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Post-breeding survival of adult and hatch-year Bank Swallows (Riparia riparia) in the Great Lakes region: a radio telemetry study

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Abstract

The post-breeding period poses significant threats to newly fledged birds due to predation, starvation, exposure to inclement weather, and collision risk prior to their first southward migration. I used automated radio telemetry to track 100 adult and 100 hatch-year Bank Swallows (*Riparia riparia*) in the Great Lakes ecoregion during the 2021 post-breeding period. Additionally, 74 hatch-year birds tracked in 2018 by Mitchell et al. were included. In 2021, daily apparent survival probability was higher for adults compared to hatch-years; we estimated that ~10% of hatch-year birds die within two weeks post-fledging but high rates of tag loss in adults and hatch-year birds precluded accurate estimation. Among hatch-year birds, there was some support that daily recapture probability was higher for those from natural lakeshore colonies compared to those from artificial aggregate pit colonies, but this could be due to inland locations of most aggregate pit colonies. Apparent survival among hatch-year birds was higher in 2018 than in 2021 and 2018 was also a drier year. Results suggest that colony type and Bank Swallow age can affect survival and recapture during the post-breeding period.

Keywords: Post-breeding, Survival, Bank Swallows, Age, Radio telemetry, Motus, RMark, Lakeshore, Aggregate pit, Mark-recapture, Aerial insectivores

Summary for Lay Audience

In Canada, groups of birds (guilds) have populations that are either increasing (e.g., birds of prey) or decreasing (e.g., aerial insectivores). Aerial insectivore populations may be decreasing due to a recent global decline in insect abundance, increased pesticides and environmental contaminant exposure through consumption of terrestrial and aquatic insects or climate change. In turn, these factors may lead to increased rates of mortality of young birds during the post-breeding period. The post-breeding period can be divided into two phases: parental dependence and independence. During the parental dependence phase, young birds are reliant on their parents for feeding and protection. During the independent phase, young birds must learn how to navigate unknown landscapes, gather food, and escape predation. Performing these actions can put young birds at a significant risk of failing to survive to their first migration. This mortality, in turn, can negatively affect the population sizes of aerial insectivores. One species in the aerial insectivore guild is the Bank Swallow (*Riparia riparia*). The Bank Swallow has been listed as Threatened in Schedule 1 of the *Species at Risk Act* (SARA) since 2017. Bank Swallows create burrows in vertical faces for nesting in two distinct areas: along natural lakeshore or in artificial human-made sand and gravel pits. My thesis aimed to estimate survival of adult and hatch-year Bank Swallows nesting in lakeshore colonies or pit colonies during the 2021 post-breeding period. Additionally, data from 2018 hatch-years provided by Dr. Greg Mitchell (Environment and Climate Change Canada) was used in this thesis. To estimate survival, birds were tracked using VHF (radio) tags. Radio tags can be detected by Motus towers to estimate movement and whether a bird has died. Results showed that lakeshore colony birds were detected by towers more than pit colony birds; this indicates a higher recapture and survival in lakeshore colony birds. Adult birds were found to have higher recapture and survival

compared to hatch-year birds. One limitation to this study was tag loss/failure. Hatch-year and adult radio tags were found to prematurely fall off, limiting the length of time birds could be tracked. Future studies should address tag failure and aim to track birds up to and beyond fall migration.

Co-Authorship Statement

All work presented in this thesis was completed under the supervision of Dr. Yolanda E. Morbey at the University of Western Ontario. All work was done in collaboration with Dr. Yolanda E. Morbey, Environment and Climate Change Canada, and Birds Canada, who helped in the development of field work, methodology, and study objectives. Data collection was performed by Christian M.M. Buchanan-Fraser, Megan Hiebert (Birds Canada) and Dr. Greg W. Mitchell. Data analysis was completed by Christian M.M. Buchanan-Fraser and Dr. Yolanda E. Morbey. This thesis has been written by Christian M.M Buchanan-Fraser and will be published with Dr. Yolanda E. Morbey and Greg W. Mitchell.

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List of Abbreviations

AIC - Akaike's Information Criterion

BBS – Breeding Bird Survey

EDT - Eastern Daylight Time

EPA - omega-3 eicosapentaenoic acid

GPS - Global Positioning System

lcl - lower confidence limit

PIM - Parameter Index Matrix

PUFA - polyunsaturated fatty acid

R - return rate

SE - standard error

ucl - upper confidence limit

Introduction

It is the consensus among biologists that the world has entered its sixth-mass extinction event (Ceballos et al. 2017, Wagner et al. 2021). Biodiversity losses have been demonstrated in various groups of organisms (Wagner et al. 2021). Terrestrial vertebrate population sizes and ranges have decreased by a third (Ceballos et al. 2017). Many species of mammals have experienced at least an 80% decline in range sizes over the last century (Ceballos et al. 2017). North American bird population numbers have decreased by 2.9 billion since 1970 (Rosenberg et al. 2019, Wagner et al. 2021). A large percentage of blame for biodiversity loss can be directed towards human activities such as hunting, deforestation causing habitat loss, agricultural expansion, industrialisation, urbanisation and human overpopulation (Maxwell et al. 2016, Ceballos et al. 2017, Sánchez-Bayo and Wyckhuys 2019).

There has been a general decline in Neotropical migrant bird populations throughout eastern North America (Robbins et al. 1989). A migratory bird’s annual cycle has distinct time periods with varying importance to overall annual survival. Guilds of migratory birds experience differential levels of survival over their annual cycle. The term “guild” refers to a group of species that use the same class of environmental resources in a similar way (Simberloff and Dayan 1991), and Canada is home to several guilds of birds. Canadian bird guilds include: waterfowl, birds of prey, wetland birds, nesting seabirds, forest birds, shorebirds, grassland birds and aerial insectivores (NABCI 2019). The average population percent change of Canadian bird guilds are changing at different rates (NABCI 2019). For example, Canadian birds of prey populations have had a +110% percent change from 1970 to 2016 while Canadian populations of aerial insectivores have had a -59% percent change from 1970 to 2016 (NABCI 2019). Aerial insectivorous birds feed on insects during flight (COSEWIC 2009). This guild includes the

Apodiformes (swifts), *Hirundinidae* (swallows), *Caprimulgiformes* (nightjars) and *Tyrannidae* (flycatchers) families (NABCI 2019). Based on population percent changes, one might ask how one guild's population percent change can be experiencing a positive amount of growth while another guild's population percent change is decreasing?

Evidence of multiple drivers affecting the decline of North American aerial insectivores have been recorded (Nebel et al. 2010, Spiller and Dettmers 2019). Potential causes of declines in aerial insectivore populations include a global decline in insect species (Sánchez-Bayo and Wyckhuys 2019), pesticides and other environmental contaminants that are ingested through terrestrial and aquatic insects (Alberts et al. 2013, Rowse et al. 2014), climate change - when species such as the Bank Swallow (*Riparia riparia*) do not advance their breeding times (Imlay et al. 2018), and non-breeding ground effects during migration or on overwintering grounds (Spiller and Dettmers 2019). In addition to these possible causes of decline, hatch-year migratory aerial insectivorous birds survival could be dependent on several separate life stages (Cox et al. 2014). Newly fledged birds need to survive their first post-breeding period and successfully survive their first southward migration. Cox et al. (2014) found mean cumulative post-breeding survival to be less than 60% from 10 days post fledge up until 50 days post-fledge for passerine birds. At 50 days post-fledge, less than 55% of fledgling passerine birds were alive (Cox et al. 2014). To put this number into context, we can use empirical survival estimates of non-breeding (i.e., migration and overwintering) Black-throated Blue Warblers (*Dendroica caerulescensfrom*) of 46% (Sillet and Holmes 2002). If we multiply the Cox et al. (2014) mean cumulative post-breeding survival estimate (55%) by Sillet and Holmes' (2002) estimate of non-breeding survival (46%), estimated first year survival is approximately 25%.

Here, I will introduce the concept of the post-breeding period and how it relates to a birds annual cycle, automated radio telemetry, the study species for my project and mark-recapture methods. After, I will present my hypotheses and predictions.

1.1 The post-breeding period

The annual life cycle of a North American migratory bird can be divided broadly into 4 periods: breeding in North America, southward migration, overwintering in North, Central, or South America, and northward migration back to the breeding grounds. One understudied life stage for migratory birds is the post-breeding period before southward migration (Cox et al. 2014). For fledglings, the post-breeding period can be divided into two stages: reliance on parents for feeding and protection and when fledglings are independent from their parents but have not dispersed or migrated (Cox et al. 2014). During the first stage of the post-breeding period, adults must ensure dependent fledglings are provided food. Adults will continue to feed newly fledged birds after they have fledged from the nest and provide additional post-fledging care such as guiding young to food resources and protection from predators (Snow 1958, Dreitz 2009, Rickenbach et al. 2011).

The post-breeding period for songbirds has been shown to be a high mortality period, especially for young hatch-year birds (Cox et al. 2014, Evans et al. 2020). In a 2014 review of 222 worldwide passerine species' fledgling post-breeding survival, Cox and colleagues found that mean cumulative post-fledging survival decreased from 100% to approximately 60% 50 days post-fledge. In a study by Evans (2018), 42% of hatch-year Southern Ontario Barn Swallows (*Hirundo rustica*) survived until their first southward migration. Since the post-breeding period is a high mortality period, it is a potentially critical life-stage for birds that may affect certain songbird population growth rates (Kershner et al. 2004). For songbirds, population growth rates are often associated with hatch-year survival (Donovan and Thompson 2001, Bonnot et al. 2011). Despite studies highlighting low post-breeding survival during the post-breeding period, it remains a severely understudied time period in the life cycle of migratory songbirds (Cox et al. 2014). One reason the post-breeding period remains understudied is because of the difficulty in tracking adults and hatch-year birds to properly estimate survival rates (Cox et al. 2014). Because of a lack of estimated post-breeding survival rates, most studies predict hatch-year songbird post-breeding survival rates to be 25-50% of the respective adult songbird annual survival rate (Ricklefs 1973, Greenberg 1980).

Factors affecting mortality during the post-breeding period have been studied (Cox et al. 2014). The post-breeding period between fledging from the nest and fall spans 2-3 months for migratory birds (Vitz and Rodewald 2011) and can be divided into two stages. During the first stage of the post-breeding period, hatch-year birds will perch in exposed sites and make begging calls to adults to encourage feeding (Vitz and Rodewald 2011). Begging calls can be conspicuous and make hatch-years more vulnerable to predation (Cox et al. 2014). In studies that were able to document mortality during the first stage of the post-breeding period, the major source of mortality was found to be predation (Anders et al. 1997, Ausprey and Rodewald 2011). In Ausprey and Rodewald (2011), fledgling Acadian flycatchers (*Empidonax virescens*) and fledgling Northern Cardinals (*Cardinalis cardinalis*) were preyed upon by Red Foxes (*Vulpes vulpes*), Coyotes (*Canis latrans*), American Red Squirrels (*Tamiascurus hudsonicus*), a Broad-winged Hawk (*Buteo platypterus*), and a domestic cat (*Felis catus*). Two important avian predators of fledgling and adult Bank Swallows are American Kestrels (*Falco sparverius*) and Merlins (*Falco columbaris*) (COSEWIC 2013). Both American Kestrels and Merlins have been observed nesting in proximity to Bank Swallow colonies (Freer 1973, Windsor and Emlen 1975, COSEWIC 2013).

The second stage of the post-breeding period is where hatch-years are especially vulnerable to mortality risks (Snow 1958, Magarth 1991, Naef-Daenzer et al. 2001). During the independent phase, hatch-years must learn how to navigate unknown landscapes, gather food resources, and avoid predation (Betts et al. 2008, Grüebler and Naef-Daenzer 2010, Dittmar et al. 2016). Performing these actions puts newly independent birds at a significant risk of failing to survive until their first southward migration (Anders et al. 1997, Berkeley et al. 2007). Hatch-year Bank Swallows will disperse and visit multiple colonies to assess their suitability as a potential breeding area in future years (Mead and Harrison 1979). The closely related Barn Swallow *(Hirundo rustica*) fledglings near Vancouver, British Columbia, Canada were found to be mobile during this phase and travel up to 19 km away from their nest at 16 days of age post-fledge (Boyton et al. 2020).

Survival rates for fledglings change as post-fledging age increases (Cox et al. 2014, Cox et al. 2018, Evans et al. 2020). In Cox et al. (2014), the age of post-fledging birds was the most frequently detected factor to influence post-fledging survival. Survival percentages differ between daily ages of fledglings (Cox et al. 2014). Survival rates have been shown to improve as fledglings age (Cox et al. 2014). Fledgling survival rates were found to level off after approximately 20 days to a survival rate similar to adults during the second stage of the post-breeding period (Cox et al. 2014). The majority of post-fledgling mortality occurs during the first three weeks post-fledging (Cox et al. 2014). Evans et al. (2020) found that apparent survival was lowest for Southern Ontario fledgling Barn Swallows between 15 to 21 days post-fledge, suggesting that the beginning of the second stage of the post-breeding period is especially important for this species. Eastern bluebird (*Sialia sialis*) fledglings show a similar survival pattern (Jackson et al. 2011). After 40 days post-fledging, overall fledgling survival rate dropped from 100% to 65.4% for 156 bluebird fledglings tracked in 2008 and 2009 (Jackson et al. 2011). Hooded warblers (*Wilsonia citrina*) fledglings radio tracked in northwestern Pennsylvania showed especially poor survival during the post-breeding period. Nineteen percent of total radio-tracked fledglings survived the first parent-dependent phase of the post-breeding period. Fledgling daily survival was lowest during the first four days post-fledging; 72% daily survival rate for the first two days post-fledging and a 69% daily survival rate for the third and fourth days post-fledging (Rush and Stutchbury 2008).

The time nestlings fledge the nest (fledging time) and nestling mass can affect survival during the post-breeding period (Jackson et al. 2011). As fledge date increases at the population level, fledgling daily survival increased by 1.18% between the first and last fledge dates of the year (Jackson et al. 2011). Cox et al. (2014) summarized post-fledging survival for 45 studies including 35 passerine species. Post-fledging age was found to influence post-fledging survival in all but 1 study (Cox et al. 2014). First-year Savannah sparrows (*Passerculus sandwichensis*) caught in New Brunswick, Canada with higher nestling mass had higher first year survival compared to nestlings with a lower nestling mass (Mitchell et al. 2011). The proportion of Savannah Sparrows surviving between years increased exponentially when plotted against nestling mass (Mitchell et al. 2011).

1.2 Automated radiotelemetry

One reason the post-breeding period is understudied in songbirds is due to difficulties in tracking individuals with high enough temporal resolution (Cox et al. 2014). Previous efforts to generate empirical estimates of post-breeding survival for hatch-year birds include the use of band recovery (Thomson et al. 1999, Webster et al. 2002, Thorup et al. 2014), mark-recapture data (e.g., Perrins 1965, Evans et al. 2020), Global Positioning Systems (GPS) (Hallworth and Marra 2015), satellite technology (Wikelski et al. 2007) and geolocators (McKinnon et al. 2013). These methods can produce biased estimates of post-breeding survival rates (Cox et al. 2014). Band recovery analyses can violate restrictive assumptions (Anderson et al. 1985) and the probability of resighting or recapturing banded birds is extremely low (Webster et al. 2002). Mark-recapture models cannot effectively distinguish between permanent emigration and individual death (Cormack 1964). GPS and satellite tags are currently too large for most migratory songbirds (Webster et al. 2002).

A unique and novel way to track the movement of flying animals is through automated radiotelemetry such as the Motus Wildlife Tracking System (http://motus.org). Motus is a global network of researchers and organizations that manage independent arrays of receiving towers over a large spatial area. Southwestern Ontario has an especially dense array of Motus towers with 40 000 km^2 of coverage (http://motus.org). Automated radio-telemetry systems are capable of recording radio tags continuously from a fixed position or mobile towers. Detection data obtained from arrays were processed through a centralized database. Motus can track thousands of unique digitally encoded radio tags on a single frequency. This allows for detection of tags by any receiver in the Motus network. Receivers continuously detect on a single frequency, as opposed to cycling through many different frequencies to find a detection, so the chances of detecting a hit are much greater than traditional non-automated methods. Each Motus tower can have 1-4 antenna which are connected to a SensorGnome receiver to allow for continuous detection. In ideal conditions, each antenna is capable of picking up a radio detection from 12-15 km away. When a tag is detected, the tag’s identity, signal strength, GPS synchronized time and the antenna the tag was detected on is recorded. All tag detections from every tag on every Motus tower are then recorded in a final data file that covers the entire Motus array (Taylor et al. 2017).

Automated radio telemetry has been used to gather a wide variety of data. Examples of automated radio telemetry use include estimating survival, measuring migratory bird stopover duration and activity, and to collect spatial behaviour (Mitchell et al. 2015, Evans 2018, Morbey et al. 2018, Deakin et al. 2019, Beauchamp et al. 2020, Bumelis 2020, Evans et al. 2020, Scardmaaglia et al. 2022). Evans et al. (2020) used Motus to estimate apparent post-breeding survival of hatch-year Barn Swallows over approximately two months of the post-breeding period. Automated radio tracking receivers have been used to track solar id-coded radiotags attached to screaming cowbirds (*Molothrus rufoaxillaris*) to test social monogamy, collect data on spatial behaviour and social mating systems (Scardmaaglia et al. 2022). Automated radiotelemetry has been used to study acorn woodpecker (*Melanerpes formicivorus*) behaviour and to construct aggregated social networks of acorn woodpecker associations (Shizuka et al. 2021).

1.3 The Bank Swallow

One species from the aerial insectivore guild that has experienced significant population decline in Ontario is the Bank Swallow (*Riparia riparia)* (Falconer et al. 2016a). Canadian Bank Swallow populations have been listed as threatened in Schedule 1 of the *Species at Risk Act* (SARA) since 2017 (Falconer et al. 2016a). From 1970 to 2012, Ontario Bank Swallow populations have declined by 6.2 percent annually or 93 percent overall (Falconer et al. 2016a). Breeding Bird Survey (BBS) data has described a significant annual decline of 8.84% per year between 1970 and 2011 (COSEWIC 2013). Based on annual Bank Swallows counts between

2009 and 2014, the overall Ontario population of Bank Swallows is estimated to be 409 000 breeding pairs (Falconer et al. 2016a). In Canada, the largest concentration of Bank Swallow occurs along the north shore of Lake Erie (COSEWIC 2013). In 2011, approximately 70 000 burrows were recorded along the North shore of Lake Erie from Point Pelee National Park, ON (41°59'31.2"N 82°29'49.2"W) to Dunnville, ON (42°51'36.0"N 79°28'15.6"W).

Bank Swallows are long-distance, diurnal migrants and have an extensive global distribution, having populations in every continent but Australia and Antarctica (COSEWIC 2013). In North America, the breeding range covers most of Canada, Alaska, and the northern two-thirds of the United States (Garrison 1999). After breeding, Bank Swallows will begin southward migration and overwinter in northern and central areas of South America (Garrison 1999). Bank Swallows arrive back to breeding grounds in Ontario from overwintering areas beginning in mid to late April up until May (Falconer et al. 2016a). Bank Swallows start to migrate back to overwintering grounds in July and will continue up until September (Falconer et al. 2016a).

Bank Swallows are the smallest swallow species in the Americas (COSEWIC 2013). Bank Swallow adult plumage can be described as gray-brown on the head mantle and rump, darker brown on the flight feathers with the underside being white (COSEWIC 2013). Juveniles can be distinguished by adults through their buff-edged wings and buff-pink wash on the throat (COSEWIC 2013). Plumage is similar in males and females, however a brood patch is present on breeding females while a cloacal protuberance is present on breeding males (COSEWIC 2013). During the breeding season, 80-95% of Bank Swallow diet frequency is composed of flies (*Diptera*), ants, bees, and wasps (*Hymenoptera*) beetles (*Coleoptera*) and true bugs (*Hemiptera*) (Garrison 1999). Terrestrial and aquatic insects and spiders (*Araneae*) are consumed by Bank

Swallows when they are locally abundant (COSEWIC 2013). The majority of adult songbird species perform the behaviour of moulting during their annual cycle, sometimes during the post-breeding period (Humphrey and Parkes 1959). Unlike most Neotropical birds, Bank Swallows moult on wintering grounds (COSEWIC 2013). Moult is energetically demanding, may strongly affect flight ability and a delayed moult can lead to a delayed start in southward migration (Jenni and Winkler 1994, Arlt and Pärt 2008).

Bank Swallows are usually single brooded in North America. Clutch size is typically 5 eggs (Falconer et al. 2016a). Bank Swallows fledge at 18 to 22 days (Garrison 1999). Bank Swallows nest in two different types of habitats. The natural habitat for Bank Swallows consists of natural vertical banks and cliffs along riparian areas such as ocean coasts, rivers, streams, lakes, and wetlands (Burke 2017, Burke et al. 2019). Lakeshore colony banks experience high levels of wind and erosion that maintain the bank's vertical face (Garrison 1999). The artificial human-made habitat for Bank Swallows includes sand and gravel pits, henceforth "aggregate pits" (Burke 2017, Burke et al. 2019). In aggregate pits, vertical faces are formed through the excavation of sand and gravel. If vertical faces are not maintained through human intervention, they will slump and stabilize causing colonies to abandon them (Ghent 2001, Lind and Stigh 2002). Approximately half of the population of Ontario Bank Swallows are estimated to occur in aggregate pit colonies and quarries (Falconer et al. 2016a).

Ecological differences have been recorded for the two types of Bank Swallow habitat in Ontario (Burke 2017, Génier et al. 2021). Southern Ontario Bank Swallow habitat persistence (ability of burrows to keep intact and functional) was found to be highest in lakeshore colonies and lowest in aggregate pit colonies (Burke 2017). Genier et al. (2021) found that Southern Ontario lakeshore Bank Swallows consumed more emergent aquatic insects compared to Bank

Swallows from aggregate pits. This may result in a nutritional disadvantage to aggregate pit Bank Swallows (Génier et al. 2021). Dietary differences have also been found in plasma polyunsaturated fatty acid (PUFA) profiles of Bank Swallows; lakeshore colony Bank Swallows consumed chironomids that had higher levels of omega-3 eicosapentaenoic acid (EPA) (Génier et al. 2021). Higher diet quality (levels of EPA) may cause lakeshore colony Bank Swallows to have higher apparent post-breeding survival compared to aggregate pit colony Bank Swallows. There is likely a nutritional cost related to diets provided to nestlings at aggregate pit colonies compared to diets provided to nestlings at lakeshore colonies (Génier et al. 2021). This could potentially create another nutritional disadvantage for birds nesting at inland pits (Génier et al. 2021).

In south-central Ontario, Bank Swallow colonies have been found to be larger along the lakeshore compared to aggregate pits (Burke 2017, Burke et al., 2021). Burke et al. (2021) found the maximum colony size of an aggregate pit colony was 1/5th the size of the largest lakeshore colony surveyed. Available nesting face was found to differ between lakeshore and aggregate pit colonies as well (Burke 2017). Burke et al. (2021) found the average size of available nesting face for Bank Swallows at lakeshore areas was 218 ± 45 m ^{2}, while the average size of available nesting face in aggregate pits was 92 ± 16m ^{2}. Natural lakeshore Bank Swallow colonies have the highest persistence (ability to be colonized by Bank Swallows in the next breeding season), followed by colonies along rivers and lastly aggregate pit colonies. Lower persistence rates in aggregate pit colonies are likely due to yearly removal procedures and relocation of aggregate resources**.** Lakeshore colonies and aggregate pit colonies generally have the same cavity occupancy rates, greater than 60% (Burke et al. 2021).

1.4 Mark-recapture methods

Mark-recapture models are used to estimate population abundance when it is impractical to count every individual. Mark-recapture models can be created essentially whenever individuals in a population can be marked in a unique and identifiable way and then recovered or resighted (Lettink and Armstrong 2003). For example, hatch-year Barn Swallows have been uniquely marked using Motus radio tags (Evans et al. 2020). Understanding the design of mark-analysis projects is especially important. Populations monitored can be open (all animals in the study have the same survival probability, capture probability, marks are not lost, length of each capture occasion is instantaneous compared to intervals between sessions) or closed (no birth, death or emigration of animals in study, all animals have the same capture probability, marks are not lost) (Lettink and Armstrong 2003). Open populations can have birth, immigration, death and emigration from the population while closed populations do not have birth, immigration, death or emigration from the population (Lettink and Armstrong 2003). Open and closed models have at least two sample sessions (Pollock 1982; Lettink and Armstrong 2003). The first session involves the capture, mark, and release of animals. The second session involves the population being resampled (Lettink and Armstrong 2003). Mark-recapture models can also be used to estimate population parameters such as survival, recruitment, and population growth rate (Lettink and Armstrong 2003). After all recapture events are performed, an encounter history can be created. Encounter histories contain 0’s (to indicate a specific individual was not detected/recaptured) and 1’s (to indicate a specific individual that was detected/recaptured).

Encounter histories can be made using automated radio telemetry detection data (e.g., Evans et al. 2020). Individuals radio tagged can be given a value of ‘1’ if they are detected by a Motus tower or a value of ‘0’ if they are not detected by a Motus tower (Evans et al. 2020).

Mark-recapture and automated radio telemetry can be used together to estimate daily apparent survival and daily recapture probability (Evans 2018, Evans et al., 2020). Two events involved in the mark-recapture of an animal are the initial capture, marking and release of an animal and its recapture at a later point in time (Cooch and Burnham 1999). Related to these two events is return rate. Return rate is the proportion of individuals marked and released on some occasion that are encountered on a subsequent occasion (Cooch and Burnham 1999). Return rate is, at minimum, the product of two events: 1) the probability of an individual surviving from the initial mark time to a future sampling occasion; apparent survival (ϕ), and 2) the probability that the marked individual is encountered during the sampling occasion alive; apparent encounter probability (p) (Cooch and Burnham 1999). Apparent survival probability is defined as survival that cannot distinguish between permanent emigration and death. Apparent encounter probability is defined as encounter probability that cannot distinguish between permanent emigration and death.

To calculate return rate, we can use the equation ($R = \phi p$). p can be further broken down by the equation $p = ([1-\gamma]p^*)$, where $1-\gamma$ is the probability that while being alive and in the superpopulation (the sum of unobservable animals outside the study area and observable animals inside the study area), the individual is available to be captured. $1-\gamma$ occurs when the animal is on the study area and 'available' to be recaptured. p^* is the probability that while alive, and in the superpopulation, an individual can be encountered. ϕ is the product of three factors: true survival, study area fidelity (the animal is observable) and tag retention. ϕ can be further broken down by the equation $\phi = SF$. S is the probability of surviving from one occasion to the next. F is the probability that conditional on surviving, the individual does not permanently leave the study area (Cooch and Burnham 1999). The full equation to calculate return rate would therefore be $R=SF(1-\gamma)p^*$.

Apparent survival has previously been modeled and estimated by using a multistate robust-design approach (Evans 2018, Evans et al. 2020). Multistate robust designs include multiple primary periods with multiple secondary periods within each primary period. In Evans et al. (2020), primary periods were represented by days (24 hours, age post-hatching in days) and secondary periods were represented by 4-hour periods within a day. Each open primary period contained multiple closed secondary periods for improved estimation of p and ϕ (Pollock 1982, White et al. 2006, Figure 1). The closed part of the approach refers to the assumption that individuals remain in the study area. During primary periods, we assume that the population is “open” to emigration and mortality. During secondary periods, we assume that the population is “closed” to emigration and mortality.

Animal movement between secondary periods can either be random or Markovian (White and Burnham, 1999). Markovian and random movement can be illustrated using γ' and γ'' (Figure 2). When γ'' is not equal to γ', movement is defined as Markovian and when γ'' is equal to γ', movement is defined as random (White and Burnham 1999). For random movement, the probability of moving between secondary periods during one primary period (i) and the next (i+1) is independent of the previous state of the system (White and Burnham 1999). During Markovian movement, the probability of moving between secondary periods during one primary period and the next is dependent on where the animal was during the previous primary period (i-1) (White and Burnham 1999).

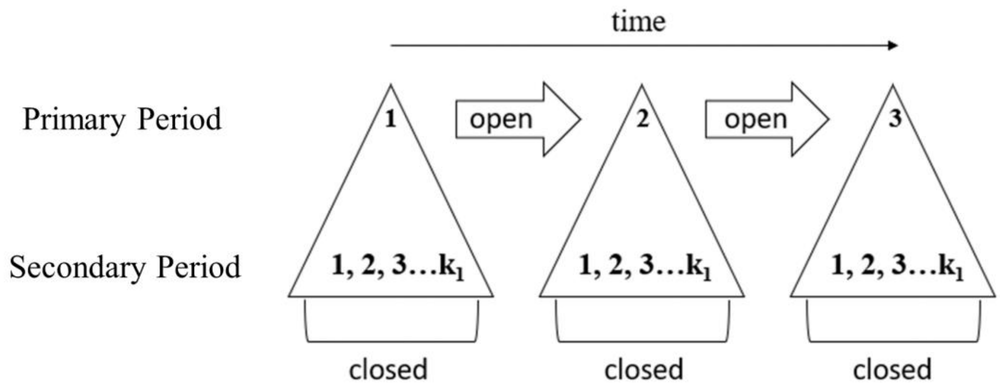

Figure 1. Illustration of robust design used (adapted from Kendall and Nichols 1995). Primary periods represent age post-hatching (days). Secondary periods represent 4 hour periods in a given primary period. The population is assumed to be open during primary periods and closed during secondary periods.

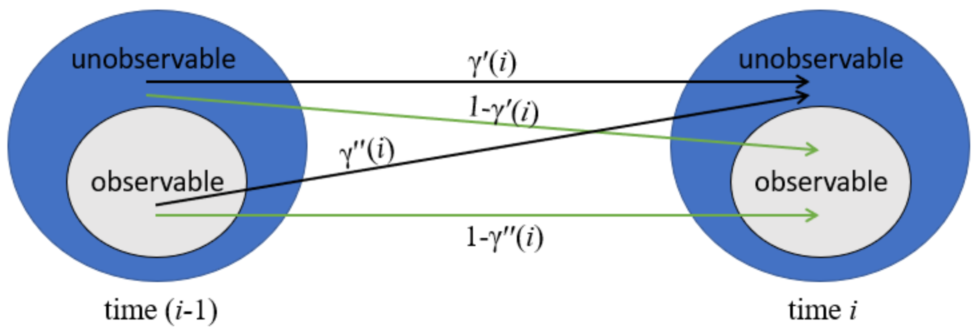

Figure 2. Relationships between γ' and γ'' (adapted from Kendall et al. 1995, 1997). γ' represents the probability that given an individual was not in the sample at time (i-1), the individual is also not present at time (i). γ'' represents the probability of an individual temporarily emigrating from the sample between sampling occasions (i-1) and (i). Green lines show individuals that are observable at time (i) while black lines show individuals that are not observable at time (i). Markovian movement occurs when γ' does not equal γ'' (difference in γ). Random emigration occurs when γ' equals γ'' (no difference in γ).

1.5 Study Objectives, Hypotheses and Predictions

The goal of my research was two-fold. First, to determine the apparent post-breeding survival probability of adult and hatch-year Bank Swallows at both lakeshore and aggregate pit colonies. Second, to test the hypothesis that apparent post-breeding survival probability depends on intrinsic and extrinsic ecological factors. The intrinsic factors of interest included sex, age class (adult vs hatch-year), wing length, mass and fat. The extrinsic factor considered was habitat type (lakeshore or aggregate pit). Based on prior empirical studies, I predict that age class, post-hatching age, wing chord, mass and habitat type will have an effect on Bank Swallow post-breeding survival. I predict that adults will have a higher apparent post-breeding survival probability compared to hatch-years. Hatch-years must successfully fledge from the nest, begin to feed for themselves and escape predation. Adults have already experienced the post-breeding period at least once before, so I believe they will be better suited to survive during the post-breeding period. I predict that as Bank Swallows' wing chord and mass increase, apparent post-breeding survival probability will increase as well. I think that birds with larger wings and more mass will be better suited to evade predators and gather food resources compared to birds with smaller wings. Finally, I predict that lakeshore colony Bank Swallows will have a higher apparent post-breeding survival probability compared to aggregate pit colony Bank Swallows. I believe that a closer proximity to open bodies of water at lakeshore colonies will allow lakeshore colony Bank Swallows to access food more readily and in turn have a higher apparent post-breeding survival probability compared to aggregate pit colony Bank Swallows.

Methods

2.1 Study area

Bank Swallows were captured in various lakeshore and aggregate pit colonies in Southwestern Ontario (Norfolk, Elgin, Oxford, Haldimand and Simcoe Counties) during the Bank Swallows' breeding period in 2018 and 2021 (Figure 3). The breeding period for Ontario populations of Bank Swallows spans from June to early August, depending on when eggs are laid in a particular year. The 2018 data was provided by G. Mitchell (Environment and Climate Change Canada).

Lakeshore colonies were located on landowner properties on the north shore of Lake Erie. All capture sites were located in ecoregion 7E (Lake Erie-Lake Ontario). Approximately 78% of ecoregion 7E is cropland or pasture space (Crins et al. 2009).

2.2 Field data collection

In 2018, hatch-year Bank Swallows were captured at 12 sites; six sites were aggregate pit colonies while the remaining 6 sites were lakeshore colonies (Figure 4). Colonies were described by type, area, latitude and longitude. Type referred to the colony type a bird was tagged at (either lakeshore or pit). Area referred to whether or not a colony was near the lakeshore (less than 15 km from shore) or if it was inland (greater than 15 km from shore). The covariate type was included to distinguish between the structural differences between lakeshore colonies and aggregate pit colonies and the area covariate was used to compare inland sites to sites along the north shore of Lake Erie. Birds were captured between 25 June 2018 and 24 July 2018, by Birds Canada personnel and 74 hatch-year birds were radio tagged in total. In 2021, hatch-year and adult Bank Swallows were captured at 12 sites; four sites were aggregate pit colonies while the remaining eight sites were lakeshore colonies (Figure 5). Bank Swallows were captured at aggregate pit colonies and lakeshore colonies between 25 May 2021 and 21 July 2021. 192 birds were radio tagged in total; 116 of radio tagged birds were adults while the remaining 72 birds were hatch-year birds.

Bank Swallows were captured using a shortened modified mist net. The modified mist net was attached to two pieces of bamboo on either end using a nut and bolt hinge. Before capturing birds, bank faces at each site with high Bank Swallow activity was monitored. Once these high activity areas were determined, each individual would take hold of one bamboo piece. The modified mist net was lifted up on either end and was quickly brought to the edge of the face. The modified mist net would then be lowered and held over the edge of the face parallel to Bank Swallow burrows. To entice birds to fly into the modified mist net, individuals could lightly stomp the ground above burrows or make a "psst-psst" alarm sound that resembles a predator warning call to other Bank Swallows (Megan Hiebert, pers. comm.). Once an appropriate amount of Bank Swallows were caught (anywhere from 1 to 10 depending on site activity and weather conditions), the mist net was raised and birds were removed. On cooler days, birds were placed into bird bags and held until they were processed. On warmer days, birds were placed in a bird box. This allowed the Bank Swallows to be in a cooler environment until they could be processed to minimize heat stress. Caught individuals were grouped into 3 different categories. Group 1: Adult Bank Swallows (for radio tagging). Group 2: Hatch-year Bank Swallows (for radio tagging). Group 3: Hatch-year Bank Swallows (for full blood sampling and central tail feather sampling). Group 3 birds were part of a different study.

All captured Bank Swallows had a standard Canadian Wildlife Service aluminum leg band (size 0C) affixed to their tarsus. Morphological characteristics were recorded for captured Bank Swallows. Sex (presence or absence of a cloacal protuberance, Pyle 1997), presence or absence of brood patch (adults only, Cowley 1999), fat score (0-8, Pyle, 1997), unflattened wing chord length (mm), and mass at capture (g) were recorded for each individual. Comments were also made regarding condition of captured birds (e.g., if a bird struggled with flying off after measurements were taken). In addition to the measurements mentioned, Group 1 and Group 2 birds had radio tags attached. Radio tags (Lotek NTQB-1; 0.29 g) were assembled into harnesses using Dritz 9345W white elastic sewing thread. Using superglue and elastic thread, 32-34 mm harnesses were created. The harnesses were glued to a radio tag and attached to a Bank Swallow using the figure 8 leg loop harness method (Rappole and Tipton 1991). Harnesses were designed to allow for muscle growth, flexion and to fall off of the bird after two months based on previous Barn Swallow (*Hirundo rustica*) research (Evans et al. 2020). The estimated tag life for radio tags used was approximately 106 days.

Group 2 birds had a small amount (<10 μl) of blood sampled. This sample was obtained by puncturing the brachial vein with a sterilized 26 G needle. Blood was collected with a heparinized capillary tube. Blood clotting was induced by applying sterile cotton gauze to the brachial vein until bleeding finished, immediately after the blood sampled was collected. If the sterile cotton gauze did not stop the bird from bleeding, a small amount of clotting liquid was applied. The small blood sample was smeared on filter paper and stored in a Ziploc bag. Small blood samples were used to sex hatch-year birds at the University of Lethbridge (Appendix 2). Whole blood samples were spun down in a centrifuge in the field to separate plasma from red blood cells. Plasma was collected by using a Hamilton syringe. Both components were stored in a liquid nitrogen dry shipper and transported to the University of Western Ontario to be stored in a -70°C freezer. Once a bird was finished being processed, the bird was immediately released close (less than 100 m) from its capture site. An additional variable called capture age (cap.age) was created by estimating the capture age of caught birds through Turner and Bryant's (1979) regression formula for estimating the length of the 9th primary feather (mm, excluding sheath) on age for Bank Swallows at 11 days of age and onwards ($y = 4.72x-51.18$, $r = 0.98$: $P < 0.001$). We calculated juvenile capture age using the adapted formula: floor((Wing-74) *(1/4.72) +20))); where floor was used to round values and Wing was wing chord length at capture. The smallest wing chord recorded in 2018 and 2021 was 74 and 20 was used in the equation as the nestling period for Bank Swallows is between 18 and 21 days. Field work was conducted under Canadian Wildlife Service permit number 10169 CL with the approval of the University at Western Ontario's animal care committee (protocol # 2020-141) (Appendix 2, Appendix 3).

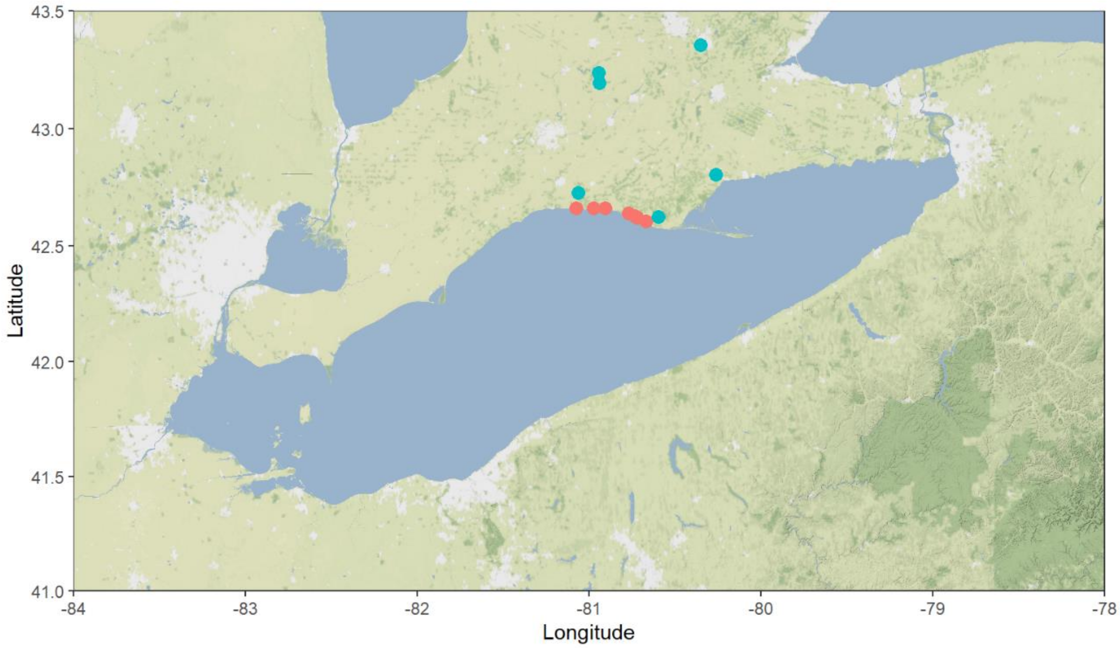

Figure 3. Colony sites sampled from during the 2018 and 2021 post-breeding period. Lakeshore colonies are shown in red while aggregate pit colonies are showed in blue (package ggmap, Kahle and Wickham 2013).

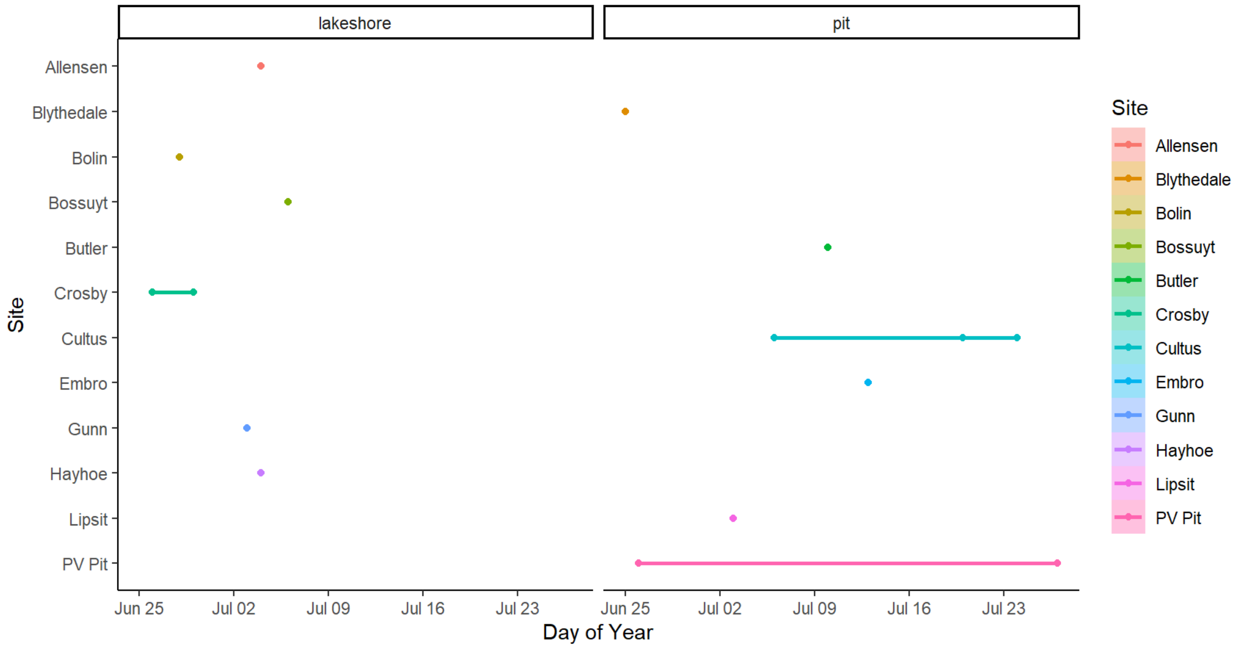

Figure 4. Bank Swallows radio tagged at a given site per day during the 2018 post-breeding period. Different sites are illustrated in different colours. The left side of the figure shows lakeshore sites while the right side of the figure shows pit sites.

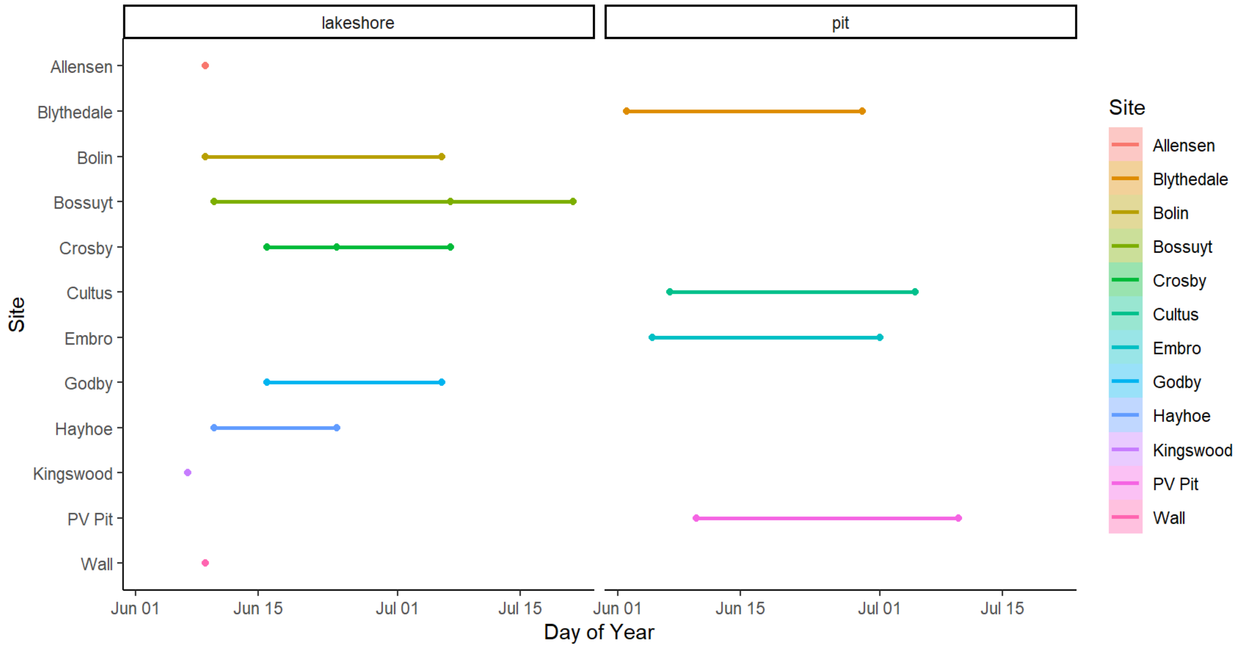

Figure 5. Bank Swallows radio tagged at a given site per day during the 2021 post-breeding period. Different sites are illustrated in different colours. The left side of the figure shows lakeshore sites while the right side of the figure shows pit sites.

2.3 Statistical analysis

2.3.1 Downloading Motus data

Bank Swallow detections were downloaded from the Motus website (Motus project 199, package motus; Brzustowski and LePage 2021). The Motus filter titled 'motusFilter' was used to identify detections that have a high probability to be false. The filter assigns runs with a value of either 0 or 1. Runs with a 'motusFilter' value of 0 are considered invalid (low probability of being true detections) while runs with a value of 1 are considered valid (high probability of being true detections). Detection data were merged with bird capture data.

2.3.2 Data filtering

The first step in the data filtering process was to remove any nighttime detections, leaving only diurnal detections as Bank Swallows commute and move primarily during the day. The daily detection frame for 2018 and 2021 was selected to be from 4:00 AM EDT to 8:30 PM EDT. One major source of error in tag detections is random radio noise (static) that can be detected and interpreted to be transmission of a tag (Birds Canada 2022). This source of error is known as a false positive. False positives were corrected by removing detections that had a run length less than three. Longer runs are associated with detections being more likely to be true detections (Birds Canada 2022). Unrealistic detections and Motus towers with unrealistic detections were removed as well. Towers with a latitude less than 41.7° or a longitude greater than -79.65° were removed. Towers with such a latitude and longitude were outside of Southwestern Ontario and did not capture Bank Swallows movement during the post-breeding period. Detections with birds travelling at an unrealistic rate were also removed.

2.3.3 Encounter history

Methods to develop encounter histories followed Evans et al. (2020). Primary periods were considered to be days. Initially, each primary period was to include five 4-hour secondary periods, similar to the Evan et al. (2020) study. We decided to instead include three 4-hour secondary periods: 4:48 am – 9:36 am (dawn), 9:36 am – 2:24 pm; (midday), 2:24 pm – 7:12 pm (dusk). Three secondary periods were chosen to capture major diel periods of activity. Detection data for 2018 contained 38 primary periods and 114 secondary periods while detection data for 2021 contained 126 primary periods and 378 secondary periods. Detection data was then transformed into an encounter history for each Bank Swallow. All individual encounter histories needed to start on a specific day (the capture occasion). The oldest hatch-year bird was radio tagged at age post-hatching day 25, therefore all encounter histories for hatch-years were aligned by age with the first encounter day assumed to be hatching day 25. Adult encounter histories similarly began on day 25 to facilitate comparison with hatch-years.

The last secondary period included in analysis was the second last primary period with at least 2 recaptures of unique birds. When birds were detected on a unique secondary period, they were given a value of '1' and when birds were not detected during a secondary period, they were given a value of '0'.

2.3.4 Robust design

To start the robust design process, the encounter history data was merged with the bird data. The bird data contained covariates of interest including: colony attributes, standardized wing chord length, mass, fat, sex, and brood patch. In 2018, capture histories were subset to include post-hatching day 25 to day 45 (21 days/primary periods and 63 secondary periods). Age post-hatching day 39 was the last day at least five hatch-year birds were detected in a secondary period; estimates past this day are likely not reliable. In 2021, adult capture histories were subset to include age post-hatching day 25 to day 45 (21 days/primary periods and 63 secondary periods) while hatch-year capture histories were subset to include age post-hatching day 25 to day 45 (21 days/primary periods and 63 secondary periods). Age post-hatching day 33 was the last day at least five hatch-year birds were detected in a secondary period while age post-hatching day 42 was the last day at least 5 adult birds were detected in a secondary period. Estimates past these days are likely not reliable. The last day included was the day with the second to last secondary period were there was at least two birds detected. Next, design data were created for 2018 and 2021 data. The Parameter Index Matrice (PIM) structure contains 3 variables of interest: ϕ (the probability of survival), p (the probability of first capture) and c (probability of recapture within a primary period). I let p = c as we assumed the probability of being first captured and recaptured at a later time were the same. The probability of being detected on the Motus array does not differ between the first capture occasion and subsequent capture occasions.

Parameter specification for models was performed, creating a list of potential models (package RMark; Laake 2013**)**. The process for finding the best model involved testing specific variables related to survival and recapture. Variables tested included: movement (random or Markovian), p_i/apparent encounter probability (probability of encounter by the Motus array at either primary period i or secondary period i), and ϕ_i (probability of surviving from sampling period i to sampling period i+1). Covariates were added to p_i and ϕ_i. To represent primary periods in the post-breeding period, the numeric value ‘time’ was used. To represent secondary periods in the post-breeding period, the categorical variable 2° was used.

Initially, the best movement model (Markovian or random) was determined for 2018 hatch-years, 2021 hatch-years and 2021 adults. Model selection assumed a quadratic or cubic relationship between survival and time and a quadratic or cubic relationship between recapture probability and time. Movement parameters for this model were either Markovian or random. Candidate models were ranked based on Akaike's Information Criterion (AIC) and the relative likelihood of each model was also determined based on model weight (w_i). A given w_i is considered as the weight of evidence in favour of model *i*; w_i can therefore be defined as the probability that model *i* is the actual best model in the set (White et al. 2006). Models were considered to have equal support when within two units of the top model ($\Delta AIC_c < 2$). The top movement type for 2018 hatch-years, 2021 hatch-years and 2021 adults was retained for the subsequent steps.

I next determined the top recapture model without covariates. Quadratic and cubic relationships between survival and time were assumed. Models of recapture with primary period (time) included constant, linear, quadratic, and cubic relationships. Recapture probability was assumed to vary among secondary periods. The top model with the lowest AICc value was chosen to move forward further in model selection. The top recapture model was then used to determine the top recapture model with covariates. Environmental recapture covariates tested included: colony type and colony area. Although colony latitude was recorded in the field, variation was better captured by colony type and colony area.

The final step was to determine the top survival parameter with covariates. The top recapture model with covariates was tested with survival models including covariates. Survival covariates tested included: colony type, colony area, wing, age, fat score, brood patch condition, sex and mass at capture. The top model with the lowest AICc value was selected as the top overall model. Top model coefficients were calculated using β (logit link function for parameter estimates). For the top 2021 model, the estimate of daily apparent mortality was calculated by subtracting the 2021 hatch-year daily apparent survival probability from the 2021 adult apparent survival probability, as 2021 adult post-breeding survival was assumed to be close or equal to 100%. Cumulative estimates of tag loss and actual mortality were calculated by subtracting daily apparent survival probabilities from 1. All statistical analyses were performed in R v. 4.1.1 (R Core Team 2021).

Results

In 2018, 74 hatch-year Bank Swallows were radio tagged from 25 June to 24 July 2018 and seventy-two birds were included in the robust design analysis. In 2021, 286 Bank Swallows were sampled from 25 May to 21 July. In the 2021 field season from 25 May to 21 July, 75 adult female birds, 41 adult male birds, 35 hatch-year female birds, 34 hatch-year male birds and 6 hatch year birds with an undetermined sex were radio tagged. Sex was determined for 69 hatch-years through blood samples. 191 birds were included in the 2021 robust design analysis. Out of the 191 birds included, 69 were hatch-years while 116 were adults.

3.1 2018 and 2021 hatch-year return rate

Return rates were aligned to begin at post-hatching day 25. Return rates for hatch-years in 2018 and 2021 both began low with less than 40% of total birds detected on a Motus tower (Figure 6). The proportion of birds detected quickly increased up until approximately post-hatching day 35 for both 2018 and 2021 birds. After day 35, detection rates rapidly decreased; at post-hatching day 40, less than 15% of hatch-year birds radio tagged in 2018 and 2021 were detected alive (Figure 6).

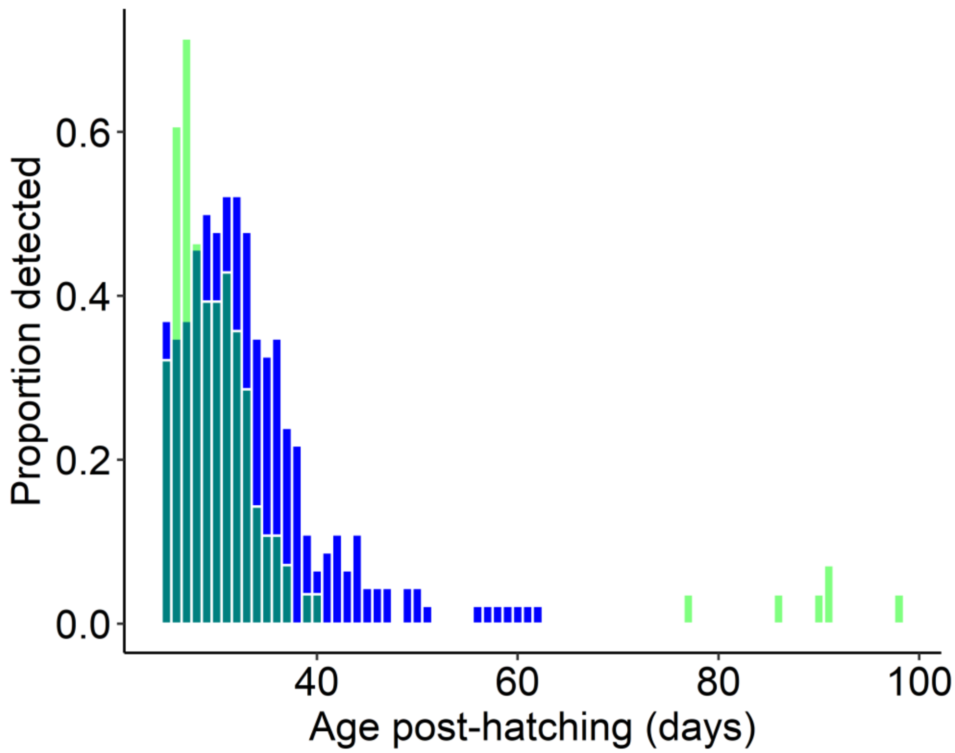

Figure 6. Proportion of hatch-year radio tagged birds that were detected on each day post-hatching in 2018 and 2021. 2018 birds are shown in blue. 2021 birds are shown in light green. The overlap between both years is shown in dark green. Detection rate sharply decreases at starting at age post-hatching day 35.

3.2 2021 hatch-year and adult return rate

Return rates were aligned to begin at post-hatching day 25. Return rate patterns were similar to patterns seen in 2018. Return rates peaked for both 2021 hatch-year and 2021 adults at approximately post-hatching day 28 (Figure 7). After post-hatching day 28, detections drastically declined (Figure 7). At age post-hatching day 40, less than 10% of hatch-years were detected and less than 20% of adults were detected (Figure 7). 2021 adults were detected further into the post-breeding period compared to 2021 hatch-year birds (Figure 7).

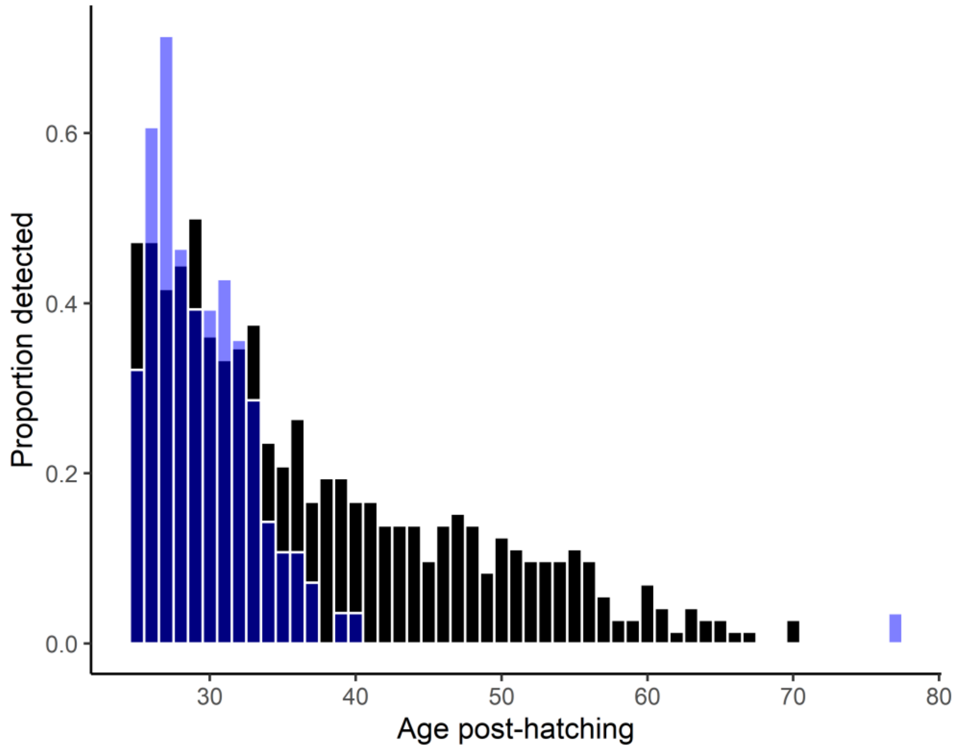

Figure 7. Proportion of adult and hatch-year radio tagged birds that were detected on each day post-hatching in 2018 and 2021. 2021 hatch-year birds are shown in lavender. 2021 adult birds are shown in gray-black. The overlap between both years is shown in dark blue. Detection rate sharply decreases at starting at age post-hatching day 35.

3.3 Movement type in 2018 and 2021

When testing for the type of movement during the post-breeding period, the top (within 2 ∆AICc values) models for 2018 hatch-year birds showed Markovian movement (Table 1). The top model for 2021 hatch-year birds showed Markovian movement (Table 2). The top models for 2021 adults showed Markovian movement (Table 3).

Table 1. Movement data output for hatch-year Bank Swallows radio tagged in 2018. ϕ represents daily survival probability. γ represents the probability of an individual being unavailable for recapture. When γ'' does not equal γ', movement between secondary periods can be defined as Markovian. The top models included Markovian movement. t represents Time (day post-fledging). p represents daily recapture probability. 2° represents secondary periods. Superscripts represent whether daily survival probability or daily recapture probability has a linear, quadratic, or polynomial relationship to Time. npar represents the number of parameters included in a model. AICc represents the corrected AIC by using npar. w_i represents how much we can attribute a model to fitting the best compared to other models. Deviance represents the difference between the null deviance and model deviance. Models with a ΔAICc value less than 2 are statistically supported.

model	npar	AICc	ΔAICc	w_i	deviance
$\phi(t + t^2 + t^3)$ $\gamma''(1)$ $\gamma'()$ $p(t + t^2 + t^3 + 2°)$	33	933.97	0	0.605	1570.23
$\phi(t + t^2 + t^3)$ $\gamma''(1)$ $\gamma'()$ $p(t + t^2 + 2°)$	32	934.83	0.85	0.395	1573.33
$\phi(t + t^2)$ $\gamma''(1)$ $\gamma'()$ $p(t + t^2 + t^3 + 2°)$	32	950.96	17.00	<0.001	1589.47
$\phi(t + t^2)$ $\gamma''(1)$ $\gamma'()$ $p(t + t^2 + 2°)$	31	952.23	18.26	<0.001	1592.98
$\phi(t + t^2 + t^3)$ $\gamma''(1)$ $\gamma'(1)$ $p(t + t^2 + t^3 + 2°)$	32	972.79	38.82	<0.001	1611.30
$\phi(t + t^2 + t^3)$ $\gamma''(1)$ $\gamma'(1)$ $p(t + t^2 + 2°)$	31	973.34	39.37	<0.001	1614.09
$\phi(t + t^2)$ $\gamma''(1)$ $\gamma'(1)$ $p(t + t^2 + t^3 + 2°)$	31	989.22	55.25	<0.001	1629.98
$\phi(t + t^2)$ $\gamma''(1)$ $\gamma'(1)$ $p(t + t^2 + 2°)$	30	990.05	56.078	<0.001	1633.04

Table 2. Movement data output for hatch-year Bank Swallows radio tagged in 2021. ϕ represents daily survival probability. γ represents the probability of an individual being unavailable for recapture. When γ'' does not equal γ', movement between secondary periods can be defined as Markovian. The top model included Markovian movement. t represents Time (day post-fledging). p represents daily recapture probability. 2° represents secondary periods. Superscripts represent whether daily survival probability or daily recapture probability has a linear, quadratic, or polynomial relationship to Time. npar represents the number of parameters included in a model. AICc represents the corrected AIC by using npar. w_i represents how much we can attribute a model to fitting the best compared to other models. Deviance represents the difference between the null deviance and model deviance. Models with a ΔAICc less than 2 are statistically supported.

model	npar	AICc	ΔAICc	w_i	deviance
$\phi(t + t^2 + t^3)$ γ''(1) γ'() $p(t + t^2 + t^3 + 2°)$	33	714.00	0	0.471	828.57
$\phi(t + t^2 + t^3)$ γ''(1) γ'(1) $p(t + t^2 + t^3 + 2°)$	32	715.05	1.04	0.279	832.17
$\phi(t + t^2)$ γ''(1) γ'() $p(t + t^2 + t^3 + 2°)$	32	716.56	2.56	0.131	833.68
$\phi(t + t^2)$ γ''(1) γ'(1) $p(t + t^2 + t^3 + 2°)$	31	717.51	3.51	0.081	837.17
$\phi(t + t^2 + t^3)$ γ''(1) γ'() $p(t + t^2 + 2°)$	32	720.11	6.11	0.022	837.24
$\phi(t + t^2 + t^3)$ γ''(1) γ'(1) $p(t + t^2 + 2°)$	31	721.07	7.06	0.014	840.72
$\phi(t + t^2)$ γ''(1) γ'() $p(t + t^2 + 2°)$	31	726.45	12.45	0.001	846.11
$\phi(t + t^2)$ γ''(1) γ'(1) $p(t + t^2 + 2°)$	30	726.99	12.99	0.001	849.17

Table 3. Movement data output for adult Bank Swallows radio tagged in 2021. ϕ represents daily survival probability. γ represents the probability of an individual being unavailable for recapture. When γ'' does not equal γ', movement between secondary periods can be defined as Markovian. The top models included Markovian movement. t represents Time (day post-fledging). p represents daily recapture probability. 2° represents secondary periods. Superscripts represent whether daily survival probability or daily recapture probability has a linear, quadratic, or polynomial relationship to Time. npar represents the number of parameters included in a model. AICc represents the corrected AIC by using npar. w_i represents how much we can attribute a model to fitting the best compared to other models. Deviance represents the difference between the null deviance and model deviance. Models with a ΔAIC$_c$ less than 2 are statistically supported.

model	npar	AICc	ΔAICc	w_i	deviance
$\phi(t + t^2 + t^3)$ $\gamma''(1)$ $\gamma'()$ $p(t + t^2 + t^3 + 2°)$	33	1663.67	0.00	0.490	2357.06
$\phi(t + t^2\ )$ $\gamma''(1)$ $\gamma'()$ $p(t + t^2 + t^3 + 2°)$	32	1663.99	0.32	0.417	2359.54
$\phi(t + t^2 + t^3)$ $\gamma''(1)$ $\gamma'()$ $p(t + t^2 + 2°)$	32	1666.99	3.32	0.093	2362.53
$\phi(t + t^2)$ $\gamma''(1)$ $\gamma'()$ $p(t + t^2 + 2°)$	31	1680.32	16.65	<0.001	2378.01
$\phi(t + t^2 + t^3)$ $\gamma''(1)$ $\gamma'(1)$ $p(t + t^2 + t^3 + 2°)$	32	1810.50	146.83	<0.001	2506.05
$\phi(t + t^2)$ $\gamma''(1)$ $\gamma'(1)$ $p(t + t^2 + t^3 + 2°)$	31	1814.25	150.58	<0.001	2511.94
$\phi(t + t^2 + t^3)$ $\gamma''(1)$ $\gamma'(1)$ $p(t + t^2 + 2°)$	31	1814.89	151.22	<0.001	2512.58
$\phi(t + t^2)$ $\gamma''(1)$ $\gamma'(1)$ $p(t + t^2 + 2°)$	30	1819.08	155.41	<0.001	2518.91

3.4 Hatch-year and adult movement paths

Hatch-year movement during the 2018 post-breeding period was concentrated along the north shore of Lake Erie (Figure 8). Dispersal and movement were evident through movement paths between sites and colonies (Figure 8). Movement during the 2021 post-breeding period was concentrated along the north shore of Lake Erie (Figure 9). During the 2021 post-breeding period, adults and hatch-years appeared to move less between sites and colonies compared to the 2018 post-breeding period (Figure 9).

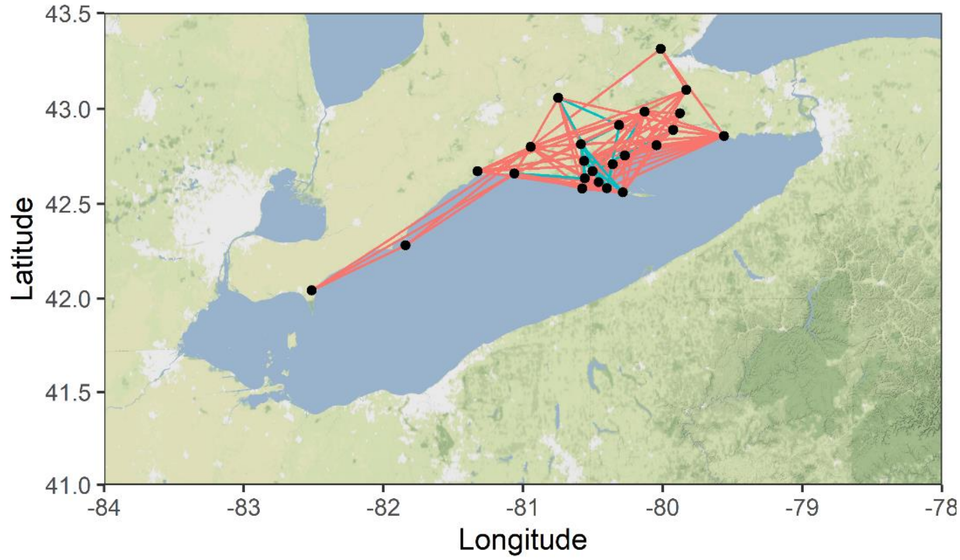

Figure 8. Movement paths for hatch-year Bank Swallows in 2018 and active Motus towers. Blue lines show movement from birds radio tagged at aggregate pit sites while red lines show movement from birds radio tagged at lakeshore sites.

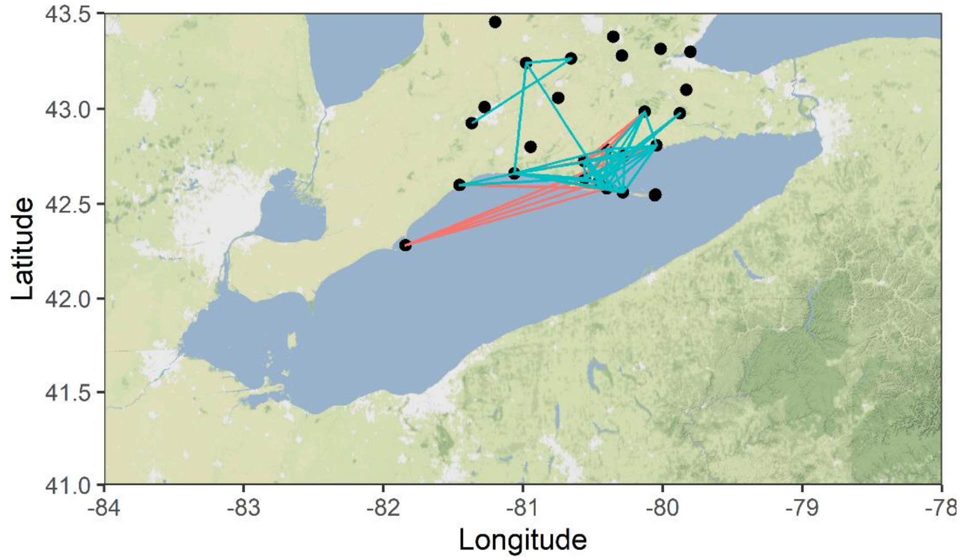

Figure 9. Movement paths for adult and hatch-year Bank Swallows in 2021 with active Motus towers. Blue lines show movement from birds radio tagged at aggregate pit sites while red lines show movement from birds radio tagged at lakeshore sites.

3.5 2018 hatch-year

Daily recapture probability was modelled for 72 birds with a confirmed wing chord length, mass, and fat score. Initial analysis found that the top model without covariates (AIC_c: 933.98, w_i: 0.580) was cubic in relationship to time (Table 4).

When testing recapture values with covariates, the top model included the covariate type (Table 5). On the logit scale, the β value for the effect of colony area being lakeshore was β_{pit} = -0.51 (-0.82, -0.20) (Table 6); corresponding to a lower daily recapture probability for aggregate pit colony birds compared to lakeshore colony birds colony birds (Figure 10). Since the confidence interval did not cover 0, this was a statistically significant effect (Table 6).

Daily apparent survival probability was modelled for 72 birds with a confirmed wing chord length, mass, and fat score. To determine the best survival models, the top recapture model (Table 5) was tested with quadratic survival, cubic survival and all possible models when including covariates. The covariates fat, sex, mass, and area had no significant effect on daily apparent survival probability. Models with an AICc value less than two included wing and type as covariates for survival (Table 7). There was a statistically significant effect of wing on daily apparent survival (β_{wing}= 0.35 (0.04, 0.65) (Table 6). Daily survival probability increased with wing length (Figure 11) and was higher at lakeshore colonies (Figure 12).

Table 4. p value assessment (without covariates) for hatch-year Bank Swallows radio tagged in 2018. t represents Time (day post-fledging). p represents daily recapture probability. 2° represents secondary periods. Superscripts represent whether daily survival probability or daily recapture probability has a linear, quadratic, or polynomial relationship to Time. npar represents the number of parameters included in a model. AICc represents the corrected AIC by using npar. w_i represents how much we can attribute a model to fitting the best compared to other models. Deviance represents the difference between the null deviance and model deviance. All models included Markovian movement. Only models with a ΔAIC_c value less than 2 are included. Models with a ΔAIC_c less than 2 are statistically supported. The top model showed a cubic relationship to p.

model	npar	AICc	ΔAICc	w_i	deviance
$\phi(t + t^2 + t^3)$ $p(t + t^2 + t^3 + 2°)$	33	933.98	0	0.580	1570.23

Table 5. p value assessment (with covariates) for hatch-year Bank Swallows radio tagged in 2018. t represents Time (day post-fledging). p represents daily recapture probability. 2° represents secondary periods. Superscripts represent whether daily survival probability or daily recapture probability has a linear, quadratic, or polynomial relationship to Time. npar represents the number of parameters included in a model. AICc represents the corrected AIC by using npar. w_i represents how much we can attribute a model to fitting the best compared to other models. Deviance represents the difference between the null deviance and model deviance. All models included Markovian movement. Only models with a ΔAIC_c value less than 2 are included. Models with a ΔAIC_c less than 2 are statistically supported. The top model included type as a covariate for p.

model	npar	AICc	ΔAICc	w_i	deviance
$\phi(t + t^2 + t^3)$ $p(t + t^2 + t^3 + 2° + Type)$	34	911.75	0	0.999	1545.74

Table 6. 2018 hatch-year top model coefficients. lcl represents the lower confidence limit. ucl represents the upper confidence limit. Compared to lakeshore birds, pit birds have a 40% lower odds of being detected.

	Estimate	SE	lcl	ucl	1-EXP(β)
ϕ: (Intercept)	0.60	0.26	0.1	1.11	
ϕ: t	1.42	0.34	0.76	2.08	
ϕ: t^2	-0.23	0.06	-0.36	-0.11	
ϕ: t^3	0.01	<0.01	<0.01	0.02	
ϕ: Wing	0.35	0.16	0.04	0.65	
ϕ: Type = pit	-0.62	0.3023	-1.21	-0.03	
γ′′: (Intercept)	-1.18	0.17	-1.52	-0.84	
γ′: (Intercept)	0.62	0.26	0.11	1.12	
p: (Intercept)	0.34	0.22	-0.09	0.77	
p: t	0.44	0.10	0.25	0.63	
p: t^2	-0.04	0.01	-0.07	-0.02	
p: t^3	<0.01	<0.01	<0.01	<0.01	
p: 2°	-1.22	0.17	-1.55	-0.88	
p: 3°	-1.19	0.17	-1.53	-0.86	
p: Type = pit	-0.51	0.16	-0.82	-0.20	0.40

Table 7. ϕ value assessment (including covariates) for hatch-year Bank Swallows radio tagged in 2018. t represents Time (day post-fledging). p represents daily recapture probability. 2° represents secondary periods. Superscripts represent whether daily survival probability or daily recapture probability has a linear, quadratic, or polynomial relationship to Time. npar represents the number of parameters included in a model. AICc represents the corrected AIC by using npar. w_i represents how much we can attribute a model to fitting the best compared to other models. Deviance represents the difference between the null deviance and model deviance. All models included Markovian movement. Only models with a ΔAIC_c value less than 2 are included. Models with a ΔAIC_c less than 2 are statistically supported. The top model included wing as a covariate for ϕ and type as a covariate for p.

model	npar	AICc	ΔAICc	w_i	deviance
$\phi(t + t^2 + t^3 + \text{Wing})\ p(t + t^2 + t^3 + 2° + \text{Type})$	35	908.97	0	0.528	834.27
$\phi(t + t^2 + t^3 + \text{Type})\ p(t + t^2 + 2° + \text{Type})$	35	909.84	0.86	0.341	1541.57

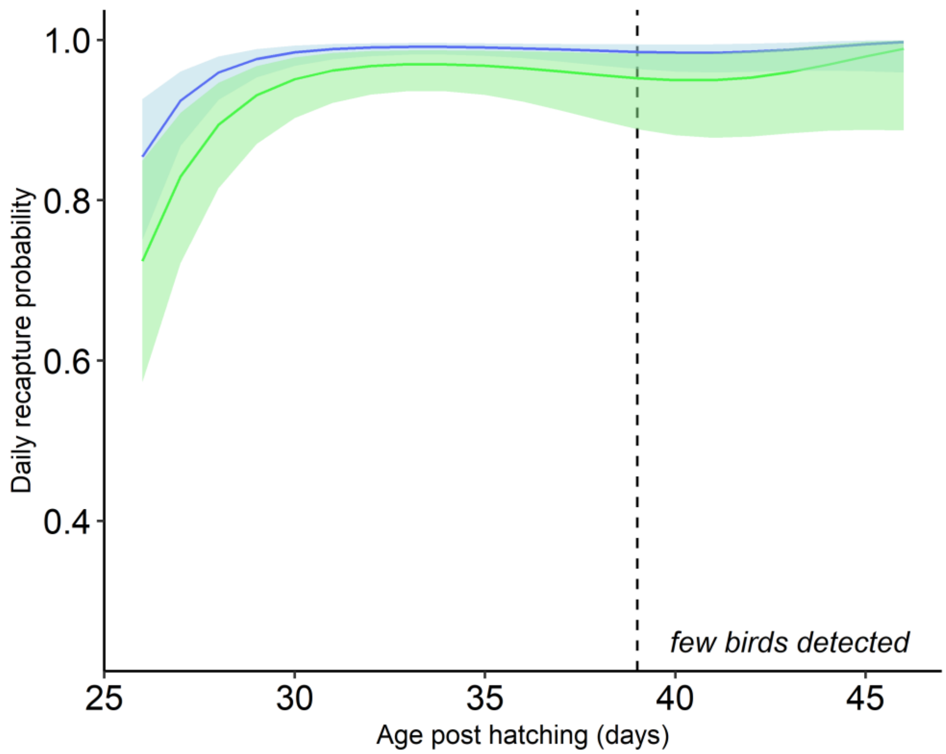

Figure 10. Daily recapture probabilities for hatch-year Bank Swallows in 2018. Lakeshore colony birds (N=42) are represented by the blue line and aggregate pit colony birds are represented by the green line. Confidence intervals for lakeshore colony birds are shown in light blue, and light green for aggregate pit colony birds. Daily recapture probability was higher for lakeshore colony birds compared to aggregate pit colony birds. The vertical line on age post hatching day 39 represents the last day at least five birds were detected in a secondary period.

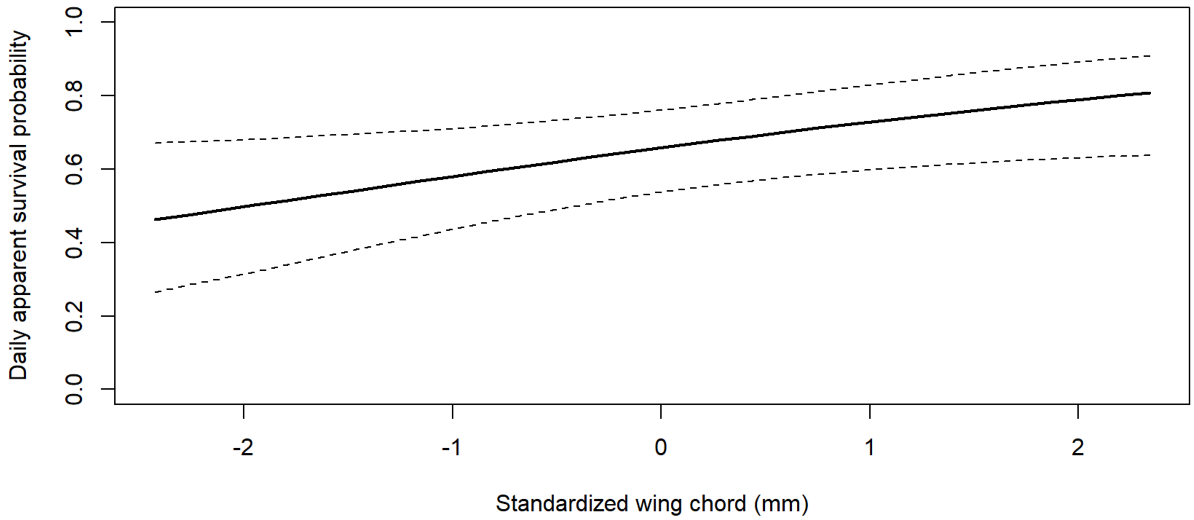

Figure 11. Mean daily apparent survival probability compared to standardized wing chord for hatch-year Bank Swallows radio tagged during the 2018 field season. Dotted lines indicate pointwise confidence intervals. Daily apparent survival probability increases as standardized wing chord length increases.

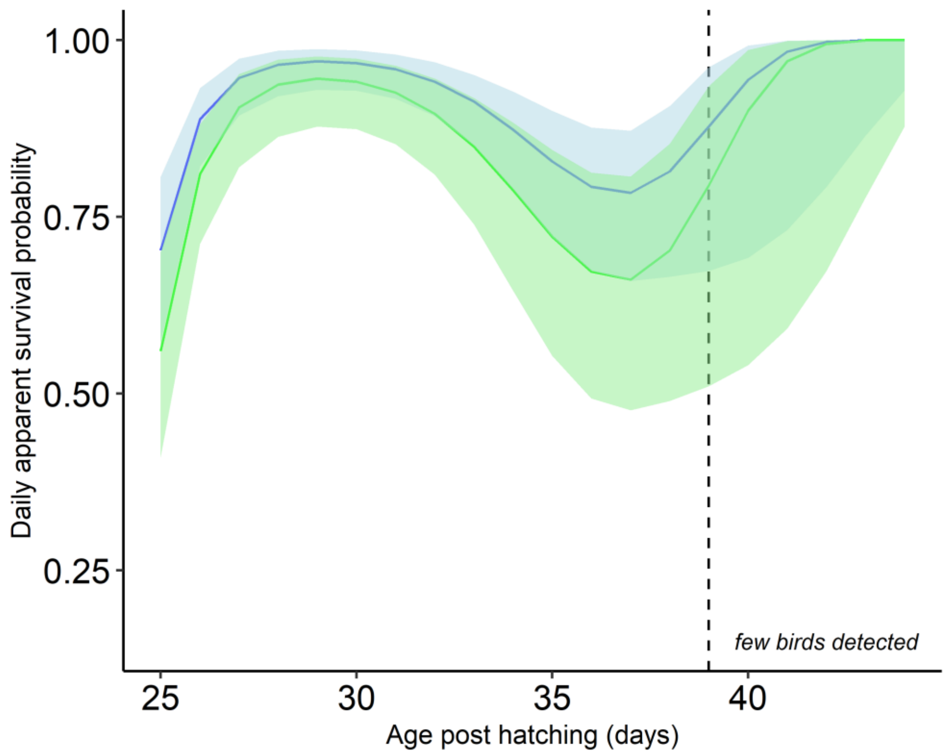

Figure 12. Daily apparent survival probability for hatch-year Bank Swallows in 2018. Lakeshore colony birds (N=42) are represented by the blue line and aggregate pit colony birds (N=30) are represented by the green line. Confidence intervals are displayed in light blue for lakeshore colony birds and light green for aggregate pit colony birds. Daily apparent survival probability began low, increased to its maximum value at approximately day 30 then decreases again. The vertical line on age post hatching day 39 represents the last day at least five birds were detected in a secondary period.

3.6 2021 hatch-year

Daily recapture probability was modelled for 69 birds with a confirmed wing chord length, mass, fat score and sex. Initial analysis found that the top model without covariates (AICc: 620.15, w_i: 0.676) was cubic in relationship to time (Table 8). When testing recapture values with covariates, the top model included colony area and the second top model included colony type as a covariate (Table 9). On the logit scale, the β value for the effect of area being lakeshore is $\beta_{lakeshore}$ = 0.70 (0.20, 1.21) (Table 10); corresponding to a higher daily recapture probability for lakeshore colony birds compared to inland colony birds (Figure 13). Since the confidence interval does not cover 0, this was a statistically significant effect.

Daily apparent survival probability was modelled for 69 birds with a confirmed wing chord length, mass, and fat score. To determine the best survival models, the top recapture model (Table 9) was tested with quadratic survival, cubic survival and all possible models when including covariates. The covariates colony area, colony type and sex had a significant effect on daily apparent survival probability. On the logit scale, the β value for the effect of colony type being pit is β_{pit} = -0.44 (-1.10. 0.21) (Table 10); corresponding to support of a higher daily apparent survival probability for lakeshore colony birds compared to pit colony. On the logit scale, the β value for the effect of colony area being lakeshore is $\beta_{lakeshore}$ = 0.53 (-0.24, 1.30) (Table 10); corresponding to support of a higher daily apparent survival probability for lakeshore colony birds compared to inland colony birds. On the logit scale, the β value for the effect of sex being female is β_{female} = 0.38 (-0.26, 1.02) (Table 10); corresponding to support of a higher daily apparent survival probability for female birds compared to male birds. Lakeshore colony birds had higher daily apparent survival probability compared to inland pit birds (Figure 14). The top model included no covariates for survival (Table 11).

Table 8. p value assessment (without covariates) for hatch-year Bank Swallows radio tagged in 2021. t represents Time (day post-fledging). p represents daily recapture probability. 2° represents secondary periods. Superscripts represent whether daily survival probability or daily recapture probability has a linear, quadratic, or polynomial relationship to Time. npar represents the number of parameters included in a model. AICc represents the corrected AIC by using npar. w_i represents how much we can attribute a model to fitting the best compared to other models. Deviance represents the difference between the null deviance and model deviance. All models included Markovian movement. Only models with a ΔAIC_c value less than 2 are included. Models with a ΔAIC_c less than 2 are statistically supported. The top model showed a cubic relationship to p.

model	npar	AICc	ΔAICc	w_i	deviance
$\phi(t + t^2 + t^3)$ $p(t + t^2 + t^3 + 2°)$	33	620.15	0	0.676	731.36
$\phi(t + t^2)$ $p(t + t^2 + t^3 + 2°)$	32	621.66	1.51	0.318	735.50

Table 9. p value assessment (with covariates) for hatch-year Bank Swallows radio tagged in 2021. t represents Time (day post-fledging). p represents daily recapture probability. 2° represents secondary periods. Superscripts represent whether daily survival probability or daily recapture probability has a linear, quadratic, or polynomial relationship to Time. npar represents the number of parameters included in a model. AICc represents the corrected AIC by using npar. w_i represents how much we can attribute a model to fitting the best compared to other models. Deviance represents the difference between the null deviance and model deviance. All models included Markovian movement. Only models with a ΔAIC_c value less than 2 are included. Models with a ΔAIC_c less than 2 are statistically supported. The top model included the covariate Area for p.

model	npar	AICc	ΔAICc	w_i	deviance
$\phi(t + t^2 + t^3)$ $p(t + t^2 + t^3 + 2° + Area)$	34	614.98	0	0.379	723.53
$\phi(t + t^2 + t^3)$ $p(t + t^2 + t^3 + 2° + Type)$	34	615.92	0.94	0.237	724.47
$\phi(t + t^2)$ $p(t + t^2 + t^3 + 2° + Area)$	33	616.16	1.18	0.210	727.37

Table 10. 2021 hatch-year top model beta coefficients. lcl represents the lower confidence limit. ucl represents the upper confidence limit. Lakeshore birds have 2x the odds of being detected compared to inland birds.

	Estimate	SE	lcl	ucl	EXP(β)
ϕ:(Intercept)	-0.08	0.26	-0.59	0.43	
ϕ: t	1.00	0.31	0.39	1.61	
ϕ: t^2	-0.16	0.06	-0.28	-0.03	
ϕ: t^3	0.01	<0.01	<0.01	0.01	
ϕ: Type = pit	-0.44	0.34	-1.10	0.21	
ϕ: Area = lakeshore	0.53	0.39	-0.24	1.30	
ϕ: Sex = female	0.38	0.33	-0.26	1.02	
γ′′:(Intercept)	-1.02	0.29	-1.59	-0.44	
γ′:(Intercept)	-0.15	0.49	-1.11	0.81	
p:(Intercept)	-0.87	0.35	-1.56	-0.19	
p: t	1.10	0.20	0.7	1.5	
p: t^2	-0.16	0.04	-0.24	-0.09	
p: t^3	0.01	<0.001	<0.001	0.01	
p: 2°	-1.19	0.23	-1.65	-0.73	
p: 3°	-1.65	0.25	-2.14	-1.17	
p: Area = lakeshore	0.70	0.26	0.20	1.21	2.01
p: Type = pit	-0.55	0.21	-0.96	-0.14	

Table 11. ϕ value assessment (including covariates) for hatch-year Bank Swallows radio tagged in 2021. t represents Time (day post-fledging). p represents daily recapture probability. 2° represents secondary periods. Superscripts represent whether daily survival probability or daily recapture probability has a linear, quadratic, or polynomial relationship to Time. npar represents the number of parameters included in a model. AICc represents the corrected AIC by using npar. w_i represents how much we can attribute a model to fitting the best compared to other models. Deviance represents the difference between the null deviance and model deviance. All models included Markovian movement. Only models with a ΔAIC_c value less than 2 are included. Models with a ΔAIC_c less than 2 are statistically supported. The top model included no covariates for ϕ and the covariate area for p.

model	npar	AICc	ΔAICc	w_i	deviance
$\phi(t + t^2 + t^3)$ $p(t + t^2 + t^3 + 2° + Area)$	34	614.98	0	0.177	723.53
$\phi(t + t^2 + t^3 + Area)$ $p(t + t^2 + t^3 + 2° + Area)$	35	615.83	0.85	0.115	721.70
$\phi(t + t^2 + t^3 + Area)$ $p(t + t^2 + t^3 + 2° + Area)$	35	615.83	0.85	0.115	721.70
$\phi(t + t^2 + t^3 + Type)$ $p(t + t^2 + t^3 + 2° + Area)$	35	615.90	0.92	0.112	721.77
$\phi(t + t^2)$ $p(t + t^2 + t^3 + 2° + Area)$	33	616.16	1.18	0.098	727.37
$\phi(t + t^2 + t^3 + Sex)$ $p(t + t^2 + t^3 + 2° + Area)$	35	616.30	1.33	0.091	722.17
$\phi(t + t^2 + t^3 + Sex)$ $p(t + t^2 + t^3 + 2° + Area)$	35	616.30	1.33	0.091	722.17
$\phi(t + t^2 + Type)$ $p(t + t^2 + t^3 + 2° + Area)$	34	616.65	1.67	0.077	725.20

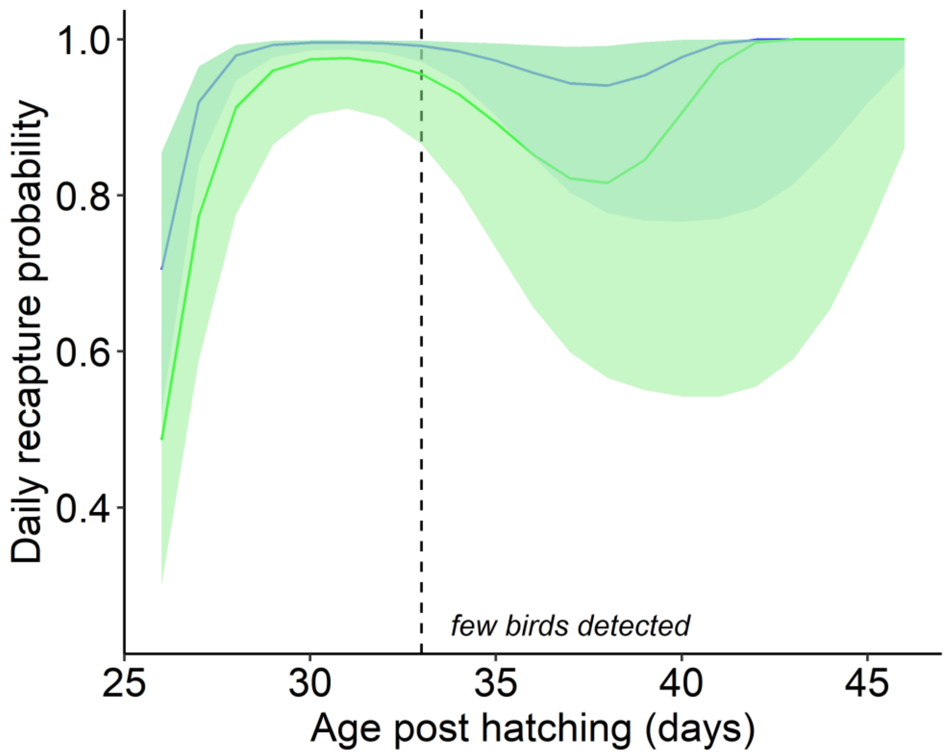

Figure 13. Daily recapture probability rates for hatch-year Bank Swallows radio tagged during the 2021 field season. Lakeshore colony birds (N=39) are represented by the blue line and aggregate pit colony birds (N=36) are represented by the green line. Confidence intervals are displayed in light blue for lakeshore colony birds and light green for aggregate pit colony birds. Daily recapture probability rates are slightly higher for lakeshore colony birds compared to inland pit colony birds. The vertical line on age post hatching day 33 represents the last day at least five birds were detected in a secondary period.

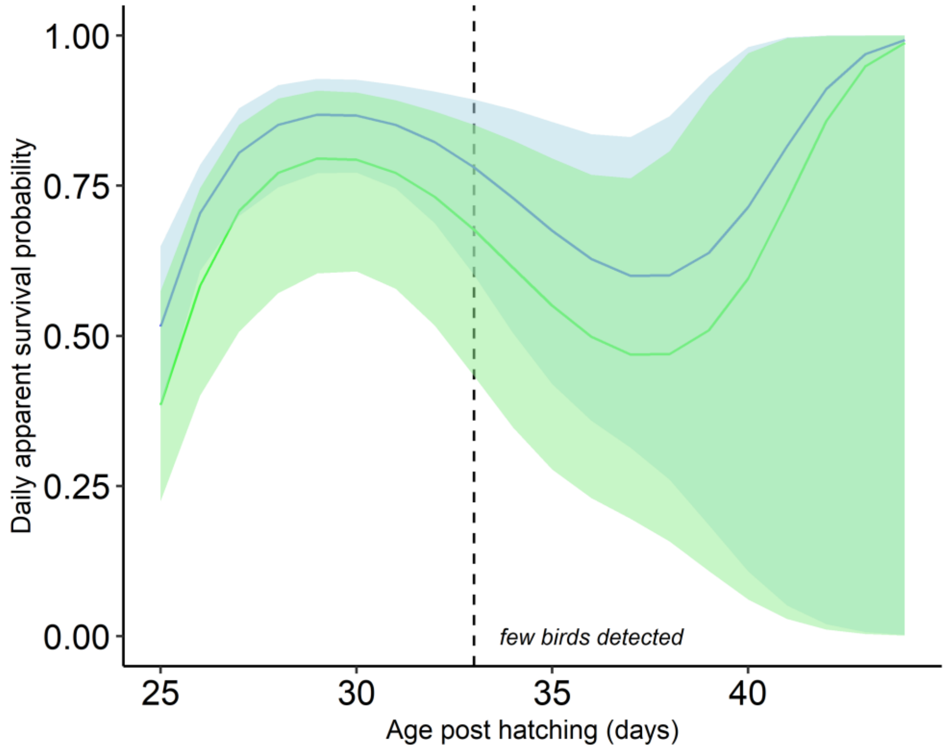

Figure 14. Daily apparent survival probabilities for lakeshore colony (N=50) and inland colony (N=19) hatch-year Bank Swallows radio tagged during the 2021 field season. Lakeshore colony birds and their confidence intervals are shown in light blue. Inland pit colony birds and their confidence intervals are shown in light green. Daily apparent survival probability rapidly increases post-fledging and reaches its peak at approximately age post-hatching day 29. After post hatching day 29, daily apparent survival probability decreases. The vertical line on age post hatching day 33 represents the last day at least five birds were detected in a secondary period.

3.7 2021 adult

Daily recapture probability was modelled for 116 birds with a confirmed wing length, mass, fat score and presence/absence of a brood patch. Initial analysis found that the top model without covariates (AIC_c: 1663.67, weight: 0.490) was cubic in relationship to time (Table 12). When testing recapture values with covariates, the top model (AIC_c: 1586.40, w_i: 1.000) included colony type as the top covariate (Table 13). There was a statistically significant effect of colony type on daily probability of recapture (β_{pit} = -1.08 (-1.32, -0.84) (Table 14); corresponding to the lower daily recapture probability at aggregate pit colonies compared to lakeshore colonies (Figure 15).

Survival rates were modelled for 116 birds with a confirmed wing length, mass, fat score and presence/absence of a brood patch. To determine the top survival model, the top recapture model (Table 13) was tested with quadratic survival, cubic survival and all possible models when including covariates. The top covariate to affect daily apparent survival probability was sex (Table 15). There was a statistically significant effect of sex on daily apparent survival (β_{female}= 0.27 (0.35, 1.41) (Table 14); corresponding to a higher daily apparent survival probability in female birds compared to adult birds (Figure 16).

Table 12. p value assessment (without covariates) for adult Bank Swallows radio tagged in 2021. t represents Time (day post-fledging). p represents daily recapture probability. 2° represents secondary periods. Superscripts represent whether daily survival probability or daily recapture probability has a linear, quadratic, or polynomial relationship to Time. npar represents the number of parameters included in a model. AICc represents the corrected AIC by using npar. w_i represents how much we can attribute a model to fitting the best compared to other models. Deviance represents the difference between the null deviance and model deviance. All models included Markovian movement. Only models with a ΔAIC_c value less than 2 are included. Models with a ΔAIC_c less than 2 are statistically supported. The top model showed a cubic relationship to p.

model	npar	AICc	ΔAICc	w_i	deviance
$\phi(t + t^2 + t^3)$ $p(t + t^2 + t^3 + 2°)$	33	1663.67	0	0.490	2357.06
$\phi(t + t^2)$ $p(t + t^2 + t^3 + 2°)$	32	1664.00	0.32	0.417	2359.54

Table 13. p value assessment (with covariates) for adult Bank Swallows radio tagged in 2021. t represents Time (day post-fledging). p represents daily recapture probability. 2° represents secondary periods. Superscripts represent whether daily survival probability or daily recapture probability has a linear, quadratic, or polynomial relationship to Time. npar represents the number of parameters included in a model. AICc represents the corrected AIC by using npar. w_i represents how much we can attribute a model to fitting the best compared to other models. Deviance represents the difference between the null deviance and model deviance. All models included Markovian movement. Only models with a ΔAIC_c value less than 2 are included. Models with a ΔAIC_c less than 2 are statistically supported. The top model included a covariate effect of colony type on p.

model	npar	AICc	ΔAICc	w_i	deviance
$\phi(t + t^2)$ $p(t + t^2 + t^3 + 2° + Type)$	33	1586.40	0	1.000	2279.79

Table 14. 2021 adult top model coefficients. lcl represents the lower confidence limit. ucl represents the upper confidence limit. Compared to lakeshore birds, pit birds have 66% lower odds of being detected. Female birds have 2.4x the odds of surviving compared to male birds.

	Estimate	SE	lcl	ucl	1-EXP(β)	EXP(β)
ϕ:(Intercept)	0.02	0.28	-0.53	0.57		
ϕ: t	1.68	0.49	0.71	2.64		
ϕ: t^2	-0.32	0.12	-0.54	-0.09		
ϕ: t^3	0.02	0.01	<0.001	0.03		
ϕ: Sex = female	0.88	0.27	0.35	1.41		2.4
γ'':(Intercept)	-0.98	0.13	-1.23	-0.72		
γ': (Intercept)	1.47	0.2	1.08	1.86		
p: (Intercept)	0.47	0.17	0.14	0.80		
p: t	0.57	0.08	0.42	0.72		
p: t^2	-0.05	0.01	-0.07	-0.03		
p: t^3	<0.001	<0.001	<0.001	<0.001		
p: 2°	-0.79	0.14	-1.07	-0.50		
p: 3°	-0.74	0.14	-1.02	-0.45		
p: Type = pit	-1.08	0.12	-1.32	-0.84	0.66	

Table 15. ϕ value assessment (including covariates) for adult Bank Swallows radio tagged in 2021. t represents Time (day post-fledging). p represents daily recapture probability. 2° represents secondary periods. Superscripts represent whether daily survival probability or daily recapture probability has a linear, quadratic, or polynomial relationship to Time. npar represents the number of parameters included in a model. AICc represents the corrected AIC by using npar. w_i represents how much we can attribute a model to fitting the best compared to other models. Deviance represents the difference between the null deviance and model deviance All models showed Markovian movement. Only models with a ΔAICc value less than 2 are included. Models with a ΔAICc less than 2 are statistically supported. The top model included a covariate effect of sex for ϕ and type for p.

model	npar	AICc	ΔAICc	w_i	deviance
ϕ($t + t^2 + t^3$ + Sex) p($t + t^2 + t^3$ + 2° + Type)	35	1565.63	0	0.88	2254.71

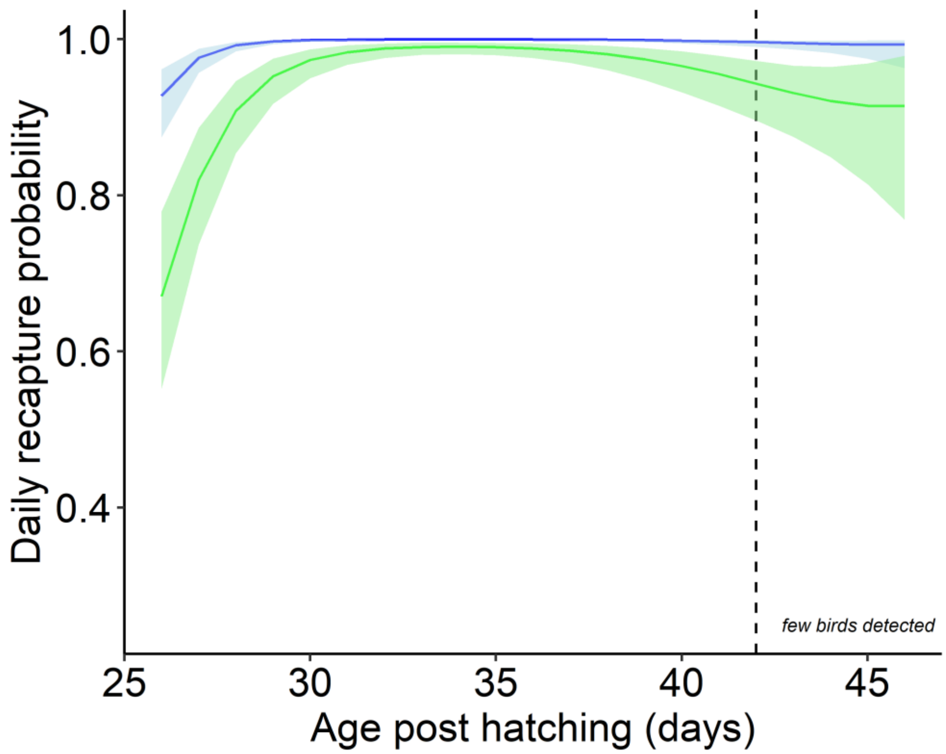

Figure 15. Daily recapture probability for adult Bank Swallows radio tagged during the 2021 field season. Lakeshore colony birds (N=76) are represented by the blue line and the green line represents aggregate pit colony birds (N=40). Daily recapture began low for aggregate pit colony birds and increased further into the post-breeding period. The vertical line on age post hatching day 42 represents the last day at least five birds were detected in a secondary period. Lakeshore colony birds had high daily recapture probabilities throughout the post-breeding period.

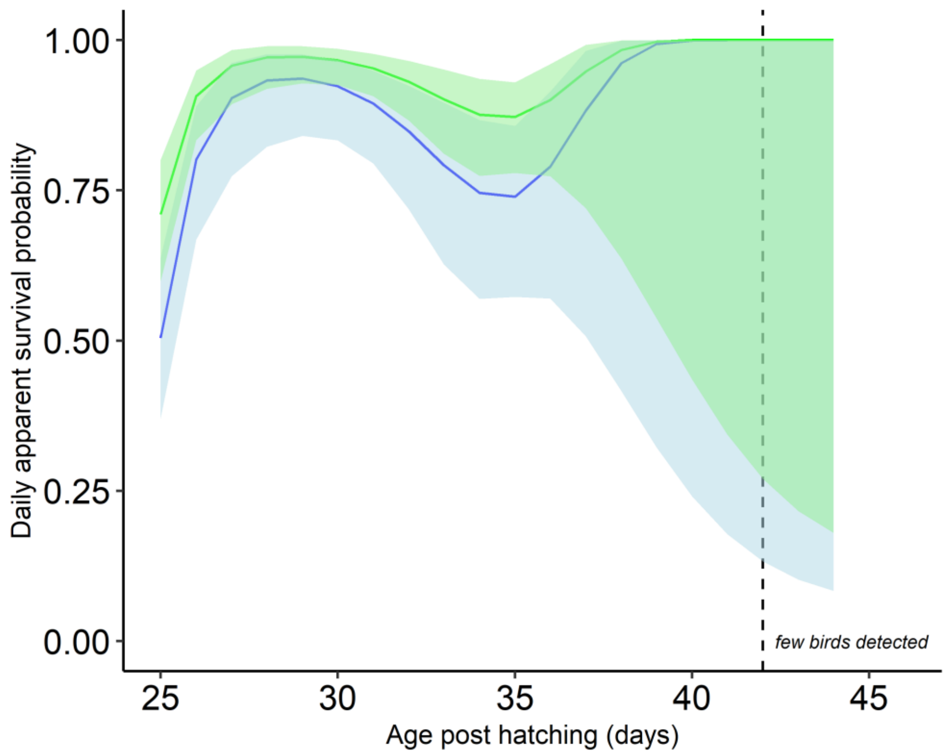

Figure 16. Daily apparent survival probability during the post-breeding period for adult Bank Swallows radio tagged during the 2021 field season. Male birds (N=20) are represented by the blue line and female birds (N=51) are represented by the green line. The vertical line on age post hatching day 42 represents the last day at least five birds were detected in a secondary period. Daily apparent survival probability followed a cubic relationship for male and female birds.

3.8 2021 hatch-year and adult comparison

Daily recapture probability began low (~0.75) for hatch-year and adult birds (Figure 19). At approximately day 30, daily recapture reached approximately 0.95 for hatch-year and adult birds (Figure 19). Daily apparent survival probability was higher in adult birds compared to hatch-year birds (Figure 20). The daily estimate of mortality for 2021 hatch-year birds was calculated by subtracting the 2021 hatch-year bird daily apparent survival probabilities from the 2021 adult daily apparent survival probabilities. The daily estimate of mortality was approximately 12.5% for hatch-year birds from age post hatching day 25 to age post-hatching day 33 (Figure 20). The cumulative estimate of tag loss and mortality for 2018 and 2021 birds was calculated by subtracting daily apparent survival probabilities from 1. We estimate that approximately 10% of hatch-year birds were lost from age post-hatching day 25 to age post-hatching day 33 (Figure 21).

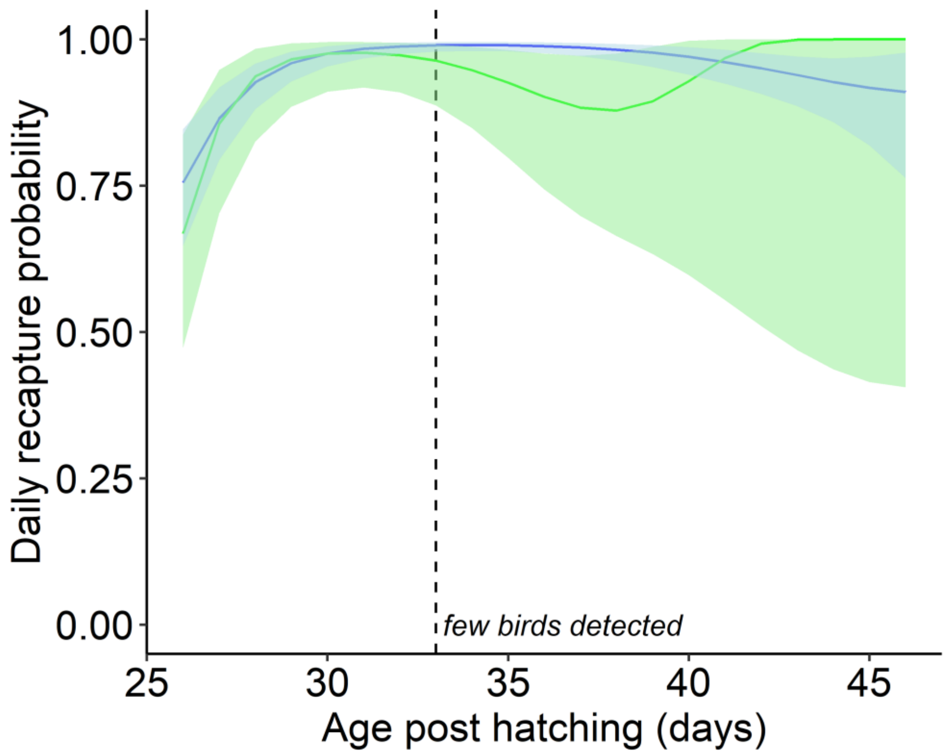

Figure 17. Daily recapture rates for hatch-year and adult Bank Swallows radio tagged during the 2021 field season. Hatch year birds (N=29) are represented by the green line, adult birds (N=71) are represented by the blue line. The vertical line on age post hatching day 33 represents the last day at least five hatch-year birds were detected in a secondary period in 2021.

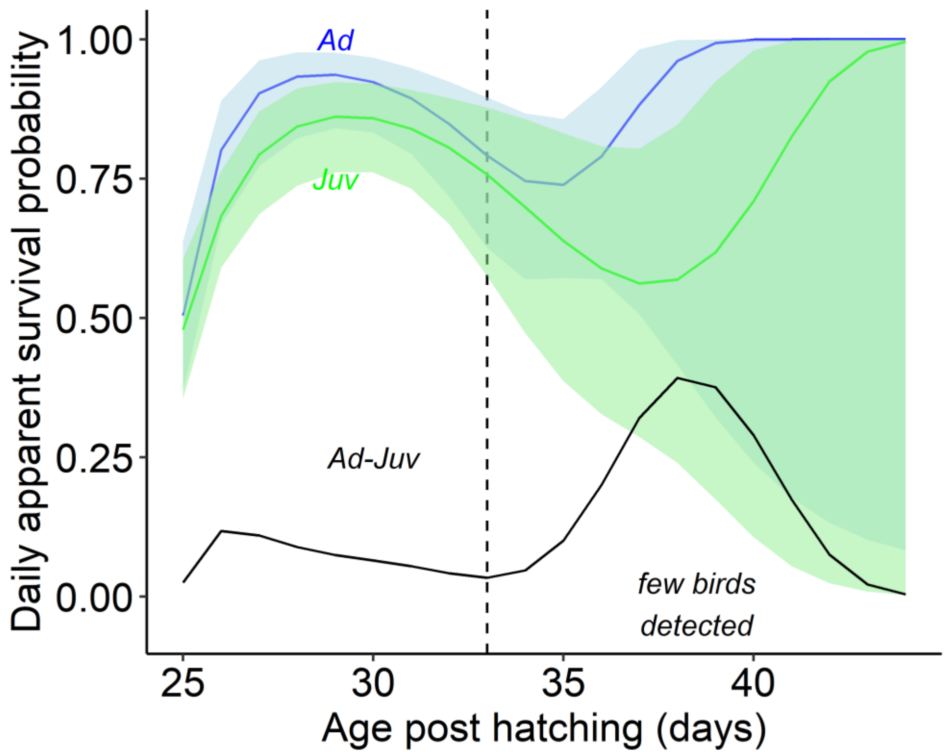

Figure 18. Daily survival rates for hatch-year and adult Bank Swallows radio tagged during the 2021 field season. Hatch year birds (N=29) are represented by the green line, adult birds (N=71) are represented by the blue line. The black line shows the daily apparent survival difference in adults and hatch-years (estimate of daily apparent mortality). The vertical line on age post hatching day 33 represents the last day at least five hatch-year birds were detected in a secondary period in 2021.

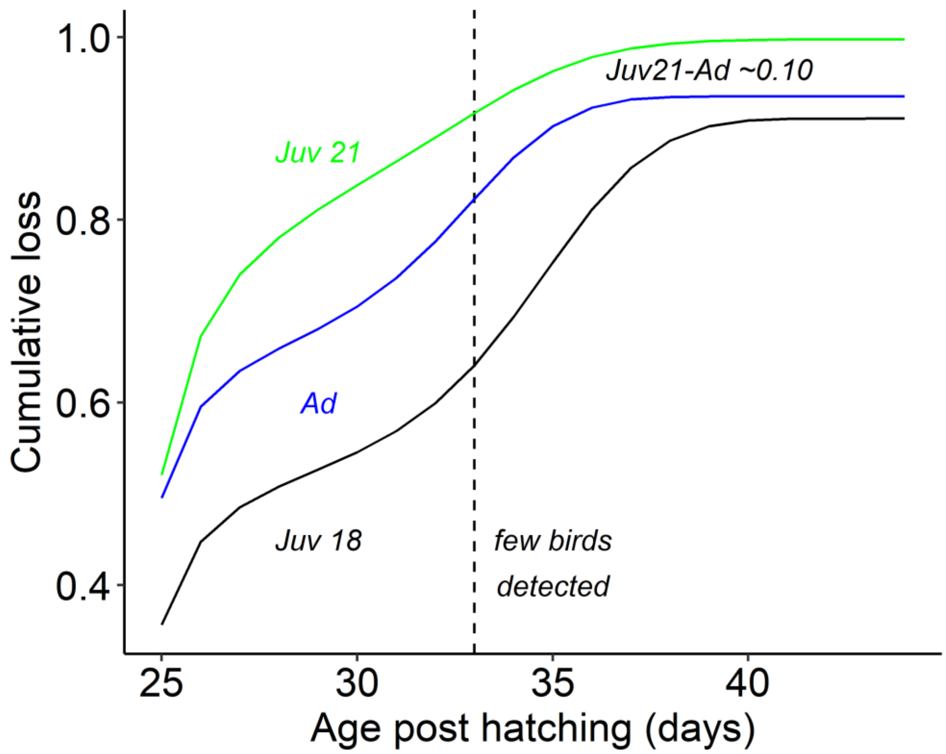

Figure 19. Cumulative estimate of tag loss and actual mortality. 2021 hatch-year birds (N=29) are represented by the green line, 2021 adult birds (N=71) are represented by the blue line and 2018 hatch-year birds (N=72) are represented by the black line. Assuming adult survival is close to 100%, the blue line shows adult tag loss. The difference between the blue and green lines is the rough estimate of 2021 hatch-year cumulative mortality. The vertical line on age post-hatching day 33 represents the last day at least five 2021 hatch-year birds were detected in a secondary period.

3.9 Morphological variability among colony types

Mean body mass at capture (±SE) and mean wing chord length at capture (±SE) did not differ between adult Bank Swallows caught at lakeshore colonies compared to adult Bank Swallows caught at aggregate pit site colonies in 2021 (Table 16, Table 17, Table 18). The random effect of colony site (e.g., Blythedale, Embro, Bossuyt) explains approximately 8% of the variation in adult mean body mass and 0% of the variation in adult wing chord (Table 18). Mean wing chord length at capture (±SE) did not differ between 2021 hatch-year Bank Swallows caught at lakeshore colonies compared to 2021 hatch-year Bank Swallows caught at aggregate pit site colonies (Table 17). The random effect of colony site explains approximately 10% of the variation in hatch-year wing chord (Table 17). However, mean body mass at capture (±SE) did significantly differ between 2021 lakeshore hatch-year Bank Swallows and 2021 aggregate pit hatch-year Bank Swallow (Table 18). 2021 lakeshore hatch-year Bank Swallows had larger masses at capture compared to 2021 aggregate pit hatch-year Bank Swallows (Figure 22). The random effect of colony site explains approximately 11% of the variation in hatch-year mass (Table 18). 2018 hatch-year birds had larger mean body mass at capture (±SE) and mean wing chord length at capture (±SE) compared to 2021 hatch-year birds (Table 16). Mean wing chord length at capture (±SE) and mean body mass at capture (±SE) did not differ between 2018 hatch-year Bank Swallows caught at lakeshore colonies compared to 2018 hatch-year Bank Swallows caught at aggregate pit site colonies (Table 17, Table 18). The random effect of colony site explains approximately 8% of the variation in wing chord and 0% of the variation in 2018 hatch-year mass (Table 17, Table 18).

Table 16. Morphological variability in mean body mass at capture and mean wing chord length at capture for adult and hatch-year birds captured at lakeshore colonies and aggregate pit colonies during the 2018 and 2021 post-breeding periods.

Year	Type	Age	Sex	Number of individuals	Mean body mass (g) (±SE)	Mean wing chord length (mm) (±SE)
2021	Lakeshore	Adult	Male	37	14.18±0.10	98.35±0.22
2021	Lakeshore	Adult	Female	56	14.19±0.10	98.36±0.22
2021	Pit	Adult	Male	11	14.38±0.10	98.33±0.27
2021	Pit	Adult	Female	37	14.38±0.10	98.32±0.26
2021	Lakeshore	Hatch-year	Male	17	12.91±0.13	89.86±0.50
2021	Lakeshore	Hatch-year	Female	19	13.00±0.12	89.96±0.48
2021	Pit	Hatch-year	Male	19	12.76±0.09	90.29±0.38
2021	Pit	Hatch-year	Female	17	12.80±0.09	90.52±0.38
2018	Lakeshore	Hatch-year	Male	542	13.35±0.03	99.50±0.07
2018	Lakeshore	Hatch-year	Female	663	14.36±0.03	99.49±0.10
2018	Pit	Hatch-year	Male	155	13.23±0.03	99.60±0.12
2018	Pit	Hatch-year	Female	194	14.52±0.03	99.54±0.11

Table 17. Effect of colony type on wing (mm) chord for 2018 hatch year, 2021 hatch-year and 2021 adult birds. A linear mixed model with a random effect of colony site was used to compare the effect of colony type on wing chord. Since all confidence intervals cover 0, there is no statistical effect of colony type on wing chord.

Group		Estimate	SE	t value	Confidence Interval
2018 hatch-year	Intercept	93.73	0.53	175.775	-
	Type = pit	-1.45	0.83	-1.748	(-3.17,0.40)
2021 hatch-year	Intercept	89.59	1.05	85.016	-
	Type = pit	-0.38	1.50	-0.251	(-3.75, 2.86)
2021 adult	Intercept	98.47	0.29	341.575	-
	Type = pit	-0.05	0.49	-0.099	(-1.04, 0.95)

Table 18. Effect of colony type on mass (g) for 2018 hatch year, 2021 hatch-year and 2021 adult birds. A linear mixed model with a random effect of colony site was used to compare the effect of colony type on mass. Confidence intervals that cover 0 show no statistical effect of colony type on mass. There is no statistical effect of colony type on mass for 2018 hatch-year and 2021 adult birds. Confidence intervals that do not cover 0 show a statistical effect of colony type on mass. There is a statistical effect of colony type on 2021 hatch-year mass.

Group		Estimate	SE	t value	Confidence Interval
2018 hatch-year	Intercept	12.92	0.13	103.030	-
	Type = pit	0.16	0.19	0.846	(-0.22, 0.58)
2021 hatch-year	Intercept	13.35	0.23	56.996	-
	Type = pit	-0.91	0.33	-2.735	(-1.69, -0.19)
2021 adult	Intercept	14.06	0.17	83.650	-
	Type = pit	0.49	0.29	1.725	(-0.12,1.10)

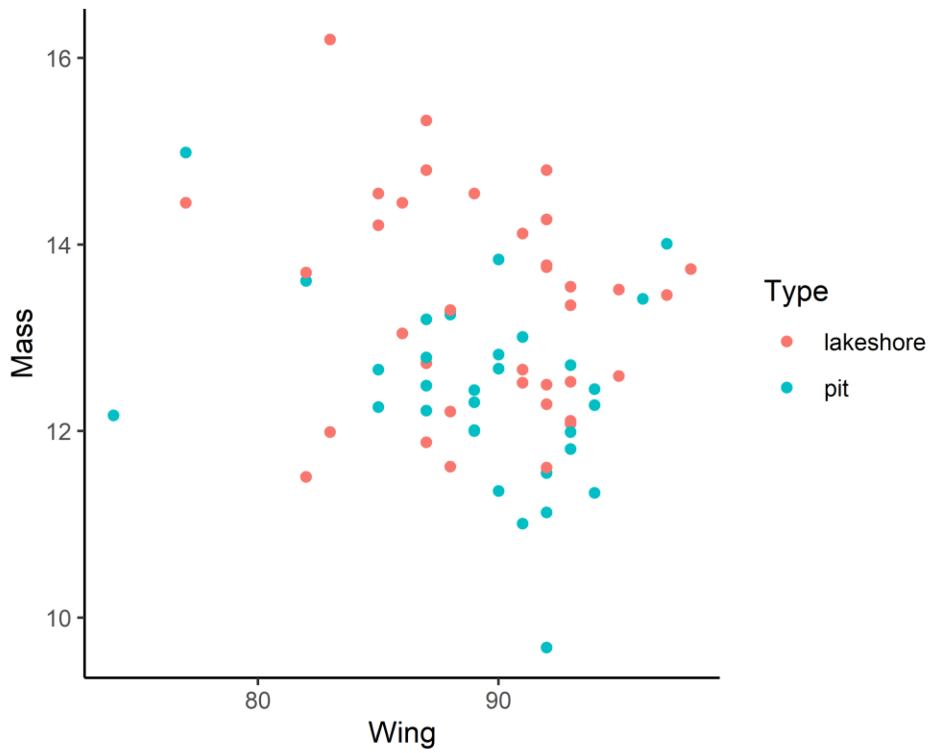

Figure 20. Standardized wing chord (mm) plotted against mass at capture (g) for hatch-year birds radio tagged in 2021. Birds radio tagged at lakeshore colonies are shown in red while birds radio tagged at aggregate pit colonies are shown in blue. Lakeshore colony birds have higher mass values compared to aggregate pit colony birds.

Discussion

The post-breeding period has been shown to be a period of high mortality for migratory birds during their annual cycle (Cox et al. 2014, Evans 2018). Increases in mortality in the post-breeding period makes this a critical life stage for migratory birds that can affect songbird population growth rates (Lang et al. 2002, Kershner et al. 2004). In my thesis, I examined daily recapture probability and daily apparent survival probability for hatch-year and adult Bank Swallows during the 2018 and 2021 post-breeding periods. During capture, morphological factors (sex, brood patch condition, fat score, wing chord length and mass) and environmental factors (colony type and colony area) were recorded and used as covariates in robust design models. Automated radio telemetry was used to acquire data for the mark recapture models, a method previously used on hatch-year Southwestern Ontario Barn Swallow (Evans 2018). Because fledglings and young birds are expected to have low survival rates during the post-breeding period (Rush and Stutchbury 2008, Jackson et al. 2011, Rickenbach et al. 2011, Cox et al. 2014, Boynton et al. 2020, Evans et al. 2020), the first hypothesis I tested was that hatch-year birds would have a lower daily apparent survival probability compared to adults.

The second hypothesis I tested was that birds radio tagged at lakeshore colonies would have a higher daily apparent survival probability compared to birds radio tagged at aggregate pit colonies. Based on fatty acid and plasma lipid stable hydrogen isotope analyses, Génier et al. (2021) found that lakeshore Bank Swallows consumed more emergent aquatic insects compared to Bank Swallows that form colonies in aggregate pits. This may result in a nutritional disadvantage to aggregate pit Bank Swallows supporting the idea that these pits are “ecological traps” (Génier et al. 2021). Habitat persistence (ability of burrows to persist and be functional) of Bank Swallows has been found to be higher at lakeshore colonies compared to aggregate pit colonies (Burke 2017). I predicted that the nutritional disadvantage and lower habitat persistence would result in a lower daily apparent survival probability for birds radio tagged at aggregate pit colonies compared to birds radio tagged at lakeshore colonies.

4.1 Radio tag retention during the post-breeding period

In this study, Lotek NTQB2-2 radio tags were fixed to elastic harnesses and then attached to Bank Swallows using the figure-8 leg loop method (Rappole and Tipton 1991). When individual encounter histories were created for birds, it was discovered that detections began to drastically lower 10 days post-tagging. I considered that the decrease in detections could be due to three possible factors: emigration from the study area, true mortality, or tag failure/loss. Emigration from the study area could not be a factor as most birds remained on the study area and were not detected south of Lake Erie during this period. The amount of time spent on post-breeding grounds has been studied in other swallow species as well (Evans 2018). Hatch-year Barn Swallows from first broods start their southward migration at around 30 days of age and hatch-year Barn Swallows from second broods start their southward migration at around 50 days of age (Evans 2018). Movement paths for Bank Swallows radio tagged in 2018 and 2021 show 0 birds crossing Lake Erie: a sign of birds beginning their southward migration (Figure 15, Figure 16). During the post-breeding period before southward migration in August, adult and hatch-year Bank Swallow roost communally and perform dusk circling behaviour in the vicinity of Long Point (Environment and Climate Change Canada 2022). Due to birds not beginning their southward migration until August, I can safely conclude that emigration from the study area did not cause the decrease in detections.

The second factor that could be the cause of decrease in detections is true mortality. True mortality does not usually increase at such a fast rate for hatch-years during the post breeding period (Cox et al. 2014). Initial daily survival rates for newly fledged hatch-years starts relatively low (~80%) and as hatch-years begin to become fully independent, daily survival rates increase further (~95%) (Naef-Daenzer and Grüebler 2016). Survival rates of fledglings during the post-breeding period improve as fledglings age (Cox et al. 2014, Naef-Daenzer and Grüebler 2016, Evans 2018, Evans et al. 2020). Fledgling survival rates level off after approximately 20 days to a relatively high survival rate similar to adults during later periods of the second stage of the post-breeding period (Cox et al. 2014). Weekly adult Barn Swallow survival during the breeding/post-breeding period is estimated to be approximately 99% (±0.007) (SE) (Grüebler et al. 2014). Total survival for adult Barn Swallow during the breeding/post-breeding period is estimated to be approximately 80% (±0.12) (SE) (Grüebler et al. 2014). A 2016 meta-analysis by Naef-Daenzer and Grüebler analyzed weekly survival estimates from 123 data series based on studies of 65 altricial species, covering weeks 1-13 post-fledging. Post-fledging survival was low immediately after fledging the nest, then steadily increased to a median weekly survival rate greater than 90% from post-fledging week 2 to week 10 (Naef-Daenzer and Grüebler 2016). This pattern in post-fledging survival was not observed in this study so I can assume the cause of the rapid decrease in detections was not solely a result of true mortality.

The third factor that could be the cause of the decrease in detections is tag failure/loss. Tag retention has been studied in aerial insectivores (Naef-Daenzer et al. 2011, Evans 2018, Evans et al. 2020). Evans et al. (2020) showed high tag retention in adult Barn Swallow. Daily apparent survival reached 100% by the end of their 56 day tracking period, suggesting radio tags did not prematurely fail in their study (Evans et al. 2020). Radio tags in the Evans et al. (2020) study had an estimated minimum lifespan of 58 days. In a separate study, Evans and colleagues examined tag retention in 38 pre-breeding adult Barn Swallows that were radio tagged and recaptured throughout the breeding season (Evans et al. 2020). The average minimum tag retention was 63.25 ± 4.70 (SE) days so tag retention was assumed to be close to or equal to 100% (Evans et al. 2020).

There are two possibilities that could have caused the decrease in detections during the post-breeding period. The first possibility is tag failure. The estimated total lifespan for tags used in my study was 106 days. Detections began to significantly drop off approximately 10 days post-tagging. While unlikely, this could be due to the batteries of the tags being faulty. The second possibility is tag loss. Motus.org lists guidelines for creating tag harnesses based on species and the mass range for a particular species. Guidelines for Bank Swallow recommend a harness size between 32-34 mm for a bird weighing between 10-13 g. The average weight of adult and hatch-year Bank Swallows tagged during my 2021 field season was 13.73 g. 126/190 birds radio tagged weighed more than the maximum limit for a 32-34 mm harness size. The average weight of hatch-year Bank Swallows tagged during the 2018 field season was 12.96 g. 36/76 birds radio tagged weighed more than the maximum limit for a 32-34 mm harness size. Perhaps birds weighing more than the recommended maximum limit influenced tag retention. A possible explanation for the sudden drop off in tag detections in hatch-years and adults is exposure to environmental factors. 27-day old Red-legged Partridge (*Alectoris rufa*) chicks had a reduced retention time for transmitters in the field due to density of bushes and exposure to environmental factors (Mateo-Moriones et al. 2012). Environmental factors may affect the tag retention time in Bank Swallows. Before breeding begins, adult male Bank Swallows excavate burrows and the nest chamber while adult female Bank Swallows build most of the nest (COSEWIC 2013). The number of burrows in a colony is almost always more than the total amount of breeding pairs (COSEWIC 2013). Adult Bank Swallow will provision their young by entering and leaving burrows prior to and around the time of fledging (COSEWIC 2013). The repetition of entering and leaving burrow entrances may impact the ability of tags to stay intact in adult Bank Swallows. Fledgling Bank Swallows will use nest burrows for roosting/resting up to one week post-fledging (COSEWIC 2013). In the United Kingdom, independent hatch-year Sand Martins (common name for Bank Swallows outside of the Americas) have been seen visiting numerous colonies during their dispersal from the nest (Mead and Harrison 1979). Visiting numerous colonies is done to assess the suitability of breeding sites for future breeding seasons (Mead and Harrison 1979). Independent hatch-year Bank Swallow in the United Kingdom will disperse several hundred kilometres and use different nightly roost sites while adults will use a single roost site close to their breeding colony (Mead and Harrison 1979). The repetitive nature of using burrows as a roosting/resting site and assessment of multiple colonies may reduce tag retention in hatch-year Bank Swallows. Ontario populations of breeding adult Bank Swallow will regularly fly 30 kilometres away from their active nests to roost overnight in marshes (Falconer et al. 2016b, Saldanha et al. 2019). It is suggested that roosting away from breeding colonies may reduce predation risk for adults, increase feeding opportunities, reduce the risk of mortality from collapsing banks, facilitate social interactions or provide alternative thermal environments (Falconer et al. 2016b, Saldanha et al. 2019). I hypothesize that common movement far away from breeding colonies for roosting activities may affect tag retention in Bank Swallows. Movement through vegetation or the sheer amount of movement during roosting activities may affect tag retention.

4.2 Morphological variability among colony types

Adult Bank Swallows did not differ in mean body mass (±SE) at capture or mean wing chord length (±SE) between colony types (Table 21). Mean body mass at capture (±SE) did significantly differ between 2021 hatch-year Bank Swallows caught at lakeshore colonies compared to hatch-years caught at aggregate pit colonies (Table 21). Lakeshore colony birds had significantly larger masses compared to aggregate pit birds (Table 21). Mean body mass at capture (±SE) did significantly differ between 2018 hatch-year Bank Swallows caught at lakeshore colonies compared to hatch-years caught at aggregate pit colonies (Table 21). Lakeshore colony birds had significantly larger masses compared to aggregate pit birds (Table 21). 2018 hatch-year Bank Swallows did have significantly larger mean body mass at capture (±SE) compared to 2021 hatch-year Bank Swallows.

I propose that 2021 hatch-year Bank Swallows at lakeshore colonies had a higher overall mean mass due to the proposed nutritional disadvantage that results from Bank Swallows nesting at inland aggregate pit sites (Génier et al. 2021). Génier et al (2021) showed stable hydrogen isotope ratios of juvenile Bank Swallow tail feathers to be higher at inland pit sites compared to lakeshore sites. Aquatic emergent chironomids have been found to have higher stable hydrogen isotope ratios compared to terrestrial dipterans. Lakeshore colony Bank Swallows consume more emergent aquatic insects compared to Bank Swallows from aggregate pits. This may result in a nutritional disadvantage to aggregate pit Bank Swallows. Dietary differences were also found in polyunsaturated fatty acid profiles of Bank Swallows; lakeshore colony Bank Swallows consumed chironomids that had higher levels of omega-3 eicosapentaenoic acid compared to aggregate pit colony Bank Swallows (Génier et al. 2021). A nutritional disadvantage for aggregate pit Bank Swallows could lead to fledglings not receiving the same quality of food as lakeshore colony Bank Swallows during the parental care phase of the post-breeding period.

4.3 Daily recapture probability during the post-breeding period

Daily recapture probability was expected to be high (greater than 70%) throughout most of the post-breeding period for adult and hatch-year birds (García-Pérez et al. 2014, Grüebler et al. 2014, Evans 2018). In 2018 and 2021, daily recapture probability was relatively high (greater than 60%) for the majority of the time birds were tagged. Hatch-year birds tagged in 2018 had low initial daily recapture probability in the first few days following fledging from the nest. Daily recapture probability increased rapidly as fledglings moved around the study area and became more likely to be detected by a Motus tower. Daily recapture probability peaked at approximately age post-hatching day 35. Daily recapture probability was highest for birds tagged at lakeshore colonies followed by birds tagged at aggregate pit sites. Hatch-year birds tagged in 2021 showed a similar pattern to hatch-years tagged in 2018. Initially, hatch-years had low daily recapture probabilities when they fledged from the nest. Daily recapture probability again increased rapidly as fledglings moved around the study area and became more likely to be detected by a Motus tower. In 2021, hatch-years daily recapture probability peaked at approximately age post-hatching day 39. Individual hatch-years radio tagged at lakeshore colonies had higher daily recapture probabilities compared to aggregate pit colony birds. Adults radio tagged in 2021 showed higher daily recapture probabilities during the post-breeding period compared to hatch-years in 2021 and 2018; the lowest daily recapture probability observed was approximately 62.5%. Individual adults radio tagged at lakeshore colonies had higher daily recapture probabilities compared to individuals radio tagged at aggregate pit sites.

The overall higher daily recapture probabilities among lakeshore colony birds makes sense given the distribution of Motus towers in Southwestern Ontario. Motus towers are particularly dense along the north shore of Lake Erie with 14 towers located within 10 km of the shore in Southwestern Ontario. Inland colonies (Blythedale pit and Embro pit) had much lower coverage from the Motus array. Within 10 km of these colonies, there is only 1 Motus tower. Using Motus, tagged birds are regularly detected by receivers greater than 20 km apart using 9-element Yagi antennas (Taylor et al. 2017). Many factors are capable of influencing detection distance such as landscape features including topography, habitat structure, and human-made structures (Taylor et al. 2017). Motus towers close (within 10 km) of the north shore of Lake Erie should have a higher probability to detect birds compared to Motus towers that are present inland (greater than 10 km from the shore). Towers on the shoreline have a lower chance of being affected by human-made structures (such as windmills and large buildings) and habitat structure (such as large dense forest areas) compared to inland towers (Taylor et al. 2017). Daily probability of recapture during the post-breeding period has been studied in aerial insectivore species (Evans et al. 2020). Hatch-year Barn Swallow showed high (greater than 70%) average daily recapture probability from day age 25 and onwards (Evans et al. 2020). Similar to my study, hatch-years initially had a low daily recapture probability that rapidly increased (Evans et al. 2020).

4.4 Daily apparent survival probability during the post-breeding period

Studies have shown low cumulative post-breeding survival in fledgling and young juvenile birds (Anders et al. 1997, Fink 2003, Styrsky et al. 2005, Rush and Stutchbury 2008, Evans et al. 2020). Findings from past studies helped form my prediction of adult Bank Swallows having higher daily apparent survival probability compared to newly fledged and young hatch-year Bank Swallows. Daily apparent survival probability for hatch-years in 2018 and 2021 began low (less than 75% in 2018 and 2021), although I could not distinguish tag loss from actual mortality. Evans et al. (2020) found that daily apparent survival probability for hatch-years Barn Swallows began relatively high (greater than 90%). In other studies, the beginning of the parental care period is a costly time for hatch-year birds (Evans 2018). Mean cumulative post-fledging survival in passerine birds drops to approximately 65% 10 days after hatch-years have fledged from the nest (Cox et al. 2014). Anders and colleagues found the risk of hatch-year predation the first week after fledging to be relatively high (Anders et al. 1997). Individuals were not capable of flying quickly, flying for long distances, or successfully avoiding predation (Anders et al. 1997). During this initial stage of the post-breeding period, fledglings are reliant on their parents for gathering food resources (Suedkamp Wells et al. 2007, Vitz and Rodewald 2011). After this initial low survival period post-fledgling, 2018 and 2021 hatch-year daily apparent survival probability increased rapidly, which is consistent with an increase in true survival. During this period, the risk of predation decreases for hatch-year birds (Anders et al. 1997). Hatch-year birds are able to fly well (compared to initially fledgling from the nest) and are also still being fed by their parents (Anders et al. 1997). After the rapid increase, daily apparent survival probability decreased at a rapid rate, which could be a sign of hatch-year birds entering into the second stage of the post-breeding period. However, I cannot rule out an increasing likelihood of tag loss. During the second stage of the post-breeding period, fledglings become independent from their parents but have not dispersed or migrated (Suedkamp Wells et al. 2007, Vitz and Rodewald 2011, Bumelis 2020). Newly independent birds must learn how to navigate unknown landscapes, gather food resources independently, and avoid predation (Betts et al. 2008, Grüebler and Naef-Daenzer 2010, Dittmar et al. 2016). Three weeks post fledging, Wood Thrush (*Hylocichla mustelina*) initial foraging attempts were loud and conspicuous as juveniles threw leaf litter while searching for invertebrates (Anders et al. 1997).

Daily apparent survival probability in 2018 and 2021 followed a similar cubic pattern with time (Evans et al. 2020). Daily apparent survival probabilities in 2018 were between 0.50 and 0.75 at age post-hatching day 25 compared to only 0.25 and 0.55 for 2021 birds (Figure 8, Figure 10). The maximum daily apparent survival probability was approximately 0.90 in 2018 and 0.80 in 2021 (Figure 8, Figure 10). Daily apparent survival probability may have been higher in 2018 due to weather conditions in 2021. Bank collapse was observed throughout the 2021 post-breeding period. There may have been an increased amount of bank collapse in the 2021 post-breeding period compared to the 2018 post-breeding period due to rainfall. Hatch-year Bank Swallows will use nest burrows for roosting/resting up to one week post-fledging (COSEWIC 2013). Returning to use nest burrows may decrease the daily apparent survival probability of hatch-years in 2021.

2018 hatch-year birds with larger wings had a higher daily apparent survival probability in the post-breeding period compared to birds with smaller wings in 2018 but not in 2021. Relative wing length has been shown to increase with fledging age and fledgling mortality decreases as relative wing length increases (Martin et al. 2018). Better-developed wings have been shown to reduce overall hatch-year mortality, as better developed wings allow fledgling birds to escape predation at a higher rate than fledglings with less developed wings (Martin et al. 2018). Adult daily survival probability was supported by the covariate sex; females had higher daily survival probabilities during the post-breeding period compared to males in 2021. Parents of fledgling Bank Swallow will both provision young in the nest for up to one week after fledging (COSEWIC 2013). Due to equal provisioning, I do not believe provisioning young affected the adult sexes differentially. Adult female Bank Swallows have been shown to spend more nights at their colony as opposed to adult males who will roost elsewhere more often (Falconer et al. 2016b). Males travelling over 30 km away from their colony to roost more often than females may explain differential mortality among the sexes. It is energetically costly to travel to and from roosting sites. Communal roosting may also allow higher rates of predation as birds gather together in large groups and become more audibly and visually conspicuous. The effects of covariates were not robust, as they were not detected in the top model for 2021 hatch-year birds. The top model for 2021 hatch-years showed a cubic relationship with survival and no covariate effects. Reliable detections for 2021 hatch-year birds began on age post-hatching day 25 and concluded on age post-hatching day 33; 9 days total. Reliable detections for 2018 hatch-year birds began on age post-hatching day 25 and concluded on age post-hatching day 39, 15 days total. Perhaps 9 days of analysis in 2021 was not enough time for covariates to significantly affect post-breeding daily apparent survival in 2021.

Similar to the hatch-year birds, adult daily apparent survival probability began low, but then increased and leveled out at approximately age post-hatching day 39. After nestlings have fledged from the nest, adults must ensure dependent fledglings are provided food and show independent behaviours near young fledglings. Adults continue to feed fledgling birds after they have fledged the nest (Snow 1958). Adults will continue to provide post-fledging care such as guiding young to food resources and protection from predators (Dreitz 2009, Rickenbach et al. 2011). Although adults may experience some true mortality, the initial decrease in adult daily apparent survival likely reflects tag loss as we expect daily apparent survival to be high and close to 100% in adults. Tag loss may be more apparent around the time nestlings are fledging from the nest due to parents provisioning their young and/or prospecting burrows. Unlike hatch-years, adults did not experience a steep decline later. Instead, daily apparent survival probability increased and recovered from the initial decline.

There was some evidence that hatch-year birds radio tagged at lakeshore colonies had higher daily apparent survival probabilities compared to birds tagged at pit colonies. The second-best model for 2018 hatch-year birds showed an effect of colony type on daily apparent survival probability. The second, third and fourth top models for 2021 hatch-year birds showed an effect of colony area and colony type on daily apparent survival probability. Bank Swallows usually feed within 1000 m of their colony but will forage greater distances if insect abundance decreases (Waugh 1979, Falconer et al. 2016a, Génier 2019, Génier et al. 2021). Through stable isotope analysis of feathers and faecal DNA metabarcoding, the Southern Ontario population of Bank Swallows was found to differ in diet based on colony area (Génier et al. 2021). Lakeshore colony birds consume more aquatic emergent insects compared to aggregate pit colony birds (Génier et al. 2021). Aquatic emergent insects contain beneficial nutrients (Hixson et al. 2015, Twining et al. 2018, Génier et al. 2021). This may create a ‘nutritional trap’ for inland aggregate pit colony birds (Génier et al. 2021). A nutritional trap could provide explanation for the lower daily probability of survival between lakeshore and inland aggregate pit birds. Lower quality and quantity of insects near pit sites could affect hatch-year body condition (Génier 2019). In turn, a lower body condition could lead to lower daily apparent survival probability.

4.5 2021 and 2018 hatch-year daily estimate of mortality and cumulative tag loss

The daily estimate of mortality during the post-breeding period was roughly estimated by subtracting the daily apparent survival probability of 2021 hatch-years from the daily apparent survival of 2021 adults. We assumed tag loss rates would be similar in adults and hatch-year birds. Adult survival during the post-breeding period was assumed to be close to 100%. Since hatch-year survival was assumed to be significantly less than 100%, the difference between adult survival and hatch-year survival was assumed to be the best estimate of daily mortality. The daily estimate of 2021 hatch-year mortality varied from less than 10% to approximately 30% throughout the post-breeding period. The daily estimate of 2021 hatch-year mortality was relatively low, less than 10%, from age post-hatching day 25 until age post-hatching day 35. From approximately age post-hatching day 36 to age post-hatching day 38, the daily estimate of mortality increased to approximately 30%. After age post-hatching day 39, the daily estimate of mortality decreases back to levels similar to post-fledging survival. At age post-hatching day 39, approximately 50% of radio tagged hatch-years in 2021 had died or lost their tags. At age post-hatching day 42, over 90% of radio tagged adults in 2021 were still alive and detected. I predict that increasing mortality rates are associated with hatch-year birds becoming independent from their parents. Hatch-years are especially vulnerable during the independent phase (Snow 1958, Magarth 1991, Naef-Daenzer et al. 2001). During this phase, hatch-years must learn to navigate unknown landscapes, gather food resources and avoid predation (Betts et al. 2008, Grüebler and Naef-Daenzer 2010, Dittmar et al. 2016). The described actions can put newly independent birds at a significant risk of failing to survive until their first southward migration (Anders et al. 1997, Berkeley et al. 2007).

Cumulative tag loss varied throughout the post-breeding period. At age post-hatching day 25, approximately 50% of 2018 hatch-year birds had lost their tags, 50% of 2021 adult birds had lost their tags and less than 40% of 2021 hatch-year birds had lost their tags. As age post-hatching increased, cumulative loss increased as well. By age post-hatching day 33, greater than 80% of 2021 hatch-year birds had lost their tags, 80% of 2021 adults had lost their tags and approximately 60% of 2018 hatch-year birds had lost their tags. We attribute the large cumulative loss values for adult and hatch-year birds to tag loss and tag failure.

4.6 Assumptions and limitations

Many assumptions were made throughout this study. I assumed that the proportion of Bank Swallows radio tagged represented all of the Southern Ontario Bank Swallow population. Adult and hatch-year birds were radio tagged at 12 different sites in 2021 and 24 sites in 2018, so I do not believe sampling bias was introduced into my study. We attempted to evenly distribute (at least 10 radio tags per hatch-year and 10 radio tags per adult) for every site in 2021. By evenly distributing radio tags at sites, I believe sampling bias was minimized.

My study was limited to two years of bird tracking in 2018 and 2021. Due to only gathering data from two post-breeding periods, generalizing findings from this study requires the assumption that the 2018 and 2021 post-breeding periods represented a typical post-breeding period for all Southern Ontario populations of adult and hatch-year Bank Swallows. Bank collapse was observed at lakeshore and aggregate pit colonies. I hypothesize that the large amount of rainfall during the 2021 post-breeding season led to an increased risk of bank collapse. Bank collapse and river flooding can often result in the death of nestlings (Garrison 1999). In 2018, fewer than 5 hatch-year birds were detected from post-hatching day 39. This can be compared to 2021 when fewer than 5 hatch-year birds were detected from post-hatching day 33. Perhaps there was higher mortality rates in 2021, possibly due to hatch-year birds having shorter wings compared to 2018 hatch-year birds.

Studies that have observed post-breeding survival often lack estimates up to the beginning of southward migration (Evans et al. 2020). This means that survival estimates during a critical part of the post-breeding period, when hatch-years can make potentially costly exploratory movements, are not quantified (Brown and Taylor 2015, Evans et al. 2020). My study had reliable detections from age post-hatching day 25 to age post-hatching day 33 for hatch year birds and from age post-hatching day 25 to age post hatching day 56 for adult birds. Canadian populations of Bank Swallows nest from mid-May to late August (Environment and Climate Change Canada, 2021). This nesting range and tag retention issue likely did not allow us to estimate daily apparent survival probability and daily recapture probability up until hatch-year birds began their migratory movements.

4.7 Future research

The findings of my study show that radio tag loss or tag failure in Southern Ontario Bank Swallows is prevalent. Hatch-year Bank Swallows were detected reliably from age post-hatching day 25 to age post-hatching day 33 while adult Bank Swallows were detected reliably from age post-hatching day 25 to age post-hatching day 56. The estimated tag life for radio tags used in this study was approximately 106 days. Therefore, a large duration of the post-breeding period was not accounted for in this study. Tag loss or tag failure may have resulted from attaching radio tags to birds through leg loop harnesses. Radio tags have been attached to Bank Swallow's trimmed feathers on the birds lower mantle using a cyanoacrylate adhesive (Raim 1978, Saldanha et al. 2019). Saldanha et al. (2019) used tags that had a minimal life expectancy (80% of total life expectancy) of 33 days. Using adhesive to attach radio tags to birds causes a relatively short retention time; with averages from studies ranging from 5-40 days (Sykes et al. 1990, Johnson et al. 1991, Bowman et al. 2002, Mong and Sandercock 2007, Saldanha et al. 2019). Future studies should compare the tag retention length between attaching radio tags using a leg loop harness or by using a cyanoacrylate adhesive directly to trimmed feathers. Another limitation was the number of post-breeding seasons analyzed in this study; the 2018 and 2021 post-breeding periods. Future studies should include multiple post-breeding periods in their analyse and estimations of daily recapture probability and daily apparent survival probability.

4.8 Conclusion

In conclusion, this project highlights the importance of the post-breeding period for migratory birds. We show that daily recapture probability was higher for Bank Swallows radio tagged at lakeshore colonies compared to Bank Swallows radio tagged at aggregate pit colonies. We also show that adult Bank Swallows have higher daily apparent survival probability compared to hatch-year Bank Swallows during the post-breeding period. An important next step is to determine why daily post-breeding recapture probability and daily post-breeding apparent survival probability rapidly decreased after age post-hatching day 39 for hatch-year birds and age post-hatching day 56 for adult birds. Possible future work could involve trying to recover lost radio tags. A manual tracking team could try to recover grounded tags; however grounded tags have a detection range less than 1 km, so this may prove difficult (Crewe et al. 2019). Our study further highlights the possibility of using the automated radio telemetry system Motus to create mark-recapture models without having to physically recapture birds in the wild.

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Appendices

Appendix 1. PCR sexing protocol used to sex hatch-year Bank Swallows during the 2021 post-breeding period.

DNA Extraction:

DNA extracted from dried blood on filter paper to equal 10 uL of blood (circle 6 mm diameter) using a modified Chelex protocol (Walsh et al. 1991; Burg and Croxall, 2001). Each sample placed in 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 hrs @ 50°C. Approximately 200 uL of solution was transferred to new tube and 300 uL 1x low TE (10 mM Tris pH 8; 0.1 mM EDTA) with 5% Chelex w/v. Some extractions diluted 1:20, some for 1:40 and 1:10 and for PCR amplification.

Primers used: P2/P8 (Griffiths R & Tiwari B (1995))

PCR conditions: (per 10 uL reaction): 2.0 uL GoFlexi Buffer 5x (Promega), 2.0 mM $MgCl_2$, 200 uM dNTP, 1.0 uM each primer, 0.5 uL M13 tag, 0.5 units GoTaq (Promega) and 1 uL 1:50 or 1:100 dilution DNA template.

Thermocycler Conditions: 1 min 30 sec @ 94°C

35 cycles of 30 sec @ 94°C

45 sec @ 48°C

45 sec @ 72°C

Final extension 5 min @ 72°C, 5 sec at 4°C.

Visualized the products using 4300 DNA analyzer Licor.

Appendix 2. Environment Canada, Canadian Wildlife Service Permit 10169 CL. Issued to Megan Hiebert.

Environment and Climate Change Canada — Environnement et changement climatique Canada

SCIENTIFIC PERMIT TO CAPTURE AND BAND MIGRATORY BIRDS
PERMIS DE CAPTURE ET DE BAGUAGE D'OISEAUX MIGRATEURS

In the Province(s) / Territories - Dans la (les) provinces(s) / territoires	Permit No. / Nº de permis
Ontario	**10169 CL**

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
MEGAN HIEBERT
[redacted]

Issue Date / Date d'émission: **2021/04/20**

Expiration Date / Date d'expiration: **2021/12/31**

Signature of Holder - Signature du détenteur	For the Minister - Pour le Ministre Name (Print) - Nom (Lettres	Signature
[redacted]	**V.DROLET-GRATTON**	[redacted]

AUTHORIZATIONS -- AUTORISATIONS

Authorized to:

- Band chicks at nest site and monitor
- Band in colonies Bank Swallow (BANS) (6160) in collab w 10911
- Band SARA listed species Bank Swallow (BANS) (6160) in collab w 10911 pursuant to Section 74 of the Species at Risk Act
- Band specific species Tree Swallow (TRES) (6140)
- Hand capture
- Take and possess blood samples Bank Swallow (BANS) (6160) (brachial vein) up to 75uL from up to 200 SAR BANS (100 HY, 100 AHY), in collab w 10911 (not to exceed 1% body mass)
- Take and possess feather samples Bank Swallow (BANS) (6160) (1 central rectrix) from up to 200 SAR BANS, in collab w 10911
- Take and possess other biological samples Bank Swallow (BANS) (6160) (fecal samples) collected opportunistically from up to 300 SAR BANS, in collab w 10911
- Trap at cavity, burrow or nest box
- Use mist nets
- Use traps
- Use (81H) radio transmitter (incl. Nanotags) on Bank Swallow (BANS) (6160)
  Lotek NTQB2-2 nanotag (0.32g) on up to 200 BANS (HY+AHY) in collab w 10911 (leg-loop harness; marker and attachment materials not to exceed 3% total body weight; Tracking data to be submitted to a public data repository according to BBO guidelines) in Ontario

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

[redacted]

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Appendix 3. University of Western Ontario, Council on Animal Care, Animal Use Protocol 2020-141. Issued to Yolanda Morbey.

Western

AUP Number: 2020-141
PI Name: Morbey, Yolanda
AUP Title: Post-breeding movement and survival of adult and first-year Bank Swallows in the Great Lakes ecoregion
Approval Date: 04/01/2021

Official Notice of Animal Care Committee (ACC) Approval:

Your new Animal Use Protocol (AUP) 2020-141:1: entitled " Post-breeding movement and survival of adult and first-year Bank Swallows in the Great Lakes ecoregion" has been APPROVED by the Animal Care Committee of the University Council on Animal Care. This approval, although valid for up to four years, is subject to annual Protocol Renewal.

Prior to commencing animal work, please review your AUP with your research team to ensure full understanding by everyone listed within this AUP.

As per your declaration within this approved AUP, you are obligated to ensure that:

1. This Animal Use Protocol is in compliance with:
   - Western's Senate MAPP 7.12 [PDF]; and
   - Applicable Animal Care Committee policies and procedures.
2. Prior to initiating any study-related activities—as per institutional OH&S policies—all individuals listed within this AUP who will be using or potentially exposed to hazardous materials will have:
   - Completed the appropriate institutional OH&S training;
   - Completed the appropriate facility-level training; and
   - Reviewed related (M)SDS Sheets.

Submitted by: Copeman, Laura on behalf of the Animal Care Committee

[redacted]

Dr.Timothy Regnault,
Animal Care Committee Chair

Animal Care Commitee
The University of Western Ontario
London, Ontario Canada N6A 5C1

Curriculum Vitae

Christian Buchanan-Fraser

Education

M.Sc. Biology
The University of Western Ontario | London, Ontario, Canada | September 2020 – May 2023

Honors Specialization in Biology
The University of Western Ontario | London, Ontario, Canada | September 2016 - May 2020

Related Work Experience

Contract: Aerial Insectivore Field Technician
Birds Canada | May 2023 – August 2023

- Capturing, mist-netting and banding Eastern Whip-poor-wills and Bank Swallows
- Day and night-time telemetry to determine habitat selection of Eastern Whip-poor-will
- Insect sampling in sites occupied by Eastern Whip-poor-will and Bank Swallows
- Collecting biological samples (blood, fecal, and feather samples)
- Fitting Eastern Whip-poor-wills and Bank Swallows with radio transmitters
- Boat surveys and burrow counts for population monitoring of Bank Swallows
- Assisting with the development of technical reports and publications
- Obtaining permission to survey sites via communicating with landowners/volunteers/public
- Ongoing landowner stewardship
- Entering and organizing data, and maintaining databases

Contract: Malaise Trap Insect Sorting
Birds Canada and the University of Western Ontario | London, Ontario, Canada | September 2022 - December 2022

- Sorting insects captured along the north shore of Lake Erie in Malaise traps during the 2022 field season down to Order

Teaching Assistant
The University of Western Ontario | London, Ontario, Canada | November 2020 - April 2021, September 2021 - April 2022, September 2022 - December 2022, January 2023 – April 2023

- Provided editing, guidance, evaluation and assistance for students in the second-year undergraduate course Biology 2290: Scientific Methods in Biology

Volunteer: Malaise Trap Insect Sorting
Birds Canada and the University of Western Ontario | London, Ontario, Canada | December 2021 - May 2022

- Sorted insects captured along the north shore of Lake Erie in Malaise traps during the 2021 season down to Order

Biology 4999E Presentation Judge

The University of Western Ontario | London, Ontario, Canada | April 2, 2022

- Evaluated and judged fourth year Honors student presentations along with professors

M.Sc. Field Research

The University of Western Ontario | Southwestern Ontario, Canada | May 2021 - August 2021

- Captured, banded and radio tagged adult and first-year Bank Swallows in Southwestern Ontario at lakeshore and aggregate pit sites in the Norfolk, Elgin, Oxford and Haldimand counties
- Set up Malaise traps to capture insects at four field sites
- Currently working on data analysis for my M.Sc. thesis entitled "*Post-breeding survival of adult and first-year Bank Swallows in the Great Lakes ecoregion: a radio telemetry study*"

Research Assistant

The University of Western Ontario | Alma, New Brunswick, Canada | August 2020 - October 2020

- Banded, took morphological measurements and manually radio tracked songbirds for Andrew Beauchamp (PhD Candidate in the Dr. Yolanda Morbey lab at the University of Western Ontario)
- Set up pitfall and sticky insect traps

Honors Thesis

The University of Western Ontario | London, Ontario, Canada | September 2019 - April 2020

- Completed undergraduate thesis titled: *Elevated capture of songbirds at a stopover site following favourable tailwinds, but only in certain species* (unpublished) under the supervision of Dr. Yolanda Morbey and mentorship of Andrew Beauchamp

Bird Carcass Survey Volunteer

The University of Western Ontario | London, Ontario, Canada | September 2019 - November 2019

- Performed survey routes throughout the University of Western Ontario campus looking for birds that had died from window or building related collisions for Brendon Samuels (PhD Candidate)

PEL Academic STEMM Co-Op in Health Research

Schulich School of Medicine & Dentistry | London, Ontario, Canada | February 2016 - June 2016

- Created a highschool mini-thesis titled: *Interdisciplinary Study: Forearm Radial Nerve* (unpublished) in the Dr. Brian Allman lab under the supervision of Dr. Tyler Beveridge

Honours and Awards

Deans Honor List

2019 - 2020

- Undergraduate yearly average of 80% or higher

The Western Scholarship of Distinction
September 2016

- High school senior average above 88%

Conferences and Presentations

2022 Bank Swallow Working Group Annual Meeting
November 30, 2022

- Presented updates on M.Sc. thesis work

Canadian Society for Ecology and Evolution/ Ecological Society of America Conference
August 14, 2022 - August 19, 2022

- Presented a poster presentation highlighting research on my M.Sc. project

Ontario Ecology, Ethology and Evolution Colloquium
May 25, 2022 - May 27, 2022

- Presented a 12 minute oral presentation highlighting research on my M.Sc. project

Ontario Chapter of the Wildlife Society Conference
March 26, 2022

- Presented a 15 minute oral presentation highlighting research on my M.Sc. project

Friday Philosophical Seminar Series
April 9, 2021 and March 25, 2022

- Weekly seminar series ran by the Ecology and Evolution group at The University of Western Ontario
- Presented one M.Sc. entry (20 minute) talk and one M.Sc. exit (20 min) talk highlighting background information, methodology and results of my M.Sc. research

Training and Skills

Biology 9960: Quantitative Biology – Going Beyond Statistics
2022 | Graduate Course

- Learned how to form quantitative models and how to choose models for studies

Biology 9916: Statistical Modelling of Biological Data
2021 | Graduate Course

- Learned how to use R to manipulate data, create graphs and to perform statistical inference

Biology 3446: Wildlife Ecology and Management
2019 | Undergraduate Course

- Learned how to identify bird, mammal, amphibian, and reptile species that are native to Ontario
- Learned about methods that are used to study wildlife

R, RStudio, RMarkdown

- How to import data, data management, analyze and filter data, produce figures using ggplot2, how to create reports in RMarkdown

Microsoft Office Programs: MS Excel, Outlook, Word, and PowerPoint

- Organization of data in workbook, creation of figures and diagrams, how to use functions
- Writing and poster creation of theses
- Creation of oral and poster presentations

Ontario Drivers License

- G Class

Standard First Aid with CPR/AED Level C