability (p), (2) migration probability (ψ_{LM}), and (3) survival probability (Φ) separately. Each of these parameters are expected to be dependent on age so we constructed five different parameterizations in which each probability could vary linearly with age (A), non-linearly with age to the second order ($A + A^2$), non-linearly with age to the third order ($A + A^2 + A^3$), weekly based on age classes (15-21, 22-28, 23-35, 36-42, 43-49, 50-56, 57-63, 64-

70 d: A_1), and weekly for the first two weeks with the last four weeks grouped together (15-21, 22-28, 23-70 d: A_2). We grouped the last four weeks because survival can level off after the first two weeks in many species (Naef-Daenzer and Grüebler 2016). We first modeled recapture probability (*p*) while keeping migration probability and apparent survival constant. A set of candidate models were created and compared in which the top model was retained for step two and three (see Appendix D; Table D1-D2). For every candidate model, we allowed recapture probability to vary across secondary periods within primary periods (~Time) to account for the fact that our six secondary periods span an entire day and there are periods where juveniles are less active (e.g. roosting). In 2016, we also included the county nestlings were tagged in as a predictor of recapture probability because the density of Motus towers is higher in Norfolk county (Figure 2-1). Recapture candidate models were created to examine the relationship with each of the age parameterizations on its own and with the additive effects of brood and sex for 2017. Secondly, we modeled the probability of migrating with the top recapture model while keeping apparent survival constant. We again created a set of candidate models for comparison where the probability of migrating could vary with each of the age parameterizations on its own and with the additive effects of brood and sex (2017 only; see Appendix D; Table D3-D4). The top model was retained and used in the final step where we modeled apparent survival. In this last step, a set of candidate models were again created and compared for apparent survival following the same procedure outlined above, but also including body condition. This resulted in a total of 20 candidate models for 2016 and 40 candidate models for 2017 (see Appendix D; Table D5-D6). A body condition index was calculated as the residuals of mass controlling for structural size where wing length was used for structural size for 2016 and tarsus was used for structural size in 2017 (Vitz and Rodewald 2011; Jones et al. 2016). We used tarsus instead of wing length to

obtain our condition measure for 2017 because it had more support, however, both measures of condition are highly correlated (see Appendix E).

Candidate models were ranked based on Akaike's Information Criterion corrected for small sample size (AICc) and the relative likelihood of each model was also determined based on model weight (w_i). Models were considered to have equal support when within two units of the top model (ΔAICc < 2), except when they only differed by one parameter, the more parameterized model had a higher AICc, and that parameter's 95% confidence interval included zero (Burnham and Anderson 2002; Arnold 2010), in which case, we considered the more parsimonious model to have more support. When there were two or more competitive models for recapture probability or migration probability we chose the top model with the lowest AICc to move forward with model selection. All results and inferences were made using the top model for 2016/17 and for only the local state 'L'. The delta method was used to calculate standard errors for cumulative survival and migration probabilities (Powell 2007).

RESULTS

(a) Fledglings

We tracked 216 juvenile Barn Swallows during the post-fledging period in 2016 and 2017 using the Motus automated telemetry system in southern Ontario (n = 116 in 2016 and n = 100 in 2017). Of these, 125 were from first-brooded nests (n = 74 in 2016, n = 51 in 2017) and 91 were from second-brooded nests (n = 42 in 2016, n = 49 in 2017). DNA analysis revealed that there were 54 females and 46 males in 2017. A total of 88 juveniles were tracked until they departed for autumn migration (n = 46 for 2016, n = 42 for 2017). Departure locations were located an average of 119.08±10.47(SE) km in 2016 and

116.63±7.39(SE) km in 2017 away from natal colonies. Thirty-eight birds were never detected by the Motus array but were assumed to have fledged based on nest checks (n = 20 in 2016, n = 18 in 2017). Average fledging age was 19.5±0.1 d(SE).

(b) Survival probability

The top survival model was consistent across both years where survival varied with body condition and non-linearly with age (see Appendix D; Table D5-D6). Greatest support was found for the third-order polynomial model relating daily survival to age ($\sum w_i = 0.93$ in 2016 and $\sum w_i = 0.83$ in 2017). Specifically, daily survival was lowest during the first week when juveniles were between 15 and 21 d old (Figure 2-2). This resulted in a cumulative survival of 78.6±4.1(SE)% in 2016 and 72.8±5.9(SE)% in 2017 (Figure 2-3). After that, daily survival continued to increase until juveniles were 25-30 d old, where daily survival plateaued before decreasing again between the ages of 30 and 45-50 d (Figure 2-2). During the last three weeks of tracking, daily survival increased to 100% by 66 d in 2016 and 60 d in 2017. Cumulative survival across 8 wks of the post-fledging period was 39.9±6.2(SE)% in 2016 and 44.2±6.2(SE)% in 2017 (Figure 2-3).

We found considerable support for body condition influencing daily apparent survival in both years ($\sum w_i = 0.87$ in 2016 and $\sum w_i = 0.90$ in 2017). Our body condition index ranged from -4.29 to 3.18 in 2016 and from -6.38 to 4.90 in 2017. Body condition had a positive effect on daily survival probability with individuals in better condition at the time of radio tagging experiencing higher daily apparent survival (Figure 2-4). We found no evidence that survival differed between broods in 2016 (model 2 Table D5: $\beta_{\text{Brood Two}} = -0.19$; 95% CI -0.78–0.40) or 2017 (model 3 Table D6: $\beta_{\text{Brood Two}} = -0.09$; 95% CI -0.79–0.61). We also

found no evidence that survival differed between sexes in 2017 (model 2 Table D6: β_{Male} = -0.17; 95% CI -0.80–0.47).

(c) Migration probability

The top migration model was the same in both years where the probability of migrating depended on brood and curvilinearly on age (see Appendix D; Table D3-D4), although there was equal support for a linear relationship with age (ΔAICc < 2). We found considerable support for differences in migration probability across broods ($\sum w_i$ = 1.00 in 2016 and 2017; Table D3-D4). Individuals from second broods migrated earlier than first brooded individuals relative to their age (Figure 2-3; Table D7). Specifically, individuals from second broods started migrating around 30 d of age compared to individuals from first broods whom started migrating around 50 d of age (Figure 2-3).

(d) Recapture probability

Top models for recapture probability in 2016 and 2017 both had considerable support (w_i = 1.00; see Appendix D; Table D1-D2). In 2016/2017, recapture probability was lowest in the first week of tracking and increased until the third week when juveniles were about 30-35 d old (Appendix F; Figure F1). After this peak, recapture probability decreased slightly before increasing during the final weeks of tracking. In both years, recapture probability varied depending on time of day (secondary period) where it was lowest during the first and last four h of the day and the highest in the middle of the day (Figure F1). Recapture probability differed with brood in each year with second-brooded juveniles having higher recapture probability in 2016 but lower recapture probability in 2017 when compared to first broods (Table D7). Recapture probability was higher for individuals tagged in Norfolk county in

2016 where the Motus array was denser (Table D7). Lastly, in 2017, males had higher recapture probability than females (Table D7).

DISCUSSION

Using a novel automated telemetry array that covers about 60,000 km^2 in southern Ontario, we provide the first measurement of apparent survival for juvenile songbirds monitored continuously from fledging until autumn migration (approximately 2 months). Our results show that less than half (mean 42%; 39.9±6.2[SE]% in 2016 and 44.2±6.2[SE]%) of fledgling Barn Swallows survive to migrate, providing definitive evidence that survival during this period is critical to population limitation. To put this in context, we can use empirical estimates of non-breeding (i.e. migration and wintering) survival of the adult Black-throated Blue Warbler (*Dendroica caerulescensfrom*) from Sillett and Holmes (~46%; Sillett and Holmes 2002) and multiply it by our average post-fledging survival (42%) to get an estimated first year survival of approximately 19%. We believe this is conservative given juvenile non-breeding survival is expected to be lower than adults (Faaborg et al. 2010). Given a reproductive output of 2.1 female fledglings (average 4.2 fledglings per pair from our study population assuming 50:50 sex ratio; Kusack et al., unpub. ms.), only 0.41 recruits would be produced per adult female per year. This suggests females would need to survive at least 3 years to replace themselves which is not supported in our study population given a mean annual apparent survival of only 48.7% (García-Pérez et al. 2014).

Our cumulative survival estimates are higher than those of post-fledging Barn Swallows in Europe (32.2% after 21 d; Grüebler et al. 2014). They also represent the lower end of estimates from other migratory passerines that were tracked for comparable periods (e.g. 56% after 58 d for Dickcissels *Spiza americana*, 57% after 72 d for Eastern

Meadowlarks *Sturnella magna*; Suedkamp Wells et al. 2007; 42% after 56 d for Wood Thrush *Hylocichla mustelina*; Anders et al. 1997). However, given the spatial limitations of these studies we believe these estimates may be biased depending on how dispersing individuals were dealt with. For example, the study by Grüebler et al. (2014) on European Barn Swallows had a spatial scale of 100 km^2 and assumed no individuals left this area during the first three weeks (even though independent juveniles were highly mobile and could not be detected for several days; Grüebler and Naef-Daenzer 2008). This could result in lower survival estimates where mortality is confounded with dispersal. The study of juvenile Dickcissel and Eastern Meadowlark (Suedkamp Wells et al. 2007) censored individuals believed to have dispersed from study sites which may have resulted in overestimates in survival. Furthermore, this study and others lack estimates up until migration meaning that survival during a critical part of the post-fledging period, when juveniles make potentially costly exploratory movements, was not quantified (Brown and Taylor 2015). Our expanded spatial and temporal scale of tracking avoids these limitations and provides the first complete and most robust account of apparent survival across the entire post-fledging period.

Juvenile birds are particularly limited at two points during the post-fledging period; at the start of the parental care stage when juveniles have limited mobility and remain dependent on care (Anders et al. 1997; Kershner et al. 2004; Ausprey and Rodewald 2011; Vitz and Rodewald 2011) and at the onset of independence when juveniles lack experience and fend for themselves (Kershner et al. 2004; Grüebler and Naef-Daenzer 2010b; Dittmar et al. 2016). We found that apparent survival was the lowest between 15 and 21 d suggesting that the beginning of the parental care period is a costly time for juvenile Barn Swallows. Specifically, 21.4-27.2% of mortality occurred during this first week. The parental care stage

of post-fledging lasts on average 10 d in Barn Swallows (Grüebler and Naef-Daenzer 2010b). With an average fledge age of 19.5 d, the average bird would become independent at about 30 d which coincides with a decrease in daily apparent survival (Figure 2-2). Contrary to previous investigations (e.g. Anders et al. 1997; Grüebler and Naef-Daenzer 2010b), daily apparent survival in our study system was not lowest at the beginning of independence. Instead, apparent survival slowly decreased from about 30 d until about 48 d in 2016 and 43 d in 2017 suggesting the costs of being independent can last well into the independence period. We hypothesize that this could be the result from an increased exposure to threats that results from increased mobility and exploration (Brown and Taylor 2015). Our results also highlight the importance of expanding the temporal and spatial scale of post-fledging survival studies. If our study was limited to just the parental care stage (until approximately 30 d), we would have missed 20-30% of the mortality incurred during the remainder of the post-fledging period.

Nestlings in better condition are thought to be raised with a 'silver spoon' because of the subsequent benefits experienced throughout their lifetime (Stamps 2006; van de Pol et al. 2006). For juvenile Barn Swallows, daily apparent survival was positively related to body condition just prior to fledging. This is consistent with some (Vitz and Rodewald 2011; Dybala et al. 2013; Jones et al. 2016), but not all literature (Anders et al. 1997; Berkeley et al. 2007; Jackson et al. 2011) suggesting the importance of body condition might depend on species and post-fledging ecology. Timing of measurements and indices of body condition used are also other potential confounding factors. There are multiple mechanisms influencing the effect of pre-fledging body condition on post-fledging survival. During the parental care stage, individuals in better condition may be better suited to withstand inclement environmental conditions (Jones et al. 2016) or evade predators (Naef-Daenzer et al. 2001).

During the independence stage, the mechanisms working during the parental care stage would remain the same with the added cost of foraging independently. Another factor that could be working across both the parental care and independence stages is the impact of disease where individuals in poorer condition are more prone to disease (Saino et al. 1997) and this in turn impacts post-fledging survival (López-Rull et al. 2011).

Due to logistical constraints of sexing juveniles, sex is often an important, yet understudied variable in juvenile survival studies (Maness and Anderson 2013). We found no evidence that apparent survival differed between male and female juvenile Barn Swallows. However, we found evidence that males were much more likely to be encountered within the Motus array which provides some evidence of that the sexes might differ in post-fledging behaviours, but perhaps without any survival costs. For example, this could be due to sex specific movements More investigation into sex specific post-fledging behaviour of juvenile Barn Swallows is needed. In addition, we found no differences in survival between broods despite evidence of reduced survival for later brooded Barn Swallows in Europe (Grüebler and Naef-Daenzer 2010a). One possible explanation for this observation is that second-brooded individuals could have received better post-fledging parental care providing them with a buffer needed to survive and migrate at a younger age. However, this is likely at a cost during migration as second brooded individuals generally experience lower return rates (Raja-Aho et al. 2017).

One challenge of using automated telemetry to estimate post-fledging survival is that determining the timing of mortality is difficult during the parental care stage when juveniles are largely immobile and have lower probability of being detected by towers. We arranged receiving towers to optimize detection, but an ideal situation would be to have a receiving

tower at each natal site for full spatial coverage. Some individuals assumed to have died early in the post-fledging period were never detected on the Motus array and because their last encounter was within the nest, this could negatively bias survival earlier in the post-fledging period. Another challenge of using automated radio telemetry is that mortality can often be confounded with tag loss or tag death, but we found such losses were negligible (Appendix A). In terms of premature radio failure, our tags had a rated battery life of approximately 58 d which is close to the duration of tracking in our study (56 d). Daily apparent survival reached 100% by the end of tracking in both years, suggesting that radio tags did not prematurely fail in our study, and this is when we would expect tags to start dying early.

CONCLUSION

This research adds to the growing evidence that the post-fledging period is a critical time in the annual cycle of songbirds. Nearly 60% of juvenile Barn Swallows fail to survive until autumn migration which is important given mortality during the post-fledging period is additive to mortality incurred during the rest of the annual cycle (Naef-Daenzer and Grüebler 2016). A critical next step in understanding population declines of North American Barn Swallows is to examine survival across other parts of the annual cycle in order to build full-annual-cycle population models (Hostetler et al. 2015). Ultimately, our results show the value of using automated telemetry, such as Motus, to obtain unbiased survival estimates at unprecedented spatial scales. On average, juvenile Barn Swallows were last detected departing for migration over 100 km away from their natal colony and tracking individuals at this distance would be impossible without automated telemetry. We believe this approach can be can be readily adapted to new and existing data on other species and periods of the annual cycle.

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FIGURES
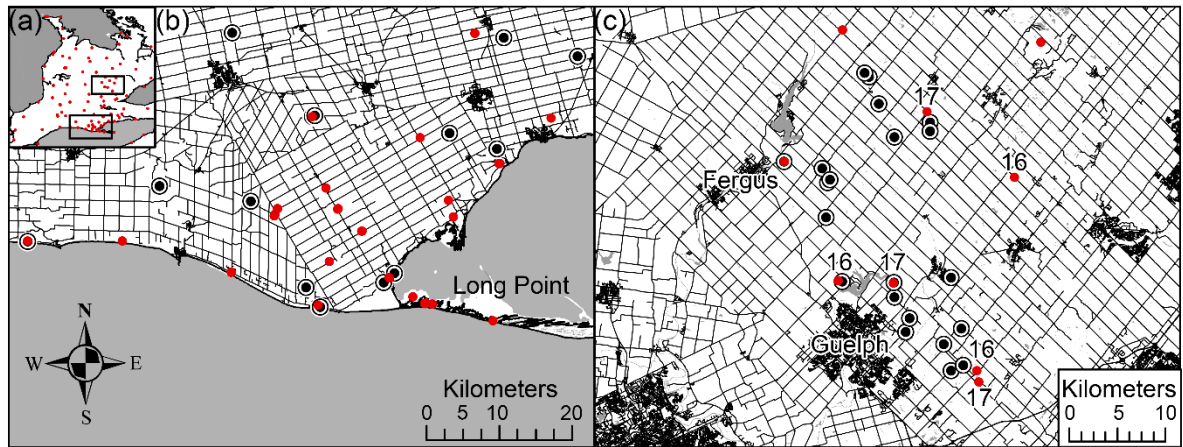
Figure 2-1. The location of study sites (black/white dots) and Motus automated radio receiving towers (red dots) within (a) southern Ontario, (b) Norfolk County, and (c) Wellington County in 2016 and 2017. Towers labeled with a specific year in Wellington County were only active that year and unlabeled towers were active both years.
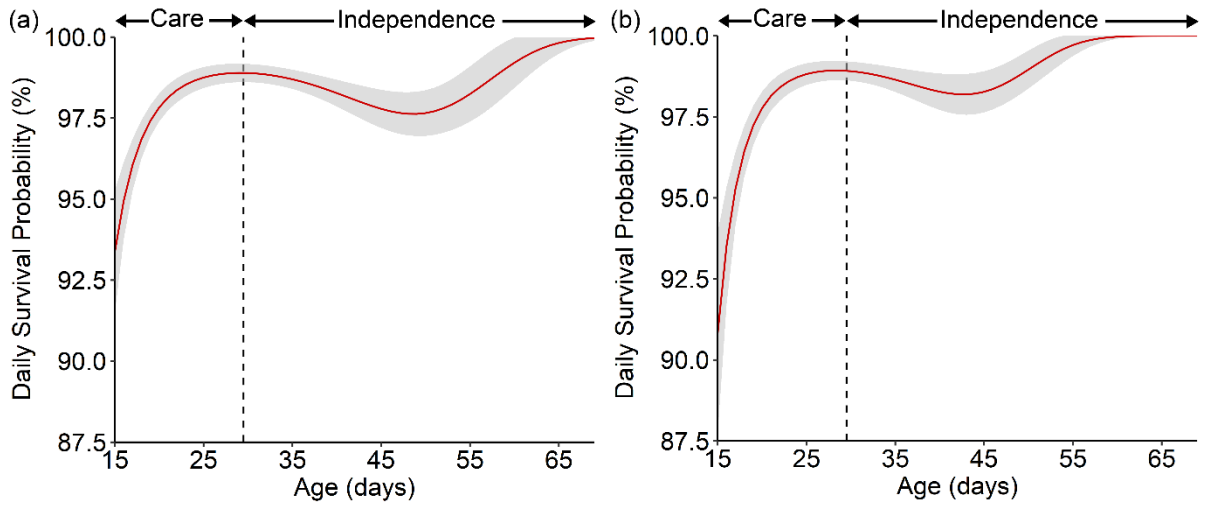
Figure 2-2. Predicted daily apparent survival probability for juvenile Barn Swallows in average condition during the post-fledging period in southern Ontario for (a) 2016 and (b) 2017. Daily apparent survival estimates are from the top model and grey areas represent the standard error. Dashed vertical line shows the average transition from parental care to independence as calculated with average fledge age plus the estimated length of parental care from Grüebler and Naef-Daenzer (2010b).
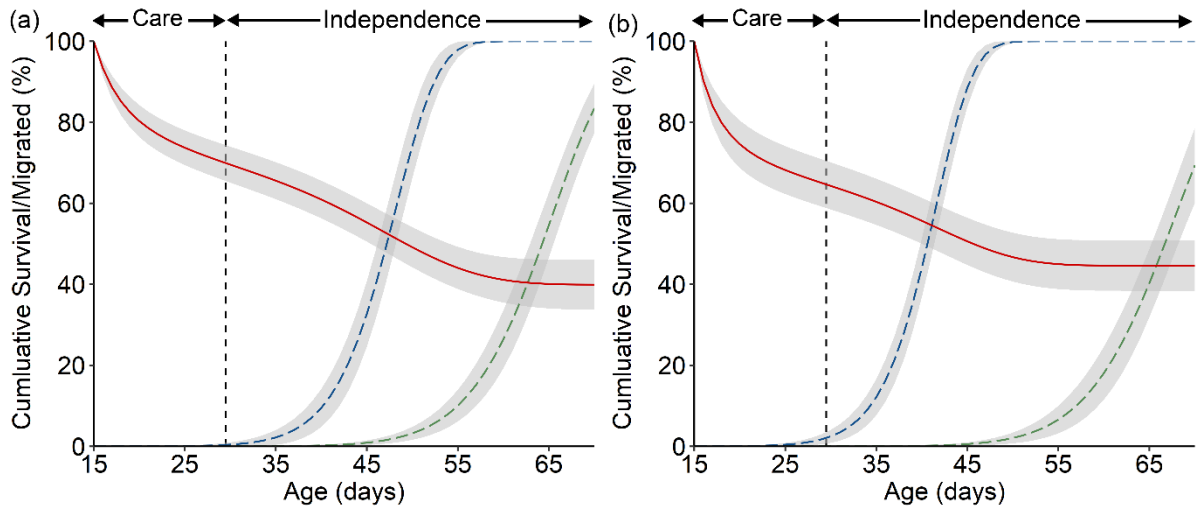
Figure 2-3. Predicted cumulative survival (solid red line) and cumulative migration from first brooded (dashed green line) and second brooded (dashed blue line) juvenile Barn Swallows in southern Ontario during the post-fledging period of (a) 2016 and (b) 2017. Cumulative survival and cumulative migrated were calculated with the top model and cumulative survival is based off of individuals in average condition. Grey areas represent standard error of the cumulative estimate. Dashed vertical line shows the average transition from parental care to independence as calculated with average fledge age plus the estimated length of parental care from Grüebler and Naef-Daenzer (2010b).
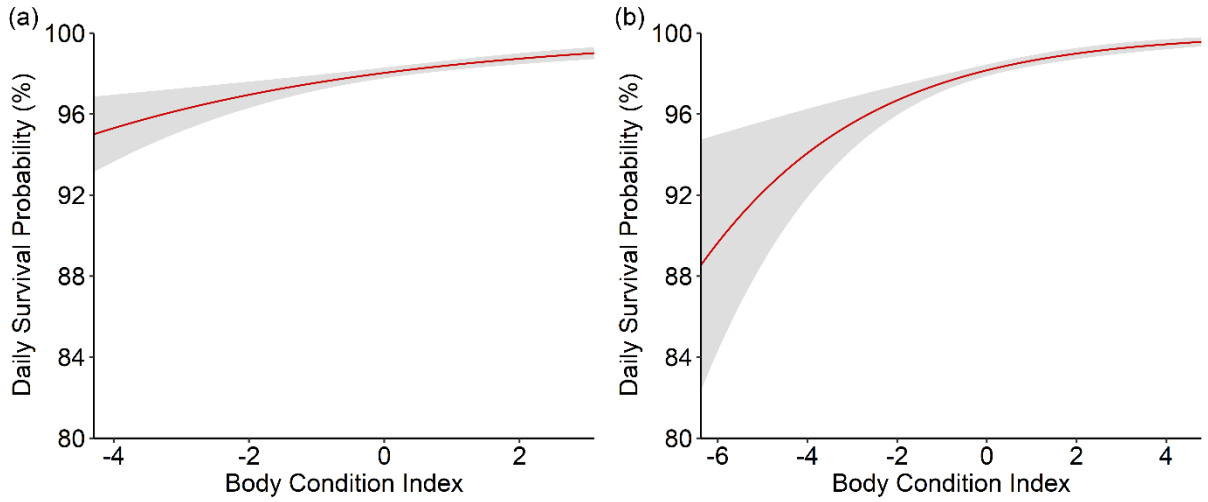
Figure 2-4. Predicted average daily apparent survival probability for juvenile Barn Swallows with different body condition in southern Ontario for (a) 2016 and (b) 2017. Range of body condition values represent the true range of radio tagged individuals in our study and the grey areas represent the standard error.

Chapter 3

The post-fledging movements of juvenile Barn Swallows (*Hirundo rustica*)

INTRODUCTION

The vertebrate annual cycle is comprised of multiple life-history stages that are behaviorally, morphologically, and physiologically distinct in order to increase individual success and survival in response to changing environmental conditions (Wingfield 2008). Migratory songbirds for example, enter a migratory state allowing them to travel great distances in order to exploit seasonal peaks of resource abundances on the breeding and wintering grounds while also avoiding adverse environmental conditions (Alerstam et al. 2003; Ramenofsky and Wingfield 2007). However, compared to resident birds, migratory songbirds have more complex annual cycles which can result in time constraints and the implementation of potentially costly time-saving strategies such as overlapping, shortening the duration, or changing the timing of life-history stages (Wingfield 2008; Tomotani et al. 2016). Ultimately, these decisions can have consequences that carry over and impact the entire annual cycle (Harrison et al. 2011).

The post-fledging period is a critical life history stage for many migratory songbirds (i.e. the time between fledging and migration; Cox et al. 2014; Naef-Daenzer and Grüebler 2016). At first, newly fledged juveniles face high mortality due to their limited mobility and dependence on parental care (Anders et al. 1997; Kershner et al. 2004; Ausprey and Rodewald 2011; Vitz and Rodewald 2011). Once independent, juveniles again face increased mortality as they become more mobile and must learn to locate and acquire resources, avoid predators, and navigate on their own (Anders et al. 1997; Rush and Stutchbury 2008; Mitchell et al. 2010; Grüebler et al. 2014; Dittmar et al. 2016). Several studies have

documented large regional and landscape-level movements during the post-fledging period that cannot be accounted for by finer scale foraging movements (Morton 1991; Brown and Taylor 2015). These movements may serve to gather information on habitat and social cues for the selection of future breeding sites and/or to build a mental map to help navigate the breeding grounds upon return the subsequent spring (hereafter 'exploration hypothesis;' Baker 1993; Betts et al. 2008; Mitchell et al. 2010; Brown and Taylor 2015). Alternatively, post-fledging movements may represent an initial displacement in the direction of migration without entering a migratory physiological state (hereafter 'migration hypothesis;' Cherry 1985; Rappole and Ballard 1987; Mitchell et al. 2010; Brown and Taylor 2015).

Current knowledge of the post-fledging period is limited despite being arguably the most important life history stage for juvenile songbirds (Kershner et al. 2004; Vitz and Rodewald 2011). Our understanding of post-fledging movement is therefore also very limited and the few existing studies that have focused on movements during this period have mostly addressed fine scale movements that occur just after fledging (e.g. Kershner et al. 2004; Berkeley et al. 2007; Haché et al. 2014). The cryptic behavior and mobility of songbirds after fledging (Anders et al. 1997; Rush and Stutchbury 2008) along with technological constraints of tracking the movements of small songbirds in general (Bridge et al. 2011) has likely limited this field of investigation. Brown and Taylor (2015) were the first to investigate post-fledging movements at a broad spatial scale (100s of km) using automated radio telemetry showing juvenile songbirds can travel widely before migration. The Motus Wildlife Tracking System (hereafter 'Motus') is currently a well-established automated radio telemetry system in eastern North America that allows small birds to be tracked at large spatial and temporal extents using small lightweight radio tags (Taylor et al. 2017).

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Despite recent evidence that juvenile songbirds can move extensively prior to autumn migration, there is still little understanding of the factors driving variability in movement distances during the post-fledging period. There is also little understanding to what extent late fledging birds in double brooded species face time constraints prior to autumn migration, relative to first-brood or earlier fledging birds. Here we investigate the movements of juvenile Barn Swallows (*Hirundo rustica*) during the post-fledging period in southern Ontario using Motus. We sought to quantify the amount of movement juveniles make prior to migration and to what extent intrinsic factors such as brood, age, body condition, and sex can influence such movements. Barn Swallows produce up to two broods per breeding season providing us an opportunity to explore differences in movement patterns between early and late broods. In double brooded species, later broods often migrate at a younger age than their predecessors and this comes at a cost of valuable time on the breeding grounds to gain experience and prepare for autumn migration (Tarof et al. 2011; Meller et al. 2013; Raja-Aho et al. 2017). We expected that second broods would move less than first broods due to the time constraints of having a shorter post-fledging period prior to migration. We further hypothesized that there will be an age-specific pattern of mobility where juveniles will remain immobile for the first 10 days of the post-fledging period while they are dependent on parental care and increase their mobility thereafter. We also expected that individuals in better condition will move more because they have larger energy reserves and can afford to put more time and energy into movement. Last we predicted that juvenile females would move more extensively than males because of female biased juvenile dispersal observed in European Barn Swallows (Balbontín et al. 2009).

METHODS

(a) Study Site and Species

Barn Swallows are a small (17–20 g) aerial insectivore that breed in Canada and are primarily associated with manmade structures (e.g. barns, garages, and sheds) that provide vertical surfaces for the construction of their mud nests (Brown and Brown 1999). Barn Swallows are commonly found breeding semi-colonially and can produce up to two broods per breeding season. We studied the post-fledging movements of juvenile Barn Swallows from 19 nesting colonies in 2016 and 15 colonies in 2017 near Guelph, Ontario, Canada (43.55° N, 80.25° W). Four of the study sites were dropped in 2017 due to logistical constraints. Each nesting colony was located within barns on private property with the exception of one garage. Landcover near each nesting colony was primarily agriculture (e.g. row crop, forage, and pasture; average 65% within 1 km) and some small natural areas (e.g. ponds and treed areas; average 27% within 1 km).

(b) Nest monitoring and radio tagging

Nest monitoring and data collection varied by year. Nesting colonies were first visited in late April or early May of each year followed by weekly visits to determine the onset of laying. Once laying had commenced, we increased our site visits to at least twice a week to determine the timing of the penultimate egg which was used to determine the approximate timing of hatch using a 14 d incubation period (Brown and Brown 1999). We then visited each site just prior to hatch and continued to visit at least twice a week in 2016 or every other day in 2017 to determine hatch day. Hatch day was recorded if there was evidence of hatch on (e.g. eggshell present, only partial nest hatch, and nestlings still wet) and if hatch day

could not be recorded in this way, nestlings were aged based on feather tract development. This process was repeated again in mid-July for second nests.

Each nest was revisited for a second time when nestlings were 6-12 d old in 2016 or 8 days old in 2017 for banding and measurements. All nestlings were fitted with a uniquely numbered US Fish and Wildlife/ Canadian Wildlife Service aluminum band and mass, wing length, and tarsus (2017 only) were recorded. A subset of nests (n = 86 in 2016 and n = 101 in 2017) were visited again when nestlings were more mature and able to be fitted with a radio transmitter (ages 13-21 d old in 2016 and 15 d old in 2017). All nestlings were measured as before and one randomly selected nestling from each nest was fitted with a digitally coded transmitter (model NTQB-2, Lotek, Newmarket, Ontario) using Rappole and Tipton's (1991) two loop leg harness method. Each harness was made using elastic thread which allowed for growth, maneuverability, and eventual breakdown. Together the radio tag and harness weighed 0.43g which represents only 2.3% of the body mass of an average Barn Swallow which is below the recommended 5% cut-off (Caccamise and Hedin 1985). Each transmitter was programed with a unique identity which was transmitted every 9.7-10.1 seconds at a frequency of 166.380 MHz. This resulted in a battery life of approximately 58 days.

In 2017 only, we took blood samples from radio tagged nestlings for determination of sex. We obtained blood samples by piercing the brachial vein with a 26 gauge needle and drawing 10-20ul of blood into a micro-capillary tube. We then dried the blood on filter paper for storage at approximately -20°C for molecular analysis. Following radio tagging, on any subsequent visits to that nesting colony we made the point of checking for radio tagged nestlings in the nest to determine if fledging had occurred. Because we frequented sites more

in 2017 we were able to estimate time of fledging as the mean age between the last visit a nestling was present in the nest and the subsequent visit they were no longer present.

(c) Molecular sexing

See Chapter 2 Methods section (c).

(d) Automated radio telemetry array

See Chapter 2 Methods section (d).

(e) Data analysis

Data was analyzed using R 3.4.3 (R Core Team 2017). Detections were sorted and examined on a per bird basis. Out of the total 187 radio tagged birds, 37 were never detected on the Motus array (n = 19 in 2016 and n = 18 in 2017) and were excluded from further analysis. We also excluded one juvenile in 2017 due to the inability to obtain a blood sample for sex determination. This resulted in a total of 149 juveniles for analysis (n = 67 in 2016 and n = 82 in 2017). To get a measure of movement, we looked at all movements made by juvenile Barn Swallows from fledging up until the bird was no longer detected or had departed for autumn migration. Specifically, we calculated two measures of movement. First, we calculated cumulative daily movement distances by summing the distance between subsequent tower detections on any day an individual was detected. To avoid over estimation, we rounded detections to the nearest hour and excluded any distances < 15 km where an individual could theoretically be detected by two towers, but not have moved between them. Secondly, we calculated cumulative distance traveled during the entire post-fledging period as the sum of cumulative daily movement. It is important to note that both of these measures are not exact distances moved because each detection only indicates a bird was within 12-15 km radius of a tower. Daily movement was likely an underestimate given individuals are not always

detected. We also recorded when individuals departed for autumn migration which marked

the end of the post-fledging period. We assumed a juvenile Barn Swallow had departed for

migration if it was observed to make a southerly movement and last detected on the southern

edge of the Motus array (e.g. along Lake Erie). For all departures we recorded the date and

location. To get a measure of body condition we used data from all nestlings that were

measured at the same time as the radio tagged nestlings separated by year due to the

differences in ages of measurement in 2016 (day 13-21) vs 2017 (day 15 only). A body

condition index was calculated from the residuals of a simple linear model of body weight

controlled for structural size where we used wing length in both years.

(f) Statistical analysis

All statistical analyses were conducted using R 3.4.3 (R Core Team 2017). To test whether

intrinsic factors such as brood, age, condition, and sex influence movement we first looked at

cumulative daily movement using generalized additive mixed effects models (GAMMs;

mgcv package; Wood 2017). We chose to use GAMMs to look at daily distance moved so

that we could account for the non-liner relationship with age that we expected, and the

mixed-effects allowed for us to account for similar movements between individuals from the

same colony and individual variance in the number of days detected. We started by modeling

each year separately because we only had sex data from 2017 and our measure of condition

in each year was not comparable given the different ages that nestlings were radio tagged in

2016. We fit an initial saturated (or global) model with all of our predictor variables. All

predictor variables were treated as linear effects with the exception of age in which we

allowed for a nonlinear relationship. We also included an interaction between age and brood

in each year because of the different timelines for each brood (i.e. second broods having a

shorter post-fledging period). Therefore, our global 2016 model consisted of: cumulative

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daily movement as the response variable; brood and condition as linear predictor variables; an age by brood non-linear predictor variable; and colony and individual as a random effect. Our 2017 model consisted of cumulative daily movement as the response variable, brood, condition, and sex as linear predator variables, an age by brood non-linear predictor variable or interaction, as well as colony and individual as a random effect.

We conducted model selection using stepwise deletion of predictor variables with little support starting from our global model. Support for the dropped term was assessed using Akaike's Information Criterion corrected for small sample size (AICc) and likelihood ratio tests. If removal of the predictor decreased the AICc and removal of that term was not significant we continued with model selection (Table 3-1). If ΔAICc < 2 we chose the most parsimonious model. This resulted in the deletion of condition in both years and sex in 2017. Because the resulting models were identical in both years we chose to combine the data from each year to model the effects of brood on cumulative distance traveled. We also included year as an additional fixed effect to account for yearly variation. This resulted in a final model of: cumulative daily distance as the response variable; brood and year as linear predictors; an age by brood non-linear predictor variable; and individual and colony as random effects (Table 3-2).

Next, we tested whether intrinsic factors of brood, condition and sex influenced cumulative distance traveled using mixed effects linear models fitted with maximum likelihood methods (package nlme; Pinheiro et al. 2017). Again, we started by modeling each year separately for the same reasons as described above. We included colony as a random factor to account for possible similarities in movement patterns among individuals from the same colony. We also included whether that individual migrated as a fixed effect in each year

to account for the fact that individuals who made it to migration would have moved more to reach their departure location. We started with a saturated global model with all predictor variables and proceeded with model selection using stepwise deletion of model terms with little support as described above. Our global model for 2016 consisted of cumulative distance traveled as the response variable, condition, brood, and migrated as fixed effects, and colony as a random effect. Our global model for 2017 consisted of cumulative distance traveled as the response variable, condition, brood, sex, and migrated as fixed effects and colony as a random effect. Following model selection, we again removed condition from both years and sex from 2017 (Table 3-3). This allowed us to combine both years for one final model. We again included year as an additional fixed effect. This resulted in a final model consisting of cumulative distance traveled as the response variable, brood, migrated or not, and year as linear predictors, and site as a random effect (Table 3-4). Lastly, to validate our assumption that second broods are more time constrained than first broods, we used a simple mixed effects linear model with departure age from both years as the response variable, brood and year as fixed effects, and colony as a random effect (n = 66).

RESULTS

We successfully tracked a total of 149 juvenile barn swallows during the post-fledging period in 2016 and 2017. Of these, 24 were tracked up until migration in 2016 (n = 14 first brood and n = 10 second brood) and 42 up until migration in 2017 (n = 16 first brood and n = 26 second brood). Departures for migration averaged 117.5±6.0 (SE) km from nesting colonies. Second brooded juveniles migrated at an average age of 42.6±0.9 (SE) d which was significantly younger than first broods who migrated at an average age of 64.1±1.2(SE) d (Estimate = -20.7±1.4(SE); t-value = -14.33; p-value = < 0.0001; Figure 3-1). Juveniles from 2017 also migrated on average 4.17±1.5(SE) days younger than juveniles from 2016 (t-value

= -2.77; *p*-value = < 0.008). The average departure date for first broods was August 19±1.8(SE) d compared to September 8±0.6(SE) d for second broods.

Juvenile Barn Swallows were highly mobile during the post-fledging traveling on average 16.7±1.7(SE) km per day. We found a significant non-linear relationship between age and cumulative daily movement where juvenile swallows from both broods were relatively immobile until approximately 28-32 d old, after which time, movement increased steadily, before levelling off for second broods only, around 45 days of age (Table 3-2; Figure 3-2). After accounting for age, second broods moved significantly more than first broods traveling on average 17.9±5.7(SE) km more per day (Table 3-2; Figure 3-2). We did not find any support that body condition, sex, or year influenced cumulative daily distance moved (Table 3-1 – 3-2). Although second broods traveled more per day, they traveled on average 202.5±45.8(SE) km less in terms of cumulative total distance moved when compared to first broods (Table 3-4; Figure 3-3). First broods moved on average 403.4±37.8 (SE) km cumulatively and second broods moved an average of 243.8±28.0(SE) km cumulatively during the post fledging period. Furthermore, juveniles from either brood that made it to autumn migration traveled on average 254.0±45.8(SE) km more than juveniles that did not make it to migration (Table 3-4). Therefore, migrating juveniles from first broods traveled on average of 582.8±56.9(SE) km compared to 345.6±33.9(SE) km for second broods. We did not find any support that body condition, sex, or year influenced cumulative distance moved (Table 3-3 – 3-4).

DISCUSSION

Using a novel tracking system, we provide the first evidence for differences in regional large-scale post-fledging movements between juveniles from first and second broods

for a migratory songbird prior to autumn migration. We found that juvenile Barn Swallows moved considerable distances prior to migration. Juvenile Barn Swallows moved on average a minimum of 403.4±37.8 (SE) km if they were from first broods and 243.8±28.0(SE) km if they were from second broods (582.8±56.9[SE] km and 345.6±33.9[SE] km for migrating individuals, respectively). This is considerably more movement than expected under the migration hypothesis given migratory departure locations were on average only 117.5±6.0 (SE) km away. Our results therefore support the finding from Brown and Taylor (2015) that juveniles songbirds make indirect movements likely for the purpose of exploration prior to migration. Although, we cannot directly test the purpose of these movements, banded juvenile Barn Swallows have been re-caught at non-natal colonies 5-8km away (Bell 1962) and one of our radio tagged juveniles was detected inside a non-natal barn 3 km away (DRE pers. obs.). Furthermore, natal dispersal in Barn Swallows is often less than 30 km from their natal colony (Brown and Brown 1999). Based on this evidence it is possible that these movements are in part for the purpose of prospecting and gathering information on habitat and social cues for the selection of future breeding sites. However, given the scale of movements we observed verses the scale of dispersal we believe the post-fledging movements observed here are more likely for creating a mental map to help navigate the breeding grounds upon return the subsequent spring.

Life history theory suggests that when faced with time constraints, individuals must adopt costly time saving measures such as shortening or overlapping life history stages or delaying entry into the subsequent stage (Wingfield 2008; Mitchell et al. 2012). Here, we show that juvenile Barn Swallows from second broods migrate nearly 22 days younger than first broods resulting in considerably less time being spent on the breeding grounds. This time constraint ultimately results in second broods being less able to move as extensively

during the post-fledging period. If these movements are for the purpose of exploration, this may impact their future survival, dispersal, and breeding success due to their inability to gather information on potential future breeding areas or if navigational abilities are under-developed (Raja-Aho et al. 2017). However, second broods moved more per day at a younger age than first broods. This suggests second broods may be at least partially compensating for their short time on the breeding grounds by trying to move as much as they can in what short time they have. There is evidence that later brooded migratory birds experience accelerated development to speed up the timing of migration (Berthold 1996; Gwinner 1996; Styrsky et al. 2004). However, this is the first study to document accelerated post-fledging movements suggesting post-fledging movements might be an essential component of songbird ecology and life-histories.

As expected, post-fledging movements were strongly related to age with juveniles from both broods remaining relatively immobile until they were approximately 30 days old. This transition corresponds closely to the expected timing of independence in our study population (Evans et al. unpub. manuscript). Many studies have documented high mortality during the relatively immobile parental care stage, likely a result of their conspicuousness and vulnerability to predators (Anders et al. 1997; Berkeley et al. 2007; Ausprey and Rodewald 2011; Vitz and Rodewald 2011). However, few studies have been able to estimate survival after juveniles become highly mobile and leave their natal areas during the independent period. Recently we showed a decrease in apparent survival of juvenile Barn Swallows during the post-fledging independence period (Evans et al. unpub. manuscript). Although we were unable to determine the cause of mortality, our results here show that juveniles are move extensively during independence which has the potential to increase mortality because of possible greater exposure to predators or anthropogenic threats, such as

wind turbine, communication tower, or building collisions (e.g. Machtans et al. 2013; Rioux et al. 2013; Zimmerling et al. 2013).

Many studies have documented lower annual apparent survival for later brooded juveniles in many species including Barn Swallows (Visser and Verboven 1999; Verhulst and Nilsson 2008; Raja-Aho et al. 2017). This could be potentially because of the costs of having less time to prepare for migration and gain experiences foraging, navigating, and evading predators (Tarof et al. 2011; Raja-Aho et al. 2017). We recently showed that there was no difference in post-fledging survival of first or second brooded Barn Swallows from our study population (Evans et al. unpub. manuscript). This would suggest that if there are costs to being second brooded they would occur during migration. Our results also have important implications for survival studies of double brooded passerines. If other species have similar post-fledging behaviours where second broods migrate younger and move more sooner than this needs to be taken into account when modeling post-fledging survival. For example, Grüebler and Naef-Daenzer (2008, 2010) looked at the post-fledging apparent survival of juvenile Barn Swallows in Europe during the first three weeks of the post-fledging period. They found a seasonal decline in apparent survival of late broods; however, this decline could be explained by emigration of later broods at a younger age compared to early broods.

We did not find any evidence that either body condition or sex influenced the post-fledging movements of juvenile Barn Swallows. Body condition has been shown to influence the post-fledging movements of Ovenbirds (*Seiurus aurocapilla*) and Worm-eating Warblers (*Helmitheros vermivorum*), however, this was only 2 days after fledging and at a scale of less than 200 m (Vitz and Rodewald 2010). Many studies have documented fine scale movements

(100s of m) during the beginning of the post-fledging period, however, using automated telemetry does not allow for tracking at that scale (Kershner et al. 2004; Suedkamp Wells et al. 2008; Haché et al. 2014). Therefore, condition may only be important for small-scale movements during the post-fledging parental care period. Despite female biased dispersal in Barn Swallows we did not observe any differences in movement between sexes during the post-fledging period in this study. This could be due to the scale of natal dispersal observed in Barn Swallows which is often within 30 km of their natal colony (Brown and Brown 1999). If this is the case it might be difficult to do detect any differences between sexes using Motus at this scale. The lack of difference in movement parameters between sexes also suggests the function of post-breeding movements is for developing some sort of mental map or navigational target, as opposed to prospecting for future breeding sites, in which females should likely be moving more.

CONCLUSION

This research adds to the growing evidence that juvenile songbirds make large scale movements prior to migration suggesting that this period is a critical time of learning for juvenile songbirds. We show that birds from later broods are considerably more time constrained than those from first broods and as a result must compensate by becoming more mobile at a younger age. An essential next step would be to determine if there are any costs associated with these types of movements given evidence that survival during the post-fledging period remains the same across early and late broods. Furthermore, future research needs to definitively determine the reason for these types of movements. Our study also highlights the value of using automated radio telemetry to expand the spatial scale of post-fledging research. Previous research on the post-fledging ecology of migratory songbirds have been extremely limited to when juveniles remain close to their natal colony. We suggest

that future studies using Motus will be invaluable for understanding the ecology of songbirds

during critical periods of mobility that were once extremely difficult to investigate.

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Table 3-1. Model selection results showing stepwise deletion of non-significant terms to determine the best general additive mixed effect model explaining cumulative daily distance moved in 2016 and 2017. Smoothed terms are represented in brackets with an 's.' P-value refers to the significance of the deleted term.

2016				
Model	**df**	**AICc**	**ΔAICc**	**p-value**
Cumulative Daily Distance Travelled ~ s(Age, by= Brood) + Brood + Condition	9	9154.286	3.14	-
Cumulative Daily Distance Travelled ~ s(Age, by= Brood) + Brood	8	9151.146	0	0.6239
2017				
Model	**df**	**AICc**	**ΔAICc**	**p-value**
Cumulative Daily Distance Travelled ~ s(Age, by= Brood) + Brood + Condition + Sex	10	14391.73	3.85	-
Cumulative Daily Distance Travelled ~ s(Age, by= Brood) + Brood + Sex	9	14389.71	1.83	0.943
Cumulative Daily Distance Travelled ~ s(Age, by= Brood) + Brood	8	14387.88	0	0.6541

Table 3-2. Summary of the generalized additive mixed model predicting cumulative daily

distance moved of juvenile Barn Swallows during the post-fledging period in southern

Ontario for 2016 and 2017.

Linear Predictors				
Variable	**Estimate**	**Standard Error**	**t-value**	**p-value**
Intercept	16.698	1.737	9.611	< 0.0001
Brood Two	17.863	5.705	3.131	0.0018
2017	3.087	2.588	1.193	0.23305
Smoothed Terms				
Variable	**edf**	**Ref.df**	**F-value**	**p-value**
Brood One	3.954	3.954	85.03	< 0.0001
Brood Two	4.599	4.599	70.06	< 0.0001

Table 3-3. Model selection results showing stepwise deletion of non-significant terms to determine the best linear mixed effect model explaining cumulative distance moved in 2016 and 2017.

2016				
Model	**df**	**AICc**	**ΔAICc**	**p-value**
Cumulative Distance Traveled ~ Brood + Migrated + Condition	6	952.412	2.28	-
Cumulative Distance Traveled ~ Brood + Migrated	5	950.124	0	0.720
2017				
Model	**df**	**AICc**	**ΔAICc**	**p-value**
Cumulative Distance Traveled ~ Brood + Migrated + Condition +	7	1156.878	2.52	-
Cumulative Distance Traveled ~ Brood + Migrated + Condition	6	1155.442	1.08	0.3278
Cumulative Distance Traveled ~ Brood + Migrated	5	1154.362	0	0.2636

Table 3-4. Summary of the linear mixed model predicting cumulative distance traveled of juvenile Barn Swallows during the post-fledging period in southern Ontario for 2016 and 2017.

Variable	Estimate	Standard Error	t-value	p-value
Intercept	312.138	39.447	7.913	< 0.0001
Brood Two	-202.490	45.821	-4.419	< 0.0001
Migrated Individuals	253.980	45.800	5.546	< 0.0001
2017	-3.546	45.687	-0.078	0.938
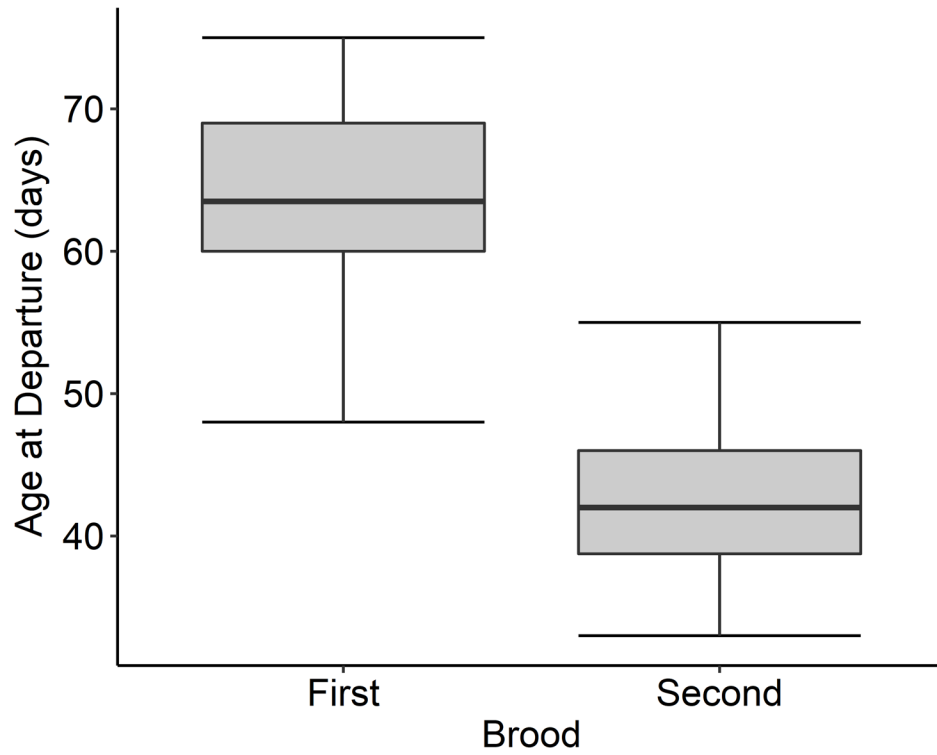
Figure 3-1. Box plots of the age of juvenile Barn Swallows at migratory departure across first and second broods in southern Ontario, Canada.
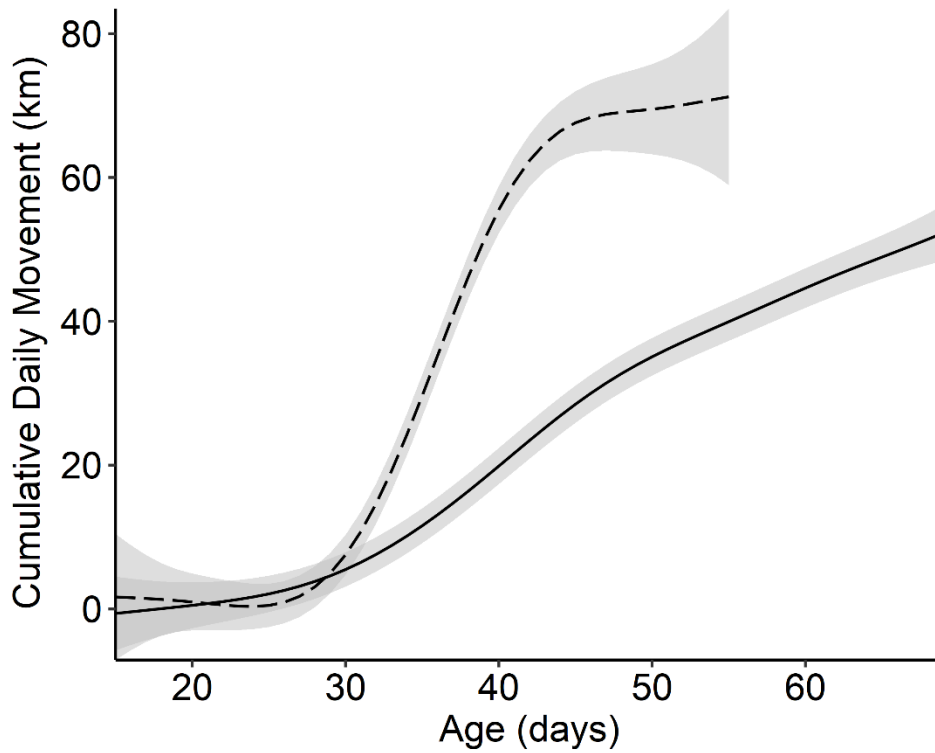
Figure 3-2. Predicted cumulative daily movement of first (solid line) and second (dashed line) brooded Barn Swallows as they age during the post-fledging period in southern Ontario, Canada.
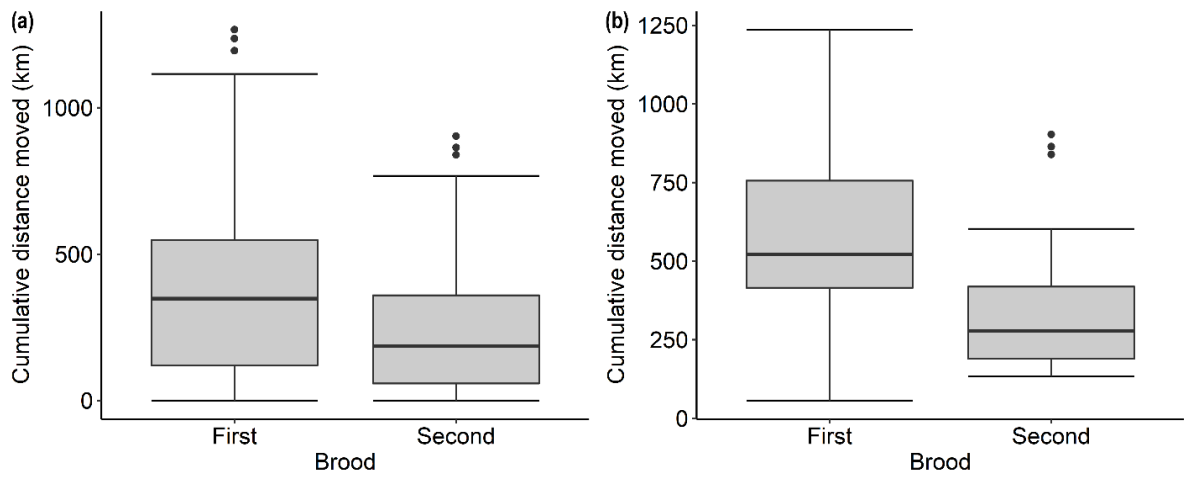
Figure 3-3. Box plots of cumulative distance travel during the post-fledging period of (a) all and (b) migrating juvenile Barn Swallows from first and second broods in southern Ontario, Canada.

Chapter 4

General Discussion

The post-fledging period is a critical life-history stage for juvenile migratory songbirds (Cox et al. 2014; Naef-Daenzer and Grüebler 2016). Existing research suggests that this period is perhaps the most important in terms of regulating population growth because of the high amount of juvenile mortality that occurs (Rush and Stutchbury 2008; Ausprey and Rodewald 2011; Vitz and Rodewald 2011). Furthermore, limited evidence to date also suggests that this period can be a time of great juvenile mobility (Morton 1991; Mitchell et al. 2010; Brown and Taylor 2015). Unfortunately, our knowledge of this life-history stage is largely incomplete due to the challenges of tracking individuals at large spatial scales (Anders et al. 1997; Rush and Stutchbury 2008). This means that previous research is missing survival estimates when juvenile songbirds are making potentially costly post-fledging movements. The goal of this thesis was to use a regional scale automated radio telemetry array (The Motus Wildlife Tracking System) to overcome previous spatial and temporal tracking limitations and, for the first time, provide insight into the post-fledging survival and movements of a juvenile songbird from fledging up until departure for fall migration. Specifically, I looked at how intrinsic factors such as brood, age, body condition, and sex can affect post-fledging survival and movement.

KEY FINDINGS

(a) Post-fledging survival and movements between broods

Later fledging broods (i.e. second broods) are much more time constrained on the breeding grounds and have less time to prepare for migration at a time when resources are potentially

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depleted or diminishing (Grüebler and Naef-Daenzer 2010; Raja-Aho et al. 2017). My results show that there are no apparent survival costs during the post-fledging period associated with being a juvenile from a second brood that fledge later in the season and migrate approximately 21 days younger. Furthermore, I show that although juveniles from second broods move less overall, they move considerably more per day compared to first broods. Taken together these results suggest that post-fledging movements are an important behaviour for juvenile Barn Swallows where birds from second broods attempt to compensate for their shorter post-fledging period by increasing their daily movements without any apparent survival costs prior to autumn migration. This is contrary to research on the post-fledging survival of Barn Swallows in Europe where there is a seasonal decline in apparent survival for second broods (Grüebler and Naef-Daenzer 2008a, 2010). However, given the spatial scale of these studies and my finding that second brooded juveniles are moving more per day, it is possible that the seasonal decline apparent survival of second broods is due to emigration rather than mortality. Furthermore, juvenile Barn Swallows from second broods have been shown to receive more parental care than individuals from first broods (Grüebler and Naef-Daenzer 2008b) and are in better condition after leaving the nest (Raja-Aho et al. 2017). Therefore, it is possible that greater parental care provides juveniles from later broods with the resources needed to increase their energy expenditure for post-fledging movements without incurring any additional survival costs. However, this possibly comes at a cost during other parts of the annual cycle because juvenile Barn Swallows from late broods still have lower rates of recruitment (Raja-Aho et al. 2017).

(b) Age effects on post-fledging survival and movement

For many species, newly fledged young are often flightless and have yet to reach full juvenile physical condition (Naef-Daenzer and Grüebler 2016). Therefore, as fledglings age they

continue to grow and develop key traits needed for locomotion (i.e. wing length and muscle growth; Jones et al. 2018). This makes juveniles extremely vulnerable during the beginning of the post-fledging period (Anders et al. 1997; Kershner et al. 2004; Ausprey and Rodewald 2011; Vitz and Rodewald 2011). Consistent with existing literature, apparent survival of juvenile Barn Swallows in this study was the lowest at the beginning of the post-fledging period and increased until they were approximately 30 days old. This also corresponded closely with cumulative daily movements where juveniles from first and second broods remained relatively immobile until about 30 days old. Although I was not able to track the termination of parental care in this study, empirical evidence suggests the parental care period of Barn Swallows lasts on average 10 days (Grüebler and Naef-Daenzer 2008b). Therefore, based on an average fledging age of 19.5 days old from my study population, the termination of parental care is expected to occur around 30 days old. Furthermore, the post-fledging independence period is often associated with juveniles leaving their natal areas and traveling widely (Grüebler et al. 2014; Brown and Taylor 2015; Dittmar et al. 2016). Juvenile Barn Swallows became highly mobile after reaching an age of 30 days old and daily cumulative movements continued to increase throughout the remainder of the post-fledging period, until about 45 days of age for second broods. At the same time when juveniles are becoming mobile, daily apparent survival decreased until about half way through the independence period. This decrease in daily survival could be associated with the costs of post-fledging movements such as high energy expenditure (Klaassen et al. 2000), increased exposure to predators (Cohen et al. 2012), and increased exposure to potential anthropogenic threats, such as collisions with buildings or towers (Machtans et al. 2013; Zimmerling et al. 2013). Ultimately, my results show the value of studying the post-fledging period in its entirety and that behaviour of juvenile Barn Swallows varies with age potentially exposing

juveniles to different factors that may influence their survival at different points during the post-fledging period.

(c) The importance of body condition for post-fledging survival and movement

Poor conditions experienced in the nest can have long lasting consequences that impact individual survival and performance throughout the annual cycle (Metcalfe and Monaghan 2001; Monaghan 2008; Mitchell et al. 2011). In this study I show that body condition in the nest is positively related to daily post-fledging apparent survival. However, body condition did not appear to influence either cumulative daily movement or cumulative movement. This might suggest that large scale post-fledging movements are independent of body condition, however, for individuals in worse condition this could come at a cost of lower survival as observed here. Individuals in poorer condition maybe less able to deal with adverse environmental conditions, may have to forage more and as a result experience greater exposure to predators, and possibly have lower immune function (Saino et al. 1997; Vitz and Rodewald 2011; Jones et al. 2017). This taken with the added costs of post-fledging movements could all be contributing to lower post-fledging survival for individuals in lower relative condition. This research adds to the growing literature that suggests that factors in the nest carry over to influence subsequent stages of the annual cycle (Naef-Daenzer et al. 2001; Vitz and Rodewald 2011).

(d) Sex effects on post-fledging survival and movement

Despite its importance, sex is often an ignored variable in studies of juvenile ecology due to the difficulties of sexing juvenile birds (Maness and Anderson 2013). In this study I found that there were no differences in survival and movement between male and female Barn Swallows. These results go hand in hand because if males and females had vastly different

behaviours during the post-fledging period we might also expect differences in survival. This is not to say that there are not different behaviours between sexes, however, these differences might not be able to be measured through movement at the scale of this study. Female Barn Swallows in Europe have greater natal dispersal than males (Balbontín et al. 2009) and therefore, if this behaviour is the same for North American populations we would expect females to move more during the post-fledging period if these movements are in part for the purpose of prospecting for future breeding sites. The absence of any differences could mean that perhaps there are no differences in male and female dispersal in North America, that post-fledging movements of juvenile Barn Swallows are not for the purpose of prospecting for future breeding sites, and/or that we could not detect any differences in movement between males and females at this scale.

CONSERVATION IMPLICATIONS

Barn Swallows were recently listed as threatened in Canada and are now protected under the Species at Risk Act (SC 2002, c 29). Thus, any research that provides insight into population regulation of this species in Canada should be invaluable to their conservation. This research shows that the post-fledging period is a critical period for Barn Swallows in Ontario and that high mortality (approximately 58%) during this period could be especially limiting to the population. Therefore, future conservation initiatives should focus on improving survival prospects of juveniles during this period. My research also suggests that factors in the nest that influence body condition could have important implications on the survival of juveniles during the post-fledging period. This means that future management plans could also focus on factors that influence body condition in the nest to improve overall survival prospects of juveniles during this critical life stage (Cox et al. 2014). Outside of species specific conservation implications, these results also show how invaluable Motus could be for

determining the survival of other threatened or at-risk species in Canada. In addition, Motus is not limited to just tracking birds, but other small flying species such as bats and insects (Taylor et al. 2017).

STUDY ASSUMPTIONS AND LIMITATIONS

The use of automated radio telemetry comes with some limitations. In the context of post-fledging survival, determining the timing of mortality is difficult during the parental care stage. Juveniles are often largely immobile during the parental care period and are often not detected until they become more mobile such as during independence. Although I purposely arranged receiving towers in such a way to optimize detection, an ideal situation would be to have a receiving tower at each natal site and full spatial coverage. Another limitation of using automated radio telemetry is that mortality can often be confounded with tag loss or tag death. As a part of another ongoing project, I observed no tag loss prior to radio death from radio tagged adult Barn Swallows that were recaptured on a weekly basis for a duration of three months in 2017 (Appendix A). I used the same methods for attaching transmitters to juveniles and adults, therefore I believe tag loss would be extremely low for juveniles as well. In terms of radio death, radio tags I used had a rated battery life of approximately 58 days which is close to the duration of tracking in my study (56 days). It is possible some tags died prematurely, however, daily apparent survival reached 100% by the end of tracking in both years and this is when I would expect tags to start dying early. Furthermore, as with any radio telemetry study, there is the chance that radio tagged individuals may incur lower survival. However, my radio tags only weighed 0.43g which is lighter than the radio tags used by (Naef-Daenzer and Grüebler 2014) which found no adverse effects of their radio tags on juvenile Barn Swallows in Europe. Lastly, mortality is often confounded with emigration which results in negatively biased apparent survival

estimates (Lebreton et al. 1992). Here I accounted for a large portion of emigration by taking into account migratory individuals. It is possible that some individuals made it out of Ontario without getting detected but with the high number of towers within the Motus array in southern Ontario (>80 towers) I believe this would be rare.

In the context of post-fledging movements, the use of automated telemetry is also limited in some ways. Locational accuracy is a limitation as radio tagged birds can be detected at a distance up to 15 km away (Taylor et al. 2017). This means that the exact location of an individual cannot be ascertained with automated radio telemetry at this point in time. Therefore, calculating daily cumulative movements and total cumulative movement is just as estimate or index for how much juvenile Barn Swallows are moving. Furthermore, based on this scale of detection, fine scale movements such as foraging are likely not detected and thus estimated movements represent a minimum amount of movement or are better characterized as cumulative amount of landscape level movements. Lastly, based on the unequal density and spatial extent of the Motus array there are areas in southern Ontario in which juveniles would be less likely to be detected and this could reduce the amount of estimated movement, however, there is no reason to expect that birds with different life-history characteristics (e.g., sex, brood, etc.) are more or less likely to move to these areas in the array.

FUTURE DIRECTIONS

There are numerous directions future research should consider in order to get a full picture of Barn Swallow post-fledging survival. Firstly, understanding the major causes of mortality for juveniles during the post-fledging period would be an important next step and provide valuable information for Barn Swallow conservation. Additionally, identifying key habitat

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used by juveniles throughout the post-fledging period would be another valuable next step. Many studies to date have looked at habitat associations of songbirds at the beginning of the post-fledging period (Anders et al. 1998; Berkeley et al. 2007; Ausprey and Rodewald 2011), however, there is little to no information on habitat use after juveniles become independent and travel widely. Lastly, other parts of the annual cycle need to be investigated to successfully pinpoint the timing of population limitation in Barn Swallows. Although the high mortality of juveniles observed in this study provides evidence that the post-fledging period is likely the most important bottleneck, without estimates from the other parts of the annual cycle one cannot say for certain.

CONCLUSIONS

In conclusion, this research represents an important advance in the understanding of the post-fledging ecology of migratory songbirds. A key post-fledging review by Cox et al. (2014) argues that only the first three weeks of the post-fledging period should be examined for species management, however, my results might suggest otherwise. Approximately one third to one half of the estimated post-fledging mortality of juvenile Barn Swallows observed in our study occurred outside of this three-week window suggesting the post-fledging independence period is also important in terms of survival. This is also when all of the post-fledging movements occur as juveniles are rather immobile during the parental car stage. Taken together, I believe the entire post-fledging period should be investigated when logistically possible. Ultimately, this research shows the value of automated radio telemetry and hopefully it will prove invaluable for future investigations of not only post-fledging survival, but other life-history stages across other bird species and taxa.

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Appendices

APPENDIX A: TAG RETENTION IN ADULT BARN SWALLOWS

As a part of another study on the same population of Barn Swallows we radio tagged 37 adults at four different colonies prior to the breeding season. To determine if tags are lost prior to expected batter failure (~58 days) we made repeated visits throughout the breeding season in attempt to recapture tagged individuals and determine the length of tag retention. All individuals were banded using eight digit aluminum bands so if a tag was lost we could still identify individuals. Out of these 37 adults 20 were recaptured at least once again (Table A1). The average minimum tag retention was 63.25±4.70(SE) days which is higher than the expected battery length. Only one tag (319) was recorded to be lost, however, this was after being retained 78 days.

Table A1. Tag retention results for each radio tagged adult Barn Swallow (tag) showing the minimum number of days a radio tag was retained, the number of times a bird was re-caught, and if a tag was ever recorded to be lost.

Tag	Minimum Tag	Times Re-caught	Tag Lost
282	0	0	N
283	34	2	N
284	0	0	N
285	72	2	N
286	72	2	N
287	0	0	N
288	0	0	N
289	0	0	N
290	27	1	N
291	0	0	N
292	0	0	N

293	0	0	N
294	64	4	N
295	0	0	N
296	0	0	N
297	78	6	N
298	0	0	N
299	0	0	N
300	0	0	N
302	78	4	N
303	71	2	N
305	83	2	N
306	110	3	N
307	0	0	N
309	56	2	N
311	71	1	N
312	48	1	N
313	33	2	N
314	0	0	N
315	0	0	N
317	64	1	N
318	56	1	N
319	78	1	Y
321	28	3	N
322	0	0	N
323	78	3	N
324	64	5	N

To estimate the age of nestlings banded in Norfolk County in 2016 we used a regression of the known ages and wing lengths (Age ~ Wing Length) from nestlings banding in Wellington county in 2016 to predict the age of Norfolk County birds. The results of this regression are provided here ($R^2 = 0.2529$; Table B1 and figure B1).

Table B1. Linear model results from the linear model of Age ~ Wing Length used to predict the age of Norfolk County nestlings in 2016.

coefficient	estimate	standard error	t-value	p-value
Intercept	10.736	0.331	32.44	$< 2 \times 10^{-16}$
Wing	0.056	0.004	12.66	$< 2 \times 10^{-16}$
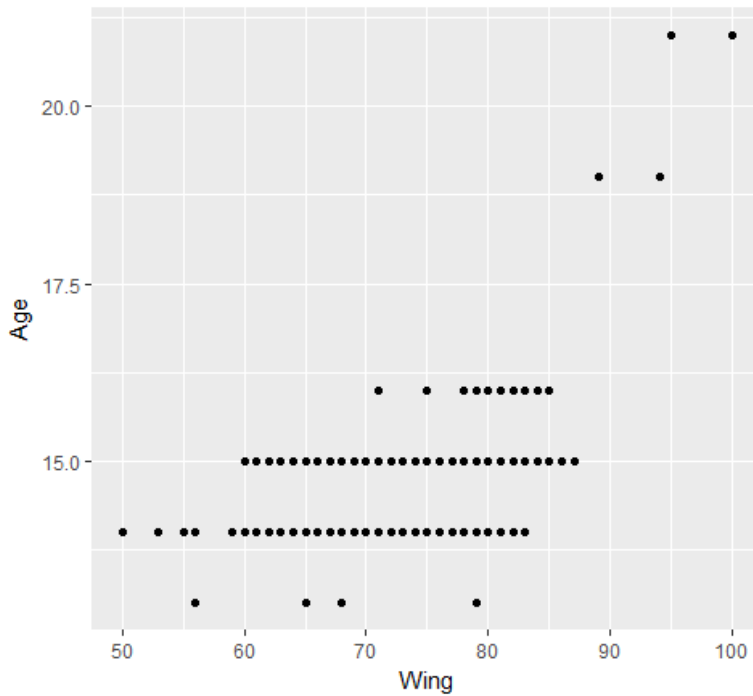
Figure B1. Relationship between nestling age and wing length used to predict the age of Norfolk County birds.

APPENDIX C: CREATING ENCOUNTER HISTORIES FROM MOTUS DATA

An encounter history is a record of whether an individual was 'captured' or not during a given sampling period and in more complex cases such as ours what state that individual was captured in. We used two states for our analysis: a local state 'L' for individuals encountered within the Motus array and a migratory state 'M' for individuals encountered at the southern edge of the array and assumed to subsequently migrate out of the Motus array. When an individual was not captured it is recorded as a '0.' Our sampling design for a robust design multistate model consisted of daily primary periods, in which apparent survival and migration probability was estimated, and six secondary periods within each primary period, in which recapture probability was estimated. We constrained our study length to 56 d which equates to a total 336 total secondary sampling periods per individual. Encounter histories were done on a per bird and per day basis by visualizing daily Motus data (figure C1). All data was stored within an excel document which could then be analyzed and manipulated in R for analysis with RMark.
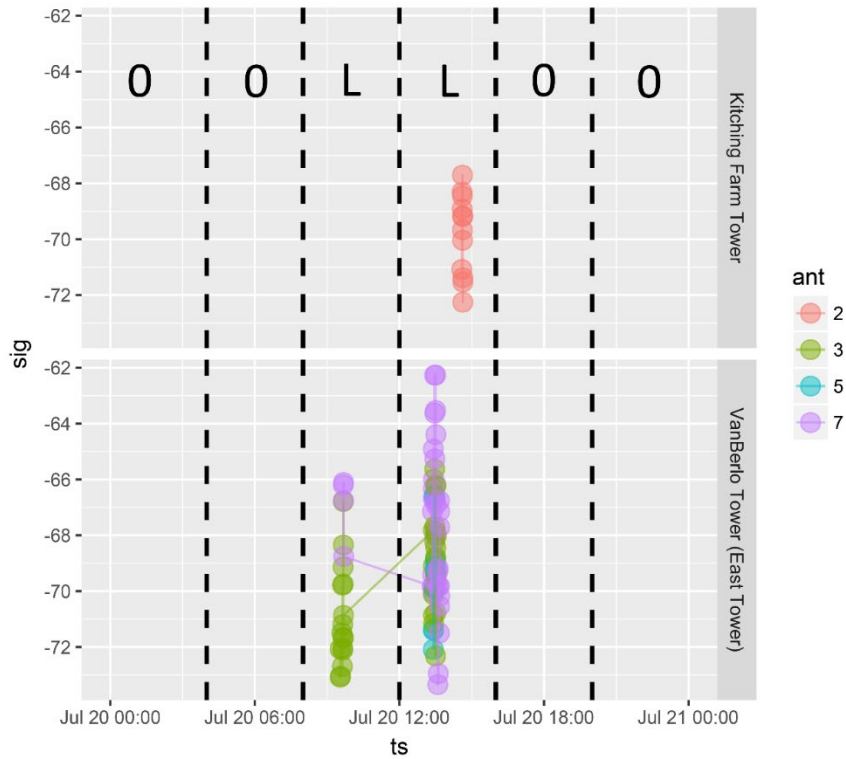
Figure C1. Visualization and creation of encounter history from Motus data. This visualization represents a single day (July 20, 2016) for a single bird (Tag 111) where it was encountered in the third and fourth secondary periods. Colors represent which antenna the bird was detected on for that given tower.

Table D1. Summary of model selection results for recapture probability of juvenile post-fledging Barn Swallows in southern Ontario in 2016. Model covariates include five different relationships with age: a linear trend (A), a second order polynomial trend (A + A^2), a third order polynomial trend (A + A^2 + A^3), a weekly age class trend (A$_1$), and a weekly age class trend for the first two weeks and the last four weeks together (A$_2$). Each age relationship was examined on its own and with the additive effect of Brood. Migration probability and apparent survival were held constant across all models. Every model also included Time and Location allowing recapture to vary across secondary periods and across the two different study areas with different tower densities.

Model	ΔAIC_c	AIC_c	k	w_i	deviance
$\Phi_{(.)} \Psi_{(.)} p_{(A+A^2+A^3+Time+Location+Brood)}$	0.00	19487.64	13	1.00	19461.55
$\Phi_{(.)} \Psi_{(.)} p_{(A_1+Time+Location+Brood)}$	29.69	19517.32	17	0.00	19483.18
$\Phi_{(.)} \Psi_{(.)} p_{(A_2+Time+Location+Brood)}$	37.88	19525.52	12	0.00	19501.44
$\Phi_{(.)} \Psi_{(.)} p_{(A+A^2+A^3+Time+Location)}$	55.15	19542.79	12	0.00	19518.71
$\Phi_{(.)} \Psi_{(.)} p_{(A_1+Time+Location)}$	88.13	19575.77	16	0.00	19543.64
$\Phi_{(.)} \Psi_{(.)} p_{(A+A^2+Time+Location+Brood)}$	104.19	19591.83	12	0.00	19567.75
$\Phi_{(.)} \Psi_{(.)} p_{(A_2+Time+Location)}$	105.96	19593.60	11	0.00	19571.54
$\Phi_{(.)} \Psi_{(.)} p_{(A+A^2+Time+Location)}$	166.70	19654.34	11	0.00	19632.27
$\Phi_{(.)} \Psi_{(.)} p_{(A+Time+Location+Brood)}$	213.39	19701.02	11	0.00	19678.96
$\Phi_{(.)} \Psi_{(.)} p_{(A+Time+Location)}$	297.00	19784.64	10	0.00	19764.58

Table D2. Summary of model selection results for recapture probability of juvenile post-fledging Barn Swallows in southern Ontario in 2017. Model covariates include five different relationships with age: a linear trend (A), a second order polynomial trend ($A + A^2$), a third order polynomial trend ($A + A^2 + A^3$), a weekly age class trend (A_1), and a weekly age class trend for the first two weeks and the last four weeks together (A_2). Each age relationship was examined on its own and with the additive effect of covariates brood and sex, individually and together. Migration probability and apparent survival were held constant across all models.

Model	ΔAIC_c	AIC_c	k	w_i	deviance
$\Phi_{(.)}\ \Psi_{(.)}\ p_{(A_1+Time+Brood+Sex)}$	0.00	17325.22	17	1.00	17291.08
$\Phi_{(.)}\ \Psi_{(.)}\ p_{(A_1+Time+Sex)}$	25.86	17351.08	16	0.00	17318.95
$\Phi_{(.)}\ \Psi_{(.)}\ p_{(A+A^2+A^3+Time+Brood+Sex)}$	34.92	17360.14	13	0.00	17334.06
$\Phi_{(.)}\ \Psi_{(.)}\ p_{(A+A^2+A^3+Time+Sex)}$	61.49	17386.71	12	0.00	17362.64
$\Phi_{(.)}\ \Psi_{(.)}\ p_{(A_1+Time+Brood)}$	71.19	17396.41	16	0.00	17364.28
$\Phi_{(.)}\ \Psi_{(.)}\ p_{(A_1+Time)}$	99.88	17425.11	15	0.00	17394.99
$\Phi_{(.)}\ \Psi_{(.)}\ p_{(A+A^2+A^3+Time + Brood)}$	105.11	17430.34	12	0.00	17406.26
$\Phi_{(.)}\ \Psi_{(.)}\ p_{(A+A^2+A^3+Time)}$	134.93	17460.15	11	0.00	17438.09
$\Phi_{(.)}\ \Psi_{(.)}\ p_{(A_2+Time+Sex)}$	223.56	17548.78	11	0.00	17526.72
$\Phi_{(.)}\ \Psi_{(.)}\ p_{(A_2+Time+Brood+Sex)}$	224.54	17549.77	12	0.00	17525.69
$\Phi_{(.)}\ \Psi_{(.)}\ p_{(A_2+Time+Brood)}$	287.21	17612.43	11	0.00	17590.37
$\Phi_{(.)}\ \Psi_{(.)}\ p_{(A_2+Time)}$	287.30	17612.52	10	0.00	17592.47
$\Phi_{(.)}\ \Psi_{(.)}\ p_{(A+A^2+Time+Brood+Sex)}$	289.21	17614.43	12	0.00	17590.36
$\Phi_{(.)}\ \Psi_{(.)}\ p_{(A+A^2+Time+Sex)}$	297.64	17622.86	11	0.00	17600.80
$\Phi_{(.)}\ \Psi_{(.)}\ p_{(A+A^2+Time+Brood)}$	356.57	17681.79	11	0.00	17659.73
$\Phi_{(.)}\ \Psi_{(.)}\ p_{(A+A^2+Time)}$	366.88	17692.10	10	0.00	17672.05
$\Phi_{(.)}\ \Psi_{(.)}\ p_{(A+Time +Brood+Sex)}$	391.04	17716.26	11	0.00	17694.20
$\Phi_{(.)}\ \Psi_{(.)}\ p_{(A+Time+Sex)}$	395.50	17720.72	10	0.00	17700.67
$\Phi_{(.)}\ \Psi_{(.)}\ p_{(A+Time+Brood)}$	450.16	17775.39	10	0.00	17755.33
$\Phi_{(.)}\ \Psi_{(.)}\ p_{(A+Time)}$	456.03	17781.25	9	0.00	17763.21

Table D3. Summary of model selection results for migration probability of juvenile post-fledging Barn Swallows in southern Ontario in 2016. Model covariates include five different relationships with age: a linear trend (A), a second order polynomial trend (A + A2), a third order polynomial trend (A + A2 + A3), a weekly age class trend (A1), and a weekly age class trend for the first two weeks and the last four weeks together (A2). Each age relationship was examined on its own and with the additive effect of brood. Apparent survival was held constant across all models.

Model	ΔAIC_c	AIC_c	k	w_i	deviance
$\Phi_{(.)}\ \psi_{(A+A^2+Brood)}\ p_{(A+A^2+A^3+Time+Location+Brood)}$	0.00	19347.60	16	0.36	19315.47
$\Phi_{(.)}\ \psi_{(A+Brood)}\ p_{(A+A^2+A^3+Time+Location+Brood)}$	0.14	19347.73	15	0.34	19317.62
$\Phi_{(.)}\ \psi_{(A+A^2+A^3+Brood)}\ p_{(A+A^2+A^3+Time+Location+Brood)}$	0.40	19348.00	17	0.30	19313.85
$\Phi_{(.)}\ \psi_{(A_1+Brood)}\ p_{(A+A^2+A^3+Time+Location+Brood)}$	16.94	19364.54	21	0.00	19322.32
$\Phi_{(.)}\ \psi_{(A+A^2+A^3)}\ p_{(A+A^2+A^3+Time+Location+Brood)}$	50.74	19398.34	16	0.00	19366.21
$\Phi_{(.)}\ \psi_{(A+A^2)}\ p_{(A+A^2+A^3+Time+Location+Brood)}$	59.03	19406.62	15	0.00	19376.51
$\Phi_{(.)}\ \psi_{(A)}\ p_{(A+A^2+A^3+Time+Location+Brood)}$	59.23	19406.83	14	0.00	19378.73
$\Phi_{(.)}\ \psi_{(A_1)}\ p_{(A+A^2+A^3+Time+Location+Brood)}$	66.00	19413.59	20	0.00	19373.40
$\Phi_{(.)}\ \psi_{(A_2+Brood)}\ p_{(A+A^2+A^3+Time+Location+Brood)}$	110.46	19458.05	16	0.00	19425.92
$\Phi_{(.)}\ \psi_{(A_2)}\ p_{(A+A^2+A^3+Time+Location+Brood)}$	117.16	19464.75	15	0.00	19434.64

Table D4. Summary of model selection results for migration probability of juvenile post-fledging Barn Swallows in southern Ontario in 2017. Model covariates include five different relationships with age: a linear trend (A), a second order polynomial trend (A + A2), a third order polynomial trend (A + A2 + A3), a weekly age class trend (A1), and a weekly age class trend for the first two weeks and the last four weeks together (A2). Each age relationship was examined on its own and with the additive effect of brood. Apparent survival was held constant across all models.

Model	ΔAIC_c	AIC_c	k	w_i	deviance
$\Phi_{(.)} \psi_{(A+A^2+Brood)} p_{(A_1+Time+Brood+Sex)}$	0.00	17198.25	20	0.34	17158.05
$\Phi_{(.)} \psi_{(A+A^2+A^3+Brood)} p_{(A_1+Time+Brood+Sex)}$	0.76	17199.01	21	0.23	17156.79
$\Phi_{(.)} \psi_{(A+Brood)} p_{(A_1+Time+Brood+Sex)}$	1.73	17199.98	19	0.14	17161.79
$\Phi_{(.)} \psi_{(A+A^2+Brood+Sex)} p_{(A_1+Time+Brood+Sex)}$	1.85	17200.10	21	0.13	17157.88
$\Phi_{(.)} \psi_{(A+A^2+A^3+Brood+Sex)} p_{(A_1+Time+Brood+Sex)}$	2.61	17200.86	22	0.09	17156.62
$\Phi_{(.)} \psi_{(A+Brood+Sex)} p_{(A_1+Time+Brood+Sex)}$	3.50	17201.75	20	0.06	17161.55
$\Phi_{(.)} \psi_{(A_1+Brood)} p_{(A_1+Time+Brood+Sex)}$	20.31	17218.56	25	0.00	17168.25
$\Phi_{(.)} \psi_{(A_1+Brood+Sex)} p_{(A_1+Time+Brood+Sex)}$	22.20	17220.45	26	0.00	17168.11
$\Phi_{(.)} \psi_{(A_2+Brood)} p_{(A_1+Time+Brood+Sex)}$	68.81	17267.06	20	0.00	17226.85
$\Phi_{(.)} \psi_{(A_2+Brood+Sex)} p_{(A_1+Time+Brood+Sex)}$	70.82	17269.07	21	0.00	17226.84
$\Phi_{(.)} \psi_{(A+A^2+A^3)} p_{(A_1+Time+Brood+Sex)}$	75.08	17273.33	20	0.00	17233.13
$\Phi_{(.)} \psi_{(A+A^2+A^3+Sex)} p_{(A_1+Time+Brood+Sex)}$	76.07	17274.32	21	0.00	17232.10
$\Phi_{(.)} \psi_{(A_1)} p_{(A_1+Time+Brood+Sex)}$	83.43	17281.68	24	0.00	17233.39
$\Phi_{(.)} \psi_{(A_1+Sex)} p_{(A_1+Time+Brood+Sex)}$	84.58	17282.83	25	0.00	17232.51
$\Phi_{(.)} \psi_{(A_2)} p_{(A_1+Time+Brood+Sex)}$	96.53	17294.78	19	0.00	17256.60
$\Phi_{(.)} \psi_{(A_2+Sex)} p_{(A_1+Time+Brood+Sex)}$	97.78	17296.03	19	0.00	17257.85
$\Phi_{(.)} \psi_{(A+A^2)} p_{(A_1+Time+Brood+Sex)}$	98.17	17296.42	20	0.00	17256.21
$\Phi_{(.)} \psi_{(A+A^2+Sex)} p_{(A_1+Time+Brood+Sex)}$	99.06	17297.31	20	0.00	17257.11
$\Phi_{(.)} \psi_{(A)} p_{(A_1+Time+Brood+Sex)}$	102.12	17300.37	18	0.00	17264.20
$\Phi_{(.)} \psi_{(A+Sex)} p_{(A_1+Time+Brood+Sex)}$	103.26	17301.51	19	0.00	17263.33

Table D5. Summary of model selection results for apparent survival of juvenile post-fledging Barn Swallows in southern Ontario in 2016. Model covariates include five different relationships with age: a linear trend (A), a second order polynomial trend ($A + A^2$), a third order polynomial trend ($A + A^2 + A^3$), a weekly age class trend (A_1), and a weekly age class trend for the first two weeks and the last four weeks together (A_2). Each age relationship was examined on its own and with the additive effect of covariates brood and condition.

Model	ΔAIC_c	AIC_c	k	w_i	deviance
$\Phi_{(A+A^2+A^3+Condition)}\ \Psi_{(A+A^2+Brood)}\ p_{(A+A^2+A^3+Time+Location+Brood)}$	0.00	19333.37	20	0.56	19293.17
$\Phi_{(A+A^2+A^3+Condition+Brood)}\ \Psi_{(A+A^2+Brood)}$ $p_{(A+A^2+A^3+Time+Location+Brood)}$	1.62	19335.00	21	0.25	19292.78
$\Phi_{(A+A^2+A^3)}\ \Psi_{(A+A^2+Brood)}\ p_{(A+A^2+A^3+Time+Location+Brood)}$	3.80	19337.17	19	0.08	19298.99
$\Phi_{(A+A^2+A^3+Brood)}\ \Psi_{(A+A^2+Brood)}\ p_{(A+A^2+A^3+Time+Location+Brood)}$	5.26	19338.63	20	0.04	19298.43
$\Phi_{(A+A^2+Condition)}\ \Psi_{(A+A^2+Brood)}\ p_{(A+A^2+A^3+Time+Location+Brood)}$	6.94	19340.32	19	0.02	19302.14
$\Phi_{(A+Condition)}\ \Psi_{(A+A^2+Brood)}\ p_{(A+A^2+A^3+Time+Location+Brood)}$	7.45	19340.82	18	0.01	19304.66
$\Phi_{(A_2+Condition)}\ \Psi_{(A+A^2+Brood)}\ p_{(A+A^2+A^3+Time+Location+Brood)}$	7.51	19340.88	20	0.01	19300.68
$\Phi_{(A+A^2+Condition+Brood)}\ \Psi_{(A+A^2+Brood)}\ p_{(A+A^2+A^3+Time+Location+Brood)}$	8.68	19342.05	20	0.01	19301.85
$\Phi_{(A_2+Condition+Brood)}\ \Psi_{(A+A^2+Brood)}\ p_{(A+A^2+A^3+Time+Location+Brood)}$	9.21	19342.59	21	0.01	19300.37
$\Phi_{(A_1+Condition)}\ \Psi_{(A+A^2+Brood)}\ p_{(A+A^2+A^3+Time+Location+Brood)}$	10.17	19343.54	25	0.00	19293.23
$\Phi_{(A+A^2)}\ \Psi_{(A+A^2+Brood)}\ p_{(A+A^2+A^3+Time+Location+Brood)}$	10.75	19344.12	18	0.00	19307.96
$\Phi_{(A)}\ \Psi_{(A+A^2+Brood)}\ p_{(A+A^2+A^3+Time+Location+Brood)}$	11.03	19344.40	17	0.00	19310.26
$\Phi_{(A+Condition+Brood)}\ \Psi_{(A+A^2+Brood)}\ p_{(A+A^2+A^3+Time+Location+Brood)}$	11.27	19344.64	20	0.00	19304.44
$\Phi_{(A_2)}\ \Psi_{(A+A^2+Brood)}\ p_{(A+A^2+A^3+Time+Location+Brood)}$	11.40	19344.77	19	0.00	19306.60
$\Phi_{(A_1+Condition+Brood)}\ \Psi_{(A+A^2+Brood)}\ p_{(A+A^2+A^3+Time+Location+Brood)}$	11.73	19345.10	26	0.00	19292.77
$\Phi_{(A+A^2+Brood)}\ \Psi_{(A+A^2+Brood)}\ p_{(A+A^2+A^3+Time+Location+Brood)}$	12.39	19345.76	19	0.00	19307.58
$\Phi_{(A+Brood)}\ \Psi_{(A+A^2+Brood)}\ p_{(A+A^2+A^3+Time+Location+Brood)}$	12.76	19346.13	18	0.00	19309.97
$\Phi_{(A_2+Brood)}\ \Psi_{(A+A^2+Brood)}\ p_{(A+A^2+A^3+Time+Location+Brood)}$	12.97	19346.34	20	0.00	19306.14
$\Phi_{(A_1)}\ \Psi_{(A+A^2+Brood)}\ p_{(A+A^2+A^3+Time+Location+Brood)}$	13.65	19347.03	24	0.00	19298.74
$\Phi_{(A_1+Brood)}\ \Psi_{(A+A^2+Brood)}\ p_{(A+A^2+A^3+Time+Location+Brood)}$	15.08	19348.45	25	0.00	19298.14

Table D6. Summary of model selection results for apparent survival of juvenile post-fledging Barn Swallows in southern Ontario in 2017. Model covariates include five different relationships with age: a linear trend (A), a second order polynomial trend (A + A^2), a third order polynomial trend (A + A^2 + A^3), a weekly age class trend (A$_1$), and a weekly age class trend for the first two weeks and the last four weeks together (A$_2$). Each age relationship was examined on its own and with the additive effect of covariates brood, sex, and condition.

| Model	ΔAIC$_c$	AIC$_c$	k	w_i	deviance
$\Phi_{(A+A^2+A^3+Condition)}\ \Psi_{(A+A^2+Brood)}\ p_{(A_1+Time+Brood+Sex)}$	0.00	17178.86	24	0.39	17130.57
$\Phi_{(A+A^2+A^3+Condition+Sex)}\ \Psi_{(A+A^2+Brood)}\ p_{(A_1+Time+Brood+Sex)}$	1.76	17180.62	25	0.16	17130.31
$\Phi_{(A+A^2+A^3+Condition+Brood)}\ \Psi_{(A+A^2+Brood)}\ p_{(A_1+Time+Brood+Sex)}$	1.96	17180.83	25	0.15	17130.51
$\Phi_{(A+A^2+A^3+Condition+Brood+Sex)}\ \Psi_{(A+A^2+Brood)}$ $p_{(A_1+Time+Brood+Sex)}$	3.73	17182.59	26	0.06	17130.25
$\Phi_{(A+A^2+Condition)}\ \Psi_{(A+A^2+Brood)}\ p_{(A_1+Time+Brood+Sex)}$	4.49	17183.35	23	0.04	17137.08
$\Phi_{(A+A^2+A^3)}\ \Psi_{(A+A^2+Brood)}\ p_{(A_1+Time+Brood+Sex)}$	4.66	17183.52	23	0.04	17137.26
$\Phi_{(A_2+Condition)}\ \Psi_{(A+A^2+Brood)}\ p_{(A_1+Time+Brood+Sex)}$	5.65	17184.51	24	0.02	17136.22
$\Phi_{(A+Condition)}\ \Psi_{(A+A^2+Brood)}\ p_{(A_1+Time+Brood+Sex)}$	5.92	17184.78	22	0.02	17140.54
$\Phi_{(A+A^2+Condition+Sex)}\ \Psi_{(A+A^2+Brood)}\ p_{(A_1+Time+Brood+Sex)}$	6.12	17184.99	24	0.02	17136.70
$\Phi_{(A+A^2+Condition+Brood)}\ \Psi_{(A+A^2+Brood)}\ p_{(A_1+Time+Brood+Sex)}$	6.51	17185.37	24	0.01	17137.08
$\Phi_{(A+A^2+A^3+Brood)}\ \Psi_{(A+A^2+Brood)}\ p_{(A_1+Time+Brood+Sex)}$	6.51	17185.38	24	0.01	17137.09
$\Phi_{(A+A^2+A^3+Sex)}\ \Psi_{(A+A^2+Brood)}\ p_{(A_1+Time+Brood+Sex)}$	6.53	17185.39	24	0.01	17137.10
$\Phi_{(A_2+Condition+Sex)}\ \Psi_{(A+A^2+Brood)}\ p_{(A_1+Time+Brood+Sex)}$	7.33	17186.19	25	0.01	17135.88
$\Phi_{(A_2+Condition+Brood)}\ \Psi_{(A+A^2+Brood)}\ p_{(A_1+Time+Brood+Sex)}$	7.50	17186.36	25	0.01	17136.04
$\Phi_{(A+A^2+Condition+Brood+Sex)}\ \Psi_{(A+A^2+Brood)}\ p_{(A_1+Time+Brood+Sex)}$	8.15	17187.01	25	0.01	17136.69
$\Phi_{(A+A^2+A^3+Brood+Sex)}\ \Psi_{(A+A^2+Brood)}\ p_{(A_1+Time+Brood+Sex)}$	8.37	17187.24	25	0.01	17136.92
$\Phi_{(A_2+Condition+Brood+Sex)}\ \Psi_{(A+A^2+Brood)}\ p_{(A_1+Time+Brood+Sex)}$	9.17	17188.03	26	0.00	17135.70
$\Phi_{(A+A^2)}\ \Psi_{(A+A^2+Brood)}\ p_{(A_1+Time+Brood+Sex)}$	9.35	17188.21	22	0.00	17143.97
$\Phi_{(A+Condition+Brood+Sex)}\ \Psi_{(A+A^2+Brood)}\ p_{(A_1+Time+Brood+Sex)}$	9.41	17188.28	24	0.00	17139.99
$\Phi_{(A+Condition+Sex)}\ \Psi_{(A+A^2+Brood)}\ p_{(A_1+Time+Brood+Sex)}$	9.42	17188.28	24	0.00	17139.99
$\Phi_{(A+Condition+Brood)}\ \Psi_{(A+A^2+Brood)}\ p_{(A_1+Time+Brood+Sex)}$	9.96	17188.82	24	0.00	17140.53
$\Phi_{(A_2)}\ \Psi_{(A+A^2+Brood)}\ p_{(A_1+Time+Brood+Sex)}$	10.56	17189.42	23	0.00	17143.15
$\Phi_{(A+A^2+Brood)}\ \Psi_{(A+A^2+Brood)}\ p_{(A_1+Time+Brood+Sex)}$	11.07	17189.93	23	0.00	17143.66

$\Phi_{(A+A^2+Sex)}$ $\psi_{(A+A^2+Brood)}$ $p_{(A_1+Time+Brood+Sex)}$	11.19	17190.05	23	0.00	17143.79
$\Phi_{(A)}$ $\psi_{(A+A^2+Brood)}$ $p_{(A_1+Time+Brood+Sex)}$	11.21	17190.07	21	0.00	17147.85
$\Phi_{(A_1+Condition)}$ $\psi_{(A+A^2+Brood)}$ $p_{(A_1+Time+Brood+Sex)}$	11.54	17190.41	29	0.00	17131.99
$\Phi_{(A_2+Sex)}$ $\psi_{(A+A^2+Brood)}$ $p_{(A_1+Time+Brood+Sex)}$	12.41	17191.27	24	0.00	17142.98
$\Phi_{(A_2+Brood)}$ $\psi_{(A+A^2+Brood)}$ $p_{(A_1+Time+Brood+Sex)}$	12.54	17191.41	24	0.00	17143.12
$\Phi_{(A+Brood)}$ $\psi_{(A+A^2+Brood)}$ $p_{(A_1+Time+Brood+Sex)}$	12.77	17191.64	22	0.00	17147.39
$\Phi_{(A+A^2+Brood+Sex)}$ $\psi_{(A+A^2+Brood)}$ $p_{(A_1+Time+Brood+Sex)}$	12.90	17191.76	24	0.00	17143.47
$\Phi_{(A+Sex)}$ $\psi_{(A+A^2+Brood)}$ $p_{(A_1+Time+Brood+Sex)}$	12.93	17191.79	22	0.00	17147.55
$\Phi_{(A_1+Condition+Sex)}$ $\psi_{(A+A^2+Brood)}$ $p_{(A_1+Time+Brood+Sex)}$	13.34	17192.20	30	0.00	17131.76
$\Phi_{(A_1+Condition+Brood)}$ $\psi_{(A+A^2+Brood)}$ $p_{(A_1+Time+Brood+Sex)}$	13.48	17192.35	30	0.00	17131.90
$\Phi_{(A_2+Brood+Sex)}$ $\psi_{(A+A^2+Brood)}$ $p_{(A_1+Time+Brood+Sex)}$	14.40	17193.26	25	0.00	17142.95
$\Phi_{(A+Brood+Sex)}$ $\psi_{(A+A^2+Brood)}$ $p_{(A_1+Time+Brood+Sex)}$	14.48	17193.35	23	0.00	17147.08
$\Phi_{(A_1+Condition+Brood+Sex)}$ $\psi_{(A+A^2+Brood)}$ $p_{(A_1+Time+Brood+Sex)}$	15.28	17194.14	31	0.00	17131.66
$\Phi_{(A_1)}$ $\psi_{(A+A^2+Brood)}$ $p_{(A_1+Time+Brood+Sex)}$	16.66	17195.52	28	0.00	17139.13
$\Phi_{(A_1+Brood)}$ $\psi_{(A+A^2+Brood)}$ $p_{(A_1+Time+Brood+Sex)}$	18.57	17197.44	29	0.00	17139.02
$\Phi_{(A_1+Sex)}$ $\psi_{(A+A^2+Brood)}$ $p_{(A_1+Time+Brood+Sex)}$	18.60	17197.46	29	0.00	17139.04
$\Phi_{(A_1+Brood+Sex)}$ $\psi_{(A+A^2+Brood)}$ $p_{(A_1+Time+Brood+Sex)}$	20.51	17199.37	30	0.00	17138.92

Table D7. Results from the top Huggins closed robust design multi-state model for 2016 and 2017 post-fledging juvenile Barn Swallows for survival (Φ), migration (Ψ), and recapture probabilities (p). Beta estimates (β), standard error (SE), and 95% confidence intervals (95% CI) are on the logit scale.

parameter	2016			2017		
	β	SE	95% CI	β	SE	95% CI
Φ Intercept	2.6432	0.3048	2.0457, 3.2407	2.2272	0.3685	1.5049, 2.9495
Φ Age	0.3035	0.0867	0.1336, 0.4734	0.3989	0.1102	0.1829, 0.6149
Φ Age^2	-0.0152	0.0053	-0.0255, -0.0049	-0.0222	0.0075	-0.0370, -0.0074
Φ Age^3	0.0002	0.0001	0.0000, 0.0004	0.0004	0.0001	0.0001, 0.0006
Φ Condition	0.2115	0.0865	0.0419, 0.3810	0.2501	0.0941	0.0657, 0.4344
Ψ Intercept	15.4577	2.7323	10.102, 20.813	16.0817	1.9263	12.306, 19.857
Ψ Age	-0.3876	0.1379	-0.6579, -0.1173	-0.4007	0.0990	-0.5947, -0.2067
Ψ Age^2	0.0023	0.0018	-0.0012, 0.0058	0.0025	0.0014	-0.0003, 0.0053
Ψ Brood Two	-3.8076	0.5631	-4.9112, -2.7040	-6.0433	0.8363	-7.6826, -4.4041
p Intercept	-3.5518	0.1069	-3.7614, -3.3423	-3.0539	0.0952	-3.2405, -2.8672
p Secondary Period 2	1.6543	0.0813	1.4949, 1.8137	1.8376	0.0826	1.6757, 1.9996
p Secondary Period 3	1.8166	0.0807	1.6584, 1.9747	1.9916	0.0823	1.8303, 2.1529
p Secondary Period 4	1.8105	0.0807	1.6523, 1.9686	1.9778	0.0823	1.8165, 2.1392
p Secondary Period 5	1.7673	0.0809	1.6088, 1.9258	1.6171	0.0833	1.4538, 1.7804
p Secondary Period 6	0.3915	0.0926	0.2100, 0.5731	-0.6935	0.1186	-0.9260, -0.4611
p Brood Two	0.3180	0.0422	0.2353, 0.4007	-0.2494	0.0459	-0.3394, -0.1593
p Age	0.1756	0.0124	0.1513, 0.1998	-	-	-
p Age^2	-0.0064	0.0006	-0.0075, -0.0053	-	-	-
p Age^3	0.0001	0.0000	0.0001, 0.0001	-	-	-
p Wellington County	-0.7660	0.0378	-0.8400, -0.6919	-	-	-
p Age 21-28	-	-	-	0.6238	0.9016	0.6238, 0.9016
p Age 28-36	-	-	-	1.0796	1.3575	1.0796, 1.3575
p Age 35-42	-	-	-	0.3899	0.6921	0.3899, 0.6921
p Age 42-49	-	-	-	0.0260	0.3850	0.0260, 0.3850
p Age 49-56	-	-	-	0.1371	0.5235	0.1371, 0.5235
p Age 56-63	-	-	-	0.1616	0.5599	0.1616, 0.5599
p Age 63-70	-	-	-	0.3058	0.7701	0.3058, 0.7701
p Males	-	-	-	0.3472	0.0405	0.2678, 0.4267

I used mass controlled by structural size from all juveniles ringed and measured at the same time as radioed birds to obtain an index of condition (n = 503 in 2016 and n = 420 in 2017). In 2017, I added tarsus measurements to my field protocols for radio tagging nestling Barn Swallows. To determine the better measure of condition to use for 2017 models, I compared two multistate closed robust design models with each condition measure. The condition measure obtained by using tarsus had more support then the condition measure obtained by wing length (ΔAICc = 3.89). Both condition measures were highly correlated (R^2 = 0.84; p < 1.0×10^{-16}; Figure E1).
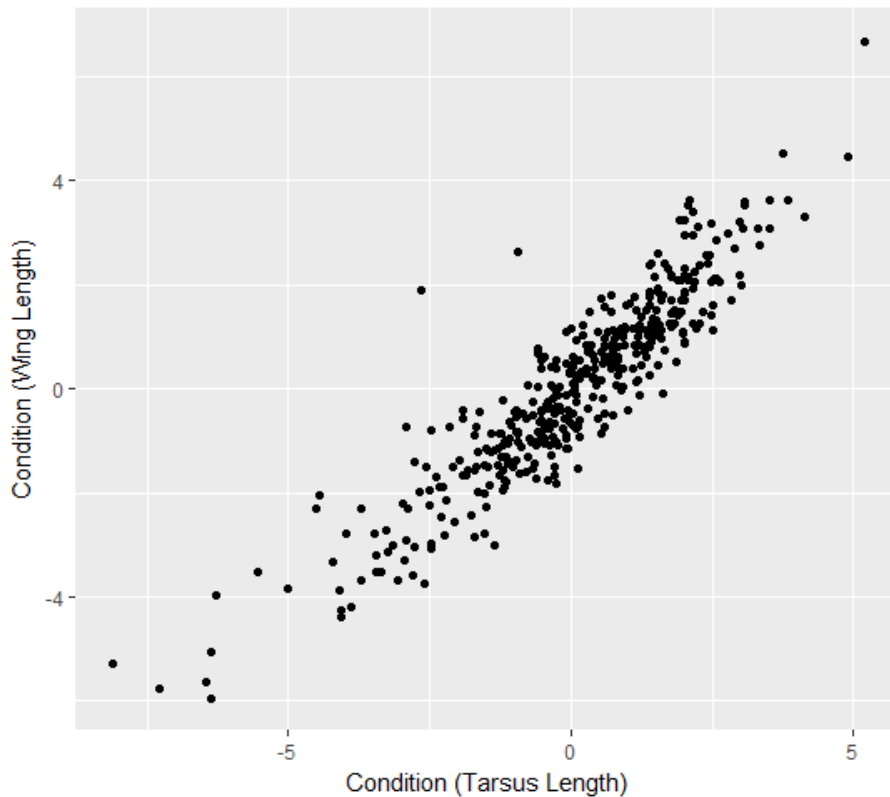
Figure E1. Correlation between body condition indices using wing length as the structural component vs using tarsus as the structural component.
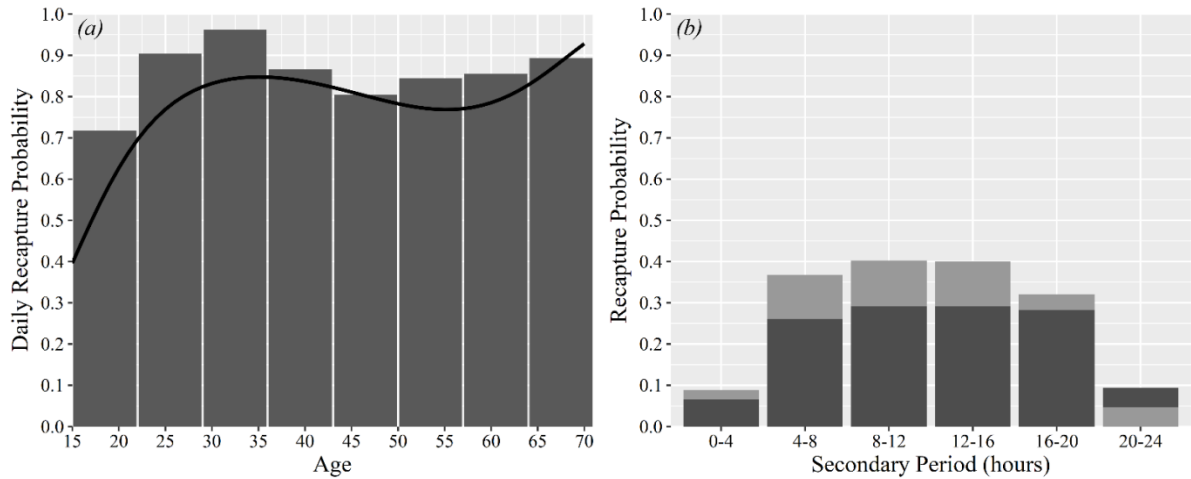
Figure F1. The relationship between: (a) age and average daily recapture probability in 2016 (black line) and 2017 (grey bars); and (b) time of day (secondary period) and average recapture probability for 2016 (dark grey) and 2017 (light grey). Average daily recapture probability represents the daily effective recapture probability $(1-(1-p_1)*(1-p_2)*(1-p_3)*(1-p_4)*(1-p_5)*(1-p_6)$; where p_1-p_6 represent the average recapture probability for each secondary period). Recapture probability was averaged across groups for each year (e.g brood).

Western

AUP Number: 2017-005
PI Name: Hobson, Keith
AUP Title: Ecology Of Migratory Songbirds In North America
Approval Date: 03/07/2017
Official Notice of Animal Use Subcommittee (AUS) Approval: Your new Animal Use Protocol (AUP) entitled "Ecology Of Migratory Songbirds In North America" has been APPROVED by the Animal Use Subcommittee of the University Council on Animal Care. This approval, although valid for four years, and is subject to annual Protocol Renewal.2017-005::1

1. This AUP number must be indicated when ordering animals for this project.
2. Animals for other projects may not be ordered under this AUP number.
3. Purchases of animals other than through this system must be cleared through the ACVS office. Health certificates will be required.

The holder of this Animal Use Protocol is responsible to ensure that all associated safety components (biosafety, radiation safety, general laboratory safety) comply with institutional safety standards and have received all necessary approvals. Please consult directly with your institutional safety officers.
Submitted by: Copeman, Laura
on behalf of the Animal Use Subcommittee
University Council on Animal Care

The University of Western Ontario
Animal Use Subcommittee / University Council on Animal Care
Health Sciences Centre, ● London, Ontario ● CANADA – N6A 5C1
PH: 519-661-2111 ext. 86768 ● FL 519-661-2028
Email: auspc@uwo.ca ● http://www.uwo.ca/animal/website/

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APPENDIX H: BANDING PERMIT

In the Province(s) / Territories - Dans la (les) provinces(s) / territoires

Ontario

Permit No. / N⁰ de permis **10685 J**

Issued under the Migratory Birds Regulations Sections 4 and 19.

If the authorizations include any species that are not protected under the Migratory Bird Convention Act, 1994, this document represents an agreement between Environment Canada and the holder for the use of federal bird bands on those species. All conditions listed on the back of this document apply.

Émis en vertu des articles 4 et 19 des règlements concernant les oiseaux migrateurs.

Si les autorisations visent des espèces qui ne sont pas protégées en vertu de la Loi de 1994 sur la convention concernant les oiseaux migrateurs, le présent document tient lieu d'entente entre Environnement Canada et le titulaire aux fins de l'utilisation de bagues fédérales sur ces espèces d'oiseaux. Toutes les conditions figurant au verso du présent document s'appliquent.

Name and Address - Nom et adresse

DEAN EVANS
62 STANLEY STREET
LONDON, ON N6C 1B1

Issue Date / Date d'émission **2017/05/08**

Expiration Date / Date d'expiration **2017/12/31**

Signature of Holder - Signature du détenteur

For the Minister - Pour le Ministre
Name (Print) - Nom (Lettres moulées)
L. LAURIN

Signature

AUTHORIZATIONS -- AUTORISATIONS

Authorized to:

- Band chicks at nest site and monitor
- Band specific species BARS and CLSW
- Hand capture
- Use mist nets
- Use (81H) Radio Transmitter (incl. nanotags) on Cliff Swallow (CLSW) (6120)
  Lotek NTQB-2 nanotag (0.35g) to adults and 15 day-old nestlings (leg-loop harness; marker and attachment materials not to exceed 4% total body weight; RADIO TRANSMITTER USE IS SUBJECT TO CERTIFICATION OF THE DEVICE BY INDUSTRY CANADA; IF IN POSSESSION OF A VALID ANIMAL CARE COMMITTEE APPROVAL) in Ontario
- Use (81H) Radio Transmitter (incl. nanotags) on Barn Swallow (BARS) (6130)
  Lotek NTQB-2 nanotag (0.35g) to adults and 15 day-old nestlings (leg-loop harness; marker and attachment materials not to exceed 4% total body weight; RADIO TRANSMITTER USE IS SUBJECT TO CERTIFICATION OF THE DEVICE BY INDUSTRY CANADA; IF IN POSSESSION OF A VALID ANIMAL CARE COMMITTEE APPROVAL) in Ontario

See Permit Conditions on the following page -- Voir les conditions du permis sur la page suivante

Page 1 / 2

Permit No.
N⁰ de permis   **10685 J**

PERMIT CONDITIONS

1. This permit is not transferable and is not valid unless it is signed by the person to whom it is issued. By signing this permit, the permittee agrees to abide by all conditions stated below and confirms that all information contained in their application was accurate. During banding activities, permittees must have their signed permit on their person at all times. Permit holders are responsible for the actions of the individuals under their supervision that conduct activities authorized under this permit, if they themselves do not have permits.
2. Permit holders will adhere to the North American Banding Council's Bander's Code of Ethics (www.nabanding.net/banders-code-of-ethics/) and the Canadian Council on Animal Care documents relevant to bird banding (CCAC guidelines on: the care and use of wildlife [www.ccac.ca/Documents/Standards/Guidelines/Wildlife.pdf], CCAC species-specific recommendations on: Birds [http://www.ccac.ca/Documents/Standards/Guidelines/Add_PDFs/Wildlife_Birds.pdf]).
3. The issuance of this permit does not exempt the permit holder from compliance with all relevant Canadian, Provincial and Territorial Laws, and Regulations otherwise applicable, nor does it exempt the permit holder from complying with applicable jurisdictional bylaws.
4. A holder of a scientific permit to capture and band migratory birds may salvage birds found dead, or killed as a result of normal banding operations, for the purpose of donating them to a public, scientific or educational institution.
5. The shipment or transport of any migratory birds or parts thereof taken under the authority of this permit must be labelled as per S.13.(1) of the Migratory Birds Regulations.
6. Unless otherwise stated, this permit does not authorize the targeted capture, banding or disturbing of species listed under the Species at Risk Act. Federally listed species at risk may be banded if captured incidentally, provided it can be done safely.
7. Only the methods specified on this permit can be used to capture birds.
8. Unless otherwise stated on this permit, the permit holder will use only the official numbered leg bands issued by the Canadian Wildlife Service.
9. Unless otherwise stated, this permit does not authorize the collection of blood, feathers and other avian biological materials.
10. The name, phone number, address and e-mail address of the permit holder will be stored in the shared North American Bird Banding Laboratory database, and may be shared with people reporting an encounter of a band used under this permit.
11. Banding and encounter data may be released to researchers and other users.
12. Permit holders will submit all required data to the Bird Banding Office as outlined in the Banding Data Submission Guidelines (see www.ec.gc.ca/BBO/ or request a copy from the BBO) or within 30 days of receiving a written request from a representative of the Minister.

Note: This permit may be suspended or cancelled if the person to whom it was issued has failed to comply with any condition set out in the permit.

CONDITIONS DU PERMIS

1. Le présent permis n'est pas transférable et n'est valide que s'il est signé par la personne à qui il a été délivré. En signant le permis, le titulaire accepte de respecter toutes les dispositions ci-dessous et confirme que tous les renseignements figurant dans sa demande étaient exacts. Durant les activités de baguage, le titulaire doit avoir son permis signé en sa possession en tout temps. Le titulaire est responsable des actions des individus sous sa supervision qui effectuent des activités autorisées par le présent permis, s'ils ne possèdent pas de permis eux-mêmes.
2. Le titulaire de permis doit respecter le Code d'éthique du bagueur du North American Banding Council (www.nabanding.net/banders-code-of-ethics/) et les documents du Conseil canadien de protection des animaux (CCPA) relatifs au baguage des oiseaux (lignes directrices du CCPA sur le soin et l'utilisation des animaux sauvages : http://www.ccac.ca/Documents/Normes/Lignes_directrices/Animaux_sauvages.pdf; recommandations spécifiques aux oiseaux : http://www.ccac.ca/Documents/Normes/Lignes_directrices/Animaux_sauvages_Oiseaux.pdf).
3. La délivrance de ce permis n'exempte pas le titulaire du permis de se conformer à toutes les lois canadiennes, provinciales et territoriales pertinentes et aux règlements par ailleurs applicables, et n'exempte pas le titulaire de se conformer aux règlements de la juridiction compétente.
4. Le titulaire d'un permis scientifique qui est autorisé à capturer et à baguer des oiseaux migrateurs peut récupérer les oiseaux tués ou trouvés morts à la suite d'opérations normales de baguage afin de les donner à un établissement public, scientifique ou d'enseignement.
5. L'envoi ou le transport de tout oiseau migrateur ou de parties d'oiseau prises sous l'autorité de ce permis doivent être étiquetés tel que décrit dans l'article 13 (1) du Règlement sur les oiseaux migrateurs.
6. Sauf indication contraire sur le permis, il est interdit de capturer, de baguer ou de déranger intentionnellement des espèces figurant sur la liste de la Loi sur les espèces en péril. Les espèces en péril figurant sur la liste fédérale peuvent être baguées si elles sont capturées de façon accidentelle, dans la mesure où il est possible de le faire en toute sécurité.
7. Seules les méthodes précisées sur le permis peuvent être utilisées pour capturer des oiseaux.
8. Sauf indication contraire sur le permis, le titulaire du permis n'utilisera que les bagues officielles numérotées délivrées par le Service canadien de la faune.
9. Sauf indication contraire sur le permis, il est interdit de prélever du sang, des plumes et tout autre matériel biologique aviaire.
10. Le nom, le numéro de téléphone, l'adresse et l'adresse de courriel du titulaire du permis seront conservés dans la base de données commune du North American Bird Banding Laboratory et peuvent être partagés avec les personnes qui signalent une bague posée au titre du présent permis.
11. Les données sur le baguage et les récupérations de bagues peuvent être communiquées à des chercheurs ou à d'autres utilisateurs.
12. Les titulaires de permis devront transmettre toutes les données requises au Bureau de baguage des oiseaux (BBO) comme le prévoit le guide sur la présentation des données de baguage (http://www.ec.gc.ca/BBO/; ou demandez une copie du guide au BBO), ou encore dans les 30 jours suivant la réception d'une demande écrite à cet effet de la part d'un représentant du ministre.

Note : Le permis peut être suspendu ou annulé si le titulaire ne se conforme pas aux conditions.

Curriculum Vitae

Dean R. Evans

PUBLICATIONS

Evans, D. R., J. Pearce, and J. R. Foote. 2017. Herring Gull Predation of Chimney Swifts at a Migratory Roost. Wilson Journal of Ornithology. 129(3):632-636.

Evans, D. R., S. L. McArthur, J. M. Bailey, J. S. Church, and M. W. Reudink. 2015. A high-accuracy, timesaving method for extracting nest watch data from video recordings. Journal of Ornithology. 156:1125– 1129.

CONFERENCE PARTICIPATION

AOS/SCO Annual Meeting 2017   East Lansing, MI   Aug. 2017
Conference Talk

Title of Talk: Adult and juvenile Bank Swallows (*Riparia riparia*) show differential post-fledging movements and departure for autumn migration

NAOC 2016   Washington, DC   Aug. 2016
Conference Poster

Poster Title: Chimney Swift Communal Roosting Varies with Atmospheric Conditions and Season

AFO/SOC-SCO/WOS 2015   Wolfville, NS   Jul. 2015
Conference Poster

Poster Title: A High-accuracy, time-saving method for extracting nest watch data from video recordings

TRU Undergraduate Research Conference   Kamloops, BC   Mar. 2015
Conference Poster

Poster Title: A High-accuracy, time-saving method for extracting nest watch data from video recordings

Respiratory Health and Sleep Science Conference   Kamloops, BC   Mar. 2014
Conference Poster

Poster Title: How does marijuana use affect sleep?

AWARDS

BSC-SCO Student Travel Award (2018)

NSERC Canadian Graduate Scholarship Master's (2017)

Queen Elizabeth II Graduate Scholarship in Science and Technology (2017-Declined)

Queen Elizabeth II Graduate Scholarship in Science and Technology (2016)

AFO / SOC-SCO / WOS Student Travel Award U

Undergraduate Research Experience Award (2014)

CUPE Local 3500 Award (2014)

Gordon R. Gore Award (2010)