

Nestling diet, quality, and post-fledging survival: Comparing two species of aerial insectivores in a gradient of agricultural intensity in Saskatchewan, Canada

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ABSTRACT

In the last decades, several species of avian aerial insectivores have experienced steep declines in different regions of North America, and no single driver has been identified. Given the common reliance of aerial insectivores on flying insects, changes in spatiotemporal availability of prey abundance and quality caused by agricultural intensification have been implicated in their decline. The quality of nestling nutrition mediated by parental selection of insect prey types (aquatic versus terrestrial) can be an important determinant of offspring health and development which, in turn, can have lasting effects on future life-stages, including the post-fledging transitional period to independence.

In 2020 and 2021, using a comparative approach between two sympatric species, Barn Swallows (*Hirundo rustica*) and Tree Swallows (*Tachycineta bicolor*), following a scale-of-effect approach, I investigated whether the intensity of agriculture was associated with parental selection of prey resources, nestling body condition and growth. Stable isotope data revealed Barn Swallows opportunistically used aquatic aerial prey resources to provision nestlings when available, whereas Tree Swallows strongly relied on aquatic-emergent prey, regardless of the availability of wetlands in the immediate area around the nest (<500 m). Although wetland cover (within 1700 m) and row-crop cover (within 500 m), showed weak but negative effects on nestling body condition of Tree and Barn Swallows, respectively, nestling quality was strongly influenced by other variables such as nest and site. Using the Motus automated telemetry technology, I tracked early post-fledging apparent survival and movements of Barn and Tree Swallows. Estimates of post-fledging survival were similar between species, declining from 88.1% and 95.5% from tagging to fledging in Barn and Tree Swallows, to an apparent daily survival of 64.1% and 59% 8 days post-fledging and 26% and 30% 14 days after fledging,

respectively. Apparent survival estimates were not related to individual factors such as body condition or age at fledging. Nevertheless, I obtained evidence that shorter development time in the nest, before reaching full locomotor development, may increase post-fledging mortality in Barn Swallows. Tree Swallow fledglings left their natal areas sooner than Barn Swallows and, after fledging, were found congregating at wetlands and marshes (> 5 km).

This work adds to the growing evidence that conservation of wetlands and naturalized areas within the agricultural landscape in the Prairie Pothole Region is important for breeding aerial insectivores, including Tree and Barn Swallows, and may be helping mitigate the negative effects of intensive agricultural crop production. This study also contributes to filling gaps in our understanding of swallow ecology during the post-fledging period, a poorly understood stage of their life cycle and an important demographic driver of annual population growth in songbirds.

NOTE TO READERS

This thesis is organized and formatted to follow the University of Saskatchewan College of Graduate and Postdoctoral Studies guidelines for a manuscript-style thesis. Chapter 1 is a general introduction and literature review, including project goals and objectives. Chapter 4 contains a general discussion and overall conclusion. Chapters 2 and 3 of this thesis are organized as manuscripts for publication in peer-reviewed scientific journals. Supporting information associated with research chapters are presented in the Appendix section. As a result of the manuscript-style format, there is some repetition of material in the introduction and methods sections of this thesis. References cited are combined and listed in the section at the end of the thesis.

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TABLE OF CONTENTS

PERMISSION TO USE	i
DISCLAIMER	ii
ABSTRACT.....	iii
NOTE TO READERS	v
ACKNOWLEDGEMENTS	vi
TABLE OF CONTENTS.....	viii
LIST OF TABLES	xi
LIST OF FIGURES	xiii
LIST OF ABBREVIATIONS.....	xvi
CHAPTER 1. General introduction	1
1.1. The declines of aerial insectivores and agricultural intensification	1
1.2. Aquatic-emergent prey source and its nutritional value to aerial insectivores	3
1.2.1. Stable Isotopes as tracers of diet source	5
1.3. The post-fledging period and tracking fledglings	9
1.4. The Prairie Pothole Region and its dynamic hydrological and ecological complexity ..	12
1.5. Focal Study Species	13
1.6. Scope of thesis.....	14
CHAPTER 2. Landscape-level effects of agricultural intensity on diet source and condition of Barn and Tree Swallow nestlings	17
ABSTRACT.....	17
2.1. INTRODUCTION.....	18
2.2. METHODS.....	22
2.2.1. Study site selection	22
2.2.2. Land use classification	24
2.2.3. Weather conditions	28
2.2.4. Nest monitoring and Nestling measurements	28
2.2.5. Blood and Feather sampling	30

2.2.6.	Terrestrial insect sampling	31
2.2.7.	Water sample collection.....	32
2.2.8.	Stable isotope analysis	32
2.2.9.	Statistical analyses	33
2.3.	RESULTS.....	36
2.3.1.	Isotopic characterization of environmental water $\delta^2\text{H}$ in natural and artificial wetlands	36
2.3.2.	Isotopic differences in $\delta^2\text{H}$ of aquatic vs terrestrial prey.....	37
2.3.3.	Comparison of $\delta^2\text{H}_f$ values of nestling Tree and Barn Swallows	38
2.3.4.	Effect of land use on $\delta^2\text{H}_f$ values in Barn and Tree Swallows.	40
2.3.5.	Effect of land use on Barn and Tree Swallow nestling body condition and daily mass gain	43
2.4.	DISCUSSION	48
2.4.1.	Environmental water and insect stable isotopes in the PPR	49
2.4.2.	Effects of agricultural intensity on differential parental selection of aquatic-emergent prey by Barn and Tree Swallows	51
2.4.3.	Effects of agricultural intensity on nestling body condition and daily mass gain ...	55
2.4.4.	Conclusions.....	58
CHAPTER 3.	Using automated radio telemetry to study early post-fledging survival and movement of Barn and Tree Swallows in Central Saskatchewan.....	61
ABSTRACT.....		61
3.1.	INTRODUCTION.....	62
3.2.	METHODS.....	66
3.2.1.	Study sites and species.....	66
3.2.2.	Nest monitoring and Nestling measurements	68
3.2.3.	Nestling tagging	70
3.2.4.	Automated telemetry array	71
3.2.5.	Manual detections	72
3.2.6.	Estimation of fledging date via change-point analysis	73

3.2.7.	Mark-recapture models and building encounter histories.....	74
3.2.8.	Statistical analysis.....	75
3.3.	RESULTS.....	78
3.3.1.	Nestling and fledging survival.....	78
3.3.2.	Apparent daily survival.....	79
3.3.3.	Detection probability	85
3.3.4.	Patterns of early post-fledging movement	87
3.4.	DISCUSSION	89
3.4.1.	Factors influencing apparent daily survival.....	90
3.4.2.	Early movements in Barn and Tree Swallows.....	95
3.4.3.	Study limitations	98
3.4.4.	Conclusion	99
CHAPTER 4.	General discussion.....	101
4.1.	SUMMARY OF FINDINGS	101
4.2.	IMPLICATIONS FOR CONSERVATION.....	102
4.3.	STUDY LIMITATIONS.....	104
4.4.	FUTURE RESEARCH	108
REFERENCES	111
APPENDIX A	144
APPENDIX B	152

LIST OF TABLES

Table 2.1 Summary of site-specific information on land use cover and colony size/nest box occupancy by year of the study. Shown are mean % and standard deviation of land use cover per site per year calculated from the land use relative cover surrounding Tree and Barn Swallow nests within a 500 m radius. This table also includes a summary of numbers of nestlings (nests) followed in 2020 and 2021, including nests that failed after laying at least one egg. For Tree Swallows, nest box occupancy (%) is also reported based on the percentage of boxes that were occupied. (*) indicates the only site where a Tree Swallow colony was previously established, and where the number of boxes available was >20.....	27
Table 2.2 Summary of $\delta^2\text{H}_f$ values (mean \pm SD) for Barn and Tree Swallows collected in 17 sites in Saskatchewan, Canada, during the breeding seasons of 2020 and 2021.	39
Table 2.3 Model selection table for linear mixed-effect models to evaluate effects of crop and water coverage (%) on $\delta^2\text{H}$ values from Tree and Barn Swallows nestling feathers. Includes six candidate models for each species, including the null model (intercept only) with only the random effect structure. All models included site ID and nest as random effects, following a nested structure. Bold indicates models with $\Delta\text{AICc}<2$, and that were averaged (See Table 2.6).....	43
Table 2.4 Summary statistics (mean \pm SD) for Barn and Tree Swallow body mass, wing length, body condition and daily mass gain from early broods. Number of nestlings included in each estimate are reported in brackets followed by the number of nests.	44
Table 2.5 Model selection table for linear mixed effect models to evaluate effects of crop and water coverage (%) on Tree and Barn Swallow nestling body condition (BCI), and daily mass gain (from Day 4 to Day 8). Shown are six candidate models for each species. All models included site ID and nest as random effects, following a nested structure. Bold indicates models with $\Delta\text{AICc}<2$ which estimates were averaged (See Table 2.6).	47
Table 2.6 Averaged model coefficients with adjusted SE and unconditional 95% confidence intervals (CI) from the best-fit models ($\Delta\text{AICc} \leq 2$ units) for Barn and Tree Swallow nestling $\delta^2\text{H}_f$, body condition and daily mass gain. (-) indicates that explanatory variables were not included in the model averaging.	48

Table 3.1 Summary statistics (mean \pm SD) of Motus nanotagged nestlings. These factors were used to evaluate potential effects on apparent survival of Tree and Barn Swallow fledglings, in 2020 and 2021. Samples sizes are included in parentheses. 81

Table 3.2 Results from the most parsimonious Huggins Robust design survival models. The reported estimates of early apparent daily post-fledging survival (ϕ), temporary migration (γ), and recapture or detection probability (p) are shown for Barn Swallows (top) and Tree Swallows (bottom) in 2020 and 2021. Beta estimates (β), Standard Error (SE) and 95% confidence intervals (CI) are reported in the logit scale. Dashes (-) indicate effects were not included in the best model. 83

Table 3.3. Model predictors evaluated on apparent post-fledging survival of Barn Swallows and Tree Swallows in 2020 and 2021, with estimates and 95% confidence intervals. Estimates were derived from the model with best age structure and each of the predictor variables. Significant effects (95% CI non-overlapping 0) are highlighted in bold. 84

Table 3.4. Summary statistics of Barn and Tree Swallow post-fledging detections reported as the mean and standard deviation (mean \pm SD). Mean age of fledging, total number of days that bird were detected in the local telemetry network after fledging, including mobile telemetry detections, number of sites were birds were detected during the summer, post-fledging latency of departure, and the maximum distance that young birds were detected by mobile telemetry on day 15. Fledging dates include minimum and maximum date of fledging of birds included in survival analysis. Maximum distance from nest was estimated based on mobile telemetry detections. Samples sizes (number of birds) are included in brackets. 88

LIST OF FIGURES

Figure 2.1. Location of the Barn and Tree Swallow study sites followed in 2020 (n=12) and 2021 (n=14). Sites were within 100km southeast of the city of Saskatoon in Central Saskatchewan. ...23

Figure 2.2 Agricultural intensity gradient measured across the study sites for each of the two study years (2020 and 2021). The plot shows % relative land use cover within 500 m radius from nest, extracted from the Annual Crop Inventory (Agriculture and Agri-Food Canada, 2020). The category of % open water was obtained from the Canadian Wetland Inventory and Sentinel2 Satellite imagery (European Space Agency, 2021). The category “Other” includes area of marshes and ephemeral wetlands, which were excluded from the analysis due to the high seasonal variability and difficulty to ground-truth.26

Figure 2.3. $\delta^2\text{H}$ values (‰) from water samples collected during three periods in the breeding season (Mid-May, Mid-June, Mid-July 2021). Samples were collected from artificial dugouts (yellow) and natural wetlands (green) based on availability at each of the 12 swallow study sites (SSP01-SSP14).37

Figure 2.4 Comparative boxplot of whole insect $\delta^2\text{H}$ values for samples at each site. Coleoptera and Nematocera were collected only in 2020 across 12 sites. A total of 70 samples were analyzed for $\delta^2\text{H}$. Sites were ordered by increasing open water coverage from low (left) to high open water coverage (right).38

Figure 2.5 Boxplot of nestling Barn Swallow and Tree Swallow $\delta^2\text{H}$ feather values (‰) sampled in 2020 and 2021 from 16 agricultural study sites in central Saskatchewan.39

Figure 2.6 Scale of effect showing model fits for nestling $\delta^2\text{H}_f$ values (plots a and c) and nestling body condition (b and d) in Barn and Tree Swallows in response to increasing buffer sizes (m) for relative proportion of open water in the landscape around the nest site. The top plots (a and b) show ΔAICc values resulting from the linear mixed effect models at each nested scale (500 to 2000 m radii, every 100 m), and using crop cover at 500 m, year, hatching date, and brood as fixed effects and site ID and nest as random effects. The dashed lines in top plots (a and b) indicate the threshold of $\Delta < 2.0$ AICc used to identify competitive models. The bottom plots (c and d) show parameter estimates (β) from models.40

Figure 2.7 Model predicted $\delta^2\text{H}_f$ values for Tree Swallows (a and c) and Barn Swallows (b and d)

nestlings and plotted against open water and annual row relative coverage at 500 m (%). Points represent individual feather data. The model predicted δ^2H_f values and 95% CIs are based on the most parsimonious model from the top models (lower ΔAIC_c), that include each of the land use variables (water or crop). δ^2H_f predicted values from 2020 are shown with light-colored lines and the darker lines are showing 2021 predicted values.42

Figure 2.8 Model predicted nestling body condition (BCI) for Tree Swallows (a and c) and Barn Swallows (b and d) plotted against % open water or % annual row relative coverage, respectively. Based on the above scale of effect analysis, buffer sizes for water coverage were 1700 m for Tree swallows and 500m for Barn Swallows. Annual row-crop coverage for both species was a 500m buffer. The model predicted BCI values and 95% CI are based on the most parsimonious model (fewest parameters) from the top models (lower ΔAIC), that include each of the land use variables (water or crop). BCI predicted values from 2020 are shown with light-colored lines and the darker lines are showing 2021 predicted values. Points represent raw data.46

Figure 3.1 Map of location of Barn and Tree Swallow colonies in central Saskatchewan. White circles represent colonies equipped with omnidirectional antennas. The blue circle indicates a site used in 2020 but removed in 2021. White triangles represent colonies equipped with 3 9-element yagi antenna stations. Yellow triangles indicate the location of additional stations with 3 9-element yagi antennas to complement the Motus telemetry network array in 2020 and 2021. Red triangles indicate new stations added to the telemetry array in 2021. Green larger circles are the expected range of detection of stations with 9-element yagi antennas (~15 km).68

Figure 3.2 Boxplot showing difference in duration of nesting period between Tree Swallows (n=68) and Barn Swallows (n=82).80

Figure 3.3 Comparative plot of predicted post-fledging apparent daily survival probability estimates for Tree Swallows (blue) and Barn Swallows (orange), in 2020 and 2021. The estimates of daily apparent survival (solid lines) were obtained from the top model (See Table 3.2). In total 41 Barn Swallow and 30 Tree Swallow fledglings were included in the analysis of apparent survival in 2020, and 38 Barn Swallow and 37 Tree Swallow fledglings were included in 2021. The shaded areas represent 95% confidence intervals.82

Figure 3.4 Predicted cumulative survival for Barn Swallows (orange) and Tree Swallows (Blue), in Central Saskatchewan during the post-fledging period of 2020 (dashed line) and 2021 (solid line). Day 0 corresponds to the day of fledging. Survival estimates were derived from the best

candidate model (See Table 3.2).....85

Figure 3.5. Comparative plot of predicted daily detection probability for Tree Swallows (blue) and Barn Swallows (orange) over time (days post-fledging), for 2020 and 2021. The two lines within the coloured area represent the two different Motus station types. The plot shows the estimates of detection probability in the early morning (04:00 – 08:00h) where probability of detection was generally higher (a and b), and at night (00:00 – 03:59h) when birds were usually roosting (c and d). The estimates of daily detection probabilities were obtained from the top-ranked model. Shaded areas represent 95% confidence intervals.86

Figure 3.6 Comparison between Tree Swallows (n=68) and Barn Swallows (n=80) showing variation in post-fledging latency to first departure from the natal site. Post-fledging latency was estimated as the number of days before fledglings stopped being detected for a whole day without being detected by the local station. Omni stations had smaller range of detection (0.5 – 1 km) than yagi stations (up to 15 km). Eight of the study colonies had omni stations while only two colonies had yagi stations.....87

Figure 3.7 Scatter plot of distance from the nest travelled by Barn and Tree Swallows (km) in relation to days after fledging. Distances were estimated based on detection data from manual or vehicle mounted mobile telemetry, using an omni-directional antenna with a 500~1000 m range of detection.....89

LIST OF ABBREVIATIONS

‰	Parts per thousand
Φ	Apparent survival
² H	Heavy hydrogen stable isotope
°C	Degrees Celsius
AICc	Akaike Information Criterion, corrected for small sample size
dB	Decibels
df	Degrees of freedom
DNA	Deoxyribonucleic acid
g	Grams
g/day	Grams per day
h	Hours
<i>k</i>	Model parameters
km	Kilometers
LCPUFA	Long Chain Poly Unsaturated Fatty Acids
LMM	Linear mixed effect model
m	Meters
MHz	Megahertz
Min	Minutes
P9	9 th primary
Sec	Second
SE	Standard error
SD	Standard deviation
SK	Saskatchewan
δ ² H	Stable-hydrogen isotope ratio (expressed in ‰)
PPR	Prairie Pothole Region
VHF	Very High Frequency

CHAPTER 1. General introduction

1.1. The declines of aerial insectivores and agricultural intensification

Avian aerial insectivores are a guild of birds that catch their insect prey during flight. Many populations of aerial insectivore species, especially swallows, swifts, and nightjars, have steeply declined in North America (Sauer et al., 2017; Smith et al., 2015; Stanton et al., 2018) and Europe (Donald et al., 2001; Newton, 2004). However, it is still unclear what factors contribute to population declines and at what stage in the life cycle those factors are operating (Cox et al., 2018).

No single cause for the sharp population declines has been identified, and the drivers and mechanisms that underpin many of these declines remain unknown. Loss of habitat quality and shifts in prey quality and abundance through agricultural intensification (Bellavance et al., 2018; Rioux Paquette et al., 2013; Stanton et al., 2016; Twining et al., 2018b), phenological mismatches, weather shifts as a result of climate change (Clark & Hobson, 2022; Cox et al., 2019; Shipley et al., 2020; Winkler et al., 2013), and increased direct and indirect effects of toxic insecticides (Hallmann et al., 2014) are some of the multiple factors that have been implicated; many of them may be acting in synergism (Spiller & Dettmers, 2019).

Although aerial insectivores share a common change point in population trends across the guild (Smith et al., 2015), population declines of aerial insectivores in North America vary geographically and among species (Michel et al., 2016). This variation suggests that different populations or species continue to be exposed to different stressors (Michel, 2021) and, possibly, during different parts of the annual cycle (Imlay et al., 2022). Nevertheless, the complex dynamics and interactions among different biological, physical, and chemical stressors make conclusions on the causes of population declines challenging (Imlay & Leonard, 2019; Michel, 2021; Spiller & Dettmers, 2019).

Since the 1970s, agricultural practices have changed in Europe and North America, in order to maximize crop yields and increase food production (Matson et al., 1997). The intensification of agricultural practices have increased the homogenization of landscapes (Benton et al., 2003), the expansion of production areas, and the intensive use of agrochemicals (Main et al., 2014; Tilman et al., 2011). These practices have also reduced or degraded marginal natural habitats, such as hedgerows and wetlands (Belanger & Grenier, 2002; Benton et al., 2003; Tschardt et al., 2005), all of which are important foraging and shelter habitats for wildlife, including farmland birds (Evans et al., 2003; Gruebler et al., 2008; Møller, 2001).

Despite the apparent spatiotemporal correlation between population declines of farmland birds, including aerial insectivores, and the intensification of agriculture (Donald et al., 2001; Newton, 2004), the link between such population trends and agriculture is still unclear. Aerial insectivores have diverse life-history traits; however, due to their shared reliance on flying insects, changes in insect abundance or availability due to agricultural intensification have been implicated in aerial insectivore population declines (Benton et al., 2002; Garrett et al., 2022b; Rioux Paquette et al., 2013). Many have suggested that agricultural intensification plays a major role in changes in insect community assemblages at a global scale (Sánchez-Bayo & Wyckhuys, 2019), with some taxa and region-specific declines (Wagner et al., 2021). Even though there is no consistent evidence of negative trends in insect populations in North America, the seasonal or regional changes in insect communities due to land use changes or other agricultural practices may still have consequences for insect consumers since low availability of food during periods of high energy demands can impact fitness and reproductive success (e.g., Seress et al., 2018; Garrett et al., 2022; but see Imlay et al. 2017) and may negatively contribute to aerial insectivore population declines (Spiller & Dettmers, 2019).

Several studies have investigated the relationship between prey availability and reproductive

success of swallows in agricultural landscapes, with mixed results depending on the focal species and the study system. In Quebec, some studies have reported adverse effects of row-cropped areas on Tree Swallow (*Tachycineta bicolor*) breeding success and the availability of insect prey (Bellavance et al., 2018; Garrett et al., 2022a; Ghilain & Belisle, 2008; Rioux Paquette et al., 2013). Recently, research assessing the effect of agricultural intensity on Barn Swallow (*Hirundo rustica*) nestling success in Ontario has found weak positive effects of cropland area on nestling condition or fledging success (Kusack et al., 2020). So far, evidence of the landscape-level effects of agriculture on aerial insectivores and the availability of insect prey remains inconclusive.

Growing evidence has recently highlighted the critical role of wetlands as sources of aquatic-emergent insects and their potential to sustain aerial insectivore populations in agricultural and natural landscapes (Berzins et al., 2021, 2022; Elgin, 2020; Génier et al., 2021). This is particularly important because aquatic-emergent insects are now known for being highly nutritious prey (Twining et al., 2019) that can drive the breeding success of some aerial insectivores (Shipley et al., 2020; Twining et al., 2018b). Nevertheless, the degradation of wetlands and exposure to pesticides and other agricultural stressors can disrupt aquatic insect community composition, abundance and phenology (Campbell et al., 2009; Cavallaro et al., 2019; Euliss & Mushet, 1999; Morrissey et al., 2015; Stenroth et al., 2015) and with that, the prey availability and prey quality for aerial insectivores.

1.2. Aquatic-emergent prey source and its nutritional value to aerial insectivores

Food availability has often been considered a limiting factor for wild animal populations (Seward et al., 2013), but the importance of the nutritional quality of food has gained recent attention for wildlife. Fatty acids represent the building blocks of fats and play key roles in cellular structure and different physiological functions of vertebrates (Hixson et al., 2015; Twining et al., 2016a). Animals can access fatty acids directly from their diet or through

biosynthesis (*de novo*)(Hixson et al., 2015). Freshwater primary producers generally produce higher amounts of omega-3 LCPUFA (EPA, 20:5n-3 and DHA, 22:6n-3), whereas these compounds are rare in vascular terrestrial plants (Hixson et al., 2015; Twining et al., 2016a). This dichotomy persists in higher trophic levels: there is evidence that aquatic and terrestrial insects are not nutritionally equivalent for consumers, in terms of concentration of long-chain polyunsaturated fatty acids (LCPUFA), in particular EPA (Twining et al., 2019). Therefore, aquatic-emergent insects from wetlands and aquatic ecosystems can be valuable aquatic-to-terrestrial subsidies of omega 3-LCPUFA for terrestrial riparian consumers such as spiders, bats, and birds (Baxter et al., 2005; Fritz et al., 2017; Kowarik et al., 2021; Twining et al., 2019).

Recent studies have highlighted the importance of the nutritional quality of diet and how, together with the abundance of available resources, it can drive fitness variation in consumers. In birds, diet quality is a strong predictor of nestling mass, body condition (Naef-Daenzer et al., 2011; Schwagmeyer & Mock, 2008), and growth (Ardia, 2006), which in turn, can have long term consequence on future stages of the life cycle such as the post-fledging period (Evans et al., 2019; Winkler et al., 2013) and migration (Mitchell et al., 2011, Naef-Daenzer et al., 2001). In Tree Swallows immunocompetence, condition, and survival can improve with higher quality prey (i.e. rich in omega-3 long-chain polyunsaturated fatty acids) (Twining et al., 2016b, 2018b). In Prothonotary Warblers (*Protonotaria citrea*), a riparian songbird, aquatic-emergent prey subsidies can positively influence nestling growth and condition (Dodson et al., 2016). In other taxa, higher emergence of aquatic prey has been correlated with faster lizard growth rates (Sabo & Power, 2002).

Despite aerial insectivores all relying on flying insect prey, the diet of different species of swallows and their reliance on aquatic-emergent prey as highly nutritious food may vary depending on foraging strategies (Bumelis et al., 2022) and dietary needs, which are related to the

capacity of insectivores to synthesize LCPUFA from precursors found in their diets (Twining et al., 2018a). Seventy five percent of Tree Swallow diets are composed of aquatic-emergent insects (Michelson et al., 2018), with a high representation of aquatic Diptera, in particular chironomid midges and other species of the suborder Chironomidae and Odonata that have a larval aquatic life stage (Beck et al., 2013; Mengelkoch et al., 2004; Michelson et al., 2018). LCPUFA-rich aquatic-emergent prey is an essential nutrient source for Tree Swallows because of their inefficiency at synthesizing omega-3 LCPUFA from molecular precursors found in terrestrial insects (Twining et al., 2018a). It is still unclear if omega-3 LCPUFAs are essential nutrients for other wild birds, including other species of aerial insectivores. Recent evidence from southern Ontario indicated that the Bank Swallow diet was predominantly composed of aerial insects from the Diptera order and chironomids were also dominant in diets of Bank Swallow nestlings when they were more available (Génier et al., 2021). Nestlings also showed differential fatty acid profiles between birds raised in inland and lakeshore sites. In contrast, aquatic insect prey appears to be a less common food source for Barn Swallow populations in North America and Europe (Kusack et al., 2022; McClenaghan et al., 2019a; Orłowski et al., 2014). The relative importance of aquatic-emergent versus terrestrial insects in Barn Swallow nestling diets has recently been investigated with respect to proximity to Lake Erie, Ontario (Génier et al., 2022) indicating that this species is much less reliant on aquatic-emergent prey.

1.2.1. Stable Isotopes as tracers of diet source

Isotopes are atoms with the same number of protons and electrons but differ in the number of neutrons (Sulzman, 2007). Stable isotopes differ from radiogenic isotopes because they do not decay over time. Stable isotopes of light elements found in our environment (C, H, N, O, S) are of hydrological, geological and biological interest because they can be used as tracers of element

flux and cycling (Clark & Fritz, 1997). Stable isotopes generally have one highly abundant light isotope and one or more that are rarer and generally heavier. Due to differences in atomic mass, stable isotopes can behave differently kinetically, and heavier stable isotopes will move slower than lighter ones (Peterson & Fry, 1987). Water molecules containing the lighter hydrogen stable isotope (H) would evaporate more readily than water molecules containing the heavier hydrogen stable isotope (^2H), and the remaining water will have a greater ratio of heavy to light stable isotopes (Clark & Fritz, 1997). These changes in isotopic ratios are due to well-described equilibrium fractionation processes.

Differences in relative abundance between heavy and light isotopes (e.g., $^2\text{H}/^1\text{H}$) in a sample can be measured using mass spectrometry. Stable isotope abundance are usually depicted as a ratio of heavy to light form, and values have a specific notation δ , representing the difference between a measurement and a standard. The following equation calculates the δ value for a specific isotope:

$$\delta^{\text{HeavyX}} = [(R_{\text{sample}} - R_{\text{Standard}}) - 1] * 1000],$$

with $R = \text{HeavyX} / \text{LightX}$

In which X is a particular element (C, N, H, O or S), Heavy refers to the heavy isotope mass of the element (^2H , ^{13}C , ^{15}N , ^{18}O or ^{34}S), R is the ratio of the heavy isotope to the light isotope ($^2\text{H}/^1\text{H}$, $^{13}\text{C}/^{12}\text{C}$, $^{15}\text{N}/^{14}\text{N}$, $^{18}\text{O}/^{16}\text{O}$, or $^{34}\text{S}/^{32}\text{S}$) of the element in the sample and the standard used in the lab. Negative δ values indicate that the sample has relatively less of the heavy isotopes compared to the standard used (Fry, 2006).

The isotopic composition of animal tissues generally reflects the isotope values of the diet and environment where they were synthesized (Hobson & Wassenaar, 2008). Different tissues are synthesized and replaced at different rates; for example, keratinous tissues (e.g., hair, feathers, or claws) or chitins (e.g., insect wings) are metabolically inert, and after formation, the isotopic

composition of these tissues remains unchanged and represents only the window of time over which those tissues were grown (Hobson, 2005). Other metabolically active tissues (e.g., blood, fat, liver) can have generally faster turnover rates (Hobson & Clark, 1992; Tieszen et al., 1983). Therefore, when choosing the right tissue, with the ratio of heavy to light stable isotopes, it is possible to learn about animal movements, diet or habitat use at different temporal and spatial scales.

Since elements predictably cycle through the environment with many opportunities for isotopic discrimination, the ratio of heavy to light stable isotopes has been widely used in ecology (Peterson & Fry, 1987). Stable isotope analysis has been a powerful tool for studying migration (reviewed in Hobson and Wassenaar 2019), food web structures (Bortolotti et al., 2013; Doucett et al., 2007; Solomon et al., 2009; Soto et al., 2013) or for providing insights into foraging and origins of diet (Bumelis et al., 2022; Cavallaro et al., 2022; Génier et al., 2021; Hobson & Clark, 1992; Michelson et al., 2018; Voigt et al., 2015).

Stable hydrogen isotope measurements have been widely used as a tool to evaluate the origins of migratory birds (Hobson, 2019; Hobson & Wassenaar, 1997). However, $\delta^2\text{H}$ has also emerged as a relatively non-invasive intrinsic marker to trace diet source origins and distinguish trophic levels (Doucett et al., 2007; Fraser et al., 2011; Solomon et al., 2009; Soto et al., 2013; Voigt et al., 2015). Hydrogen atoms are incorporated into food webs from environmental waters to plant tissues through primary production, and from there, they are transferred to higher trophic levels (Fogel & Cifuentes, 1993; Hobson, 2007). Aquatic algae discriminate against the heavier H isotope and often have a higher content of lipids which are depleted in ^2H (Doucett et al., 2007; Estep & Hoering, 1980). In terrestrial plants, water evaporates from leaves through transpiration, and the remaining water often becomes enriched in the heavier isotope relative to aquatic primary producers (Doucett et al., 2007; Hobson, 2007). Because of the differential retention of ^2H

between terrestrial and aquatic autotrophs, aquatic food webs tend to be more depleted in ^2H compared to terrestrial food webs from the same locations (Vander Zanden et al., 2016)

Differences in $\delta^2\text{H}$ values among animal species or populations have provided an opportunity to use $\delta^2\text{H}$ in dietary studies to successfully infer the origin of food sources (aquatic versus terrestrial) and aquatic-to-terrestrial linkages (Hobson et al., 1999; Soto et al., 2013). In Germany, $\delta^2\text{H}$ were used to assess the differential use of aquatic and terrestrial prey by insectivorous bats (Voigt et al., 2015). In Ontario, Canada, interspecific differences in nestling diet and differential relative use of aquatic-emergent prey of three species of sympatric aerial insectivores, Tree Swallows, Barn Swallows, and Cliff Swallows (*Petrochelidon pyrrhonota*), were assessed using $\delta^2\text{H}$ as an endogenous marker (Bumelis et al., 2022). Similarly, $\delta^2\text{H}$ was used as a tracer to study differential contribution of aquatic-emergent prey to Bank Swallow (*Riparia riparia*), Tree Swallow, and Barn Swallow nestling diets. Differences were apparent between inland and lakeshore birds, with more negative $\delta^2\text{H}$ values in Bank and Tree Swallow individuals breeding closer to aquatic ecosystems, but this was not observed in Barn Swallows (Génier et al., 2021, 2022).

The application of $\delta^2\text{H}$ as a tracer in trophic studies has shown successful results (Birchall et al., 2005). However, when interpreting $\delta^2\text{H}$ values it is necessary to account for the diverse sources of variation that can affect isotopic values in nature. H isotopic composition of tissues reflects the variability in diet and environmental water from where tissues were synthesized (Hobson et al., 1999; Soto et al., 2013). Therefore, $\delta^2\text{H}$ in food webs can be a function of biotic and environmental factors such as habitat and other life history traits of organisms (Hobson et al., 2012; Jardine et al., 2009; Reese et al., 2018; Vander Zanden et al., 2016), climate, and hydrological processes that can influence the ^2H of environmental waters (i.e. temperature, evaporation, groundwater inputs) (Bortolotti et al., 2013; Bowen et al., 2005; Clark et al., 2021).

For example, Coulton et al. (2009) studied the factors that influenced $\delta^2\text{H}$ variability in feathers of Mallards (*Anas platyrhynchos*) with known moult locations at shallow ponds in Saskatchewan. They reported that the type of wetlands used by the ducks could represent a significant source of variation in $\delta^2\text{H}$ feather values in the prairie ecosystems due to differential evapotranspiration from ponds with distinct hydroperiods.

1.3. The post-fledging period and tracking fledglings

The post-fledging stage of birds is defined as the period between fledging when birds leave the nest, and migration, dispersal and/or independence (Cox et al., 2014; Naef-Daenzer & Gruebler, 2016). In altricial birds, the departure from the nest is a key life-history stage, and is considered a bottleneck in population dynamics because it represents an abrupt transitional period from the nest to a new environment during which juvenile birds face greater challenges before achieving full independence (Berkeley et al., 2007; Cox et al., 2014). A recent meta-analysis showed that mortality within the first week of leaving the nest can be as high as 50%, with an average of 17% among different species of songbirds (Naef-Daenzer & Gruebler, 2016). The first three weeks after fledging are the most critical for survival and when higher mortality rates occur. During these period, fledglings have limited mobility, are still depend partially on parental care, and are more conspicuous and vulnerable to predators (Anders et al., 1997; Cox et al., 2014; Evans et al., 2019; Naef-Daenzer & Gruebler, 2016). After leaving the nest, fledglings remain close to the nest because they rely initially on parental food provisioning until they reach independence (Anders et al., 1997, p. 199; Cox et al., 2014; Vitz & Rodewald, 2011). As soon as young reach independence, fledglings usually leave their natal sites while still learning how to navigate, explore (Lombardo, 1987), forage, and evade predators (Anders et al., 1997; Mitchell et al., 2010). In other species, such as the common swifts (*Apus apus*), fledglings transition from a sedentary life in the nest to one of constant flight with little to no post-fledging care, foraging on

their own immediately after leaving the nest (Martins, 1997). Given this variability in fledging strategies, the condition in the nest and the development stage at the time of fledging have been identified as important predictors of post-fledging survival in some species of songbirds (e.g. Evans et al., 2019; Lindén et al., 1992; Naef-Daenzer et al., 2001; but see Sankamethawee et al., 2009).

Despite the perceived importance of the post-fledging period in determining short and long-term survival, this period has received less attention when studying reproductive success. Young birds can be cryptic, secretive and, depending on the species, fledglings can be highly mobile, making it challenging to track them (Anders et al., 1997; Rush & Stutchbury, 2008). However, use of radiotelemetry has created opportunities to collect reencounter information to estimate fledging survival, movement and habitat use (i.e. Anders et al., 1997; Boynton et al., 2020; Cormier & Taylor, 2019; Evans et al., 2019; Jones et al., 2018).

Radiotracking animals using transmitters that operate on a unique frequency and receivers that are programmed to detect that specific frequency have been used as a wildlife tracking method for over 50 years (Cochran & Lord, 1963). Traditionally, radiotracking has been limited to larger animals due to the size of the transmitters, and has relied on researchers on the ground or in aircrafts using antennas and portable receivers, limiting the scale of coverage or the number of individuals that could be tracked simultaneously. New developments in telemetry systems with miniaturization and digitization of transmitters and station automation have improved this technology's capabilities. This system has allowed the study of movements in a wide range of taxa (from mammals to insects) at a broader scale and with high temporal accuracy.

The Motus Wildlife Tracking Network (<https://motus.org>; Taylor et al., 2017) is a collaborative network of researchers, educators, NGOs and other collaborators that deploy arrays of automated radio-telemetry stations to track wildlife at local and regional levels and inter-

continental scales. Currently, more telemetry stations are located in Eastern North America.

However, the network has expanded to the rest of North America and more than 25 countries on six continents.

Motus uses very high frequency (VHF) digitally-encoded nanotags that, after being activated, emit a unique series of four pulses that together make a burst. Bursts repeat at a fixed interval (e.g., 13 secs, 19 secs), depending on the expected lifespan of the tags or the desired optimal interval to track tagged individuals. Pulse intervals and unique tag IDs are encoded in each radio transmitter. Motus Stations, which comprise a power source, a receiver, and one or more antennas tuned to a specific frequency (usually 166.38 MHz in the Western Hemisphere), are tracking continuously and can simultaneously detect multiple coded tags within the range of detection of the antennas. Automated stations also reduce the effort required to find and detect tagged animals. As such, researchers have been able to answer more questions regarding animal movement and their ecology at unprecedented spatial and temporal scales.

So far, VHF radio-telemetry and the automation of stations for the detection of tags are the most reliable option for studying post-fledging survival and tracking movement, especially in small species of songbird that disperse widely and rapidly throughout in the landscape. Thanks to this technology, Evans et al. (2020) studied the post-fledging survival of Barn Swallows from fledging to migration in Ontario, Canada. Similarly, Bumelis et al. (2020) obtained some insights into the movements of multiple species of swallows in the same study system in Ontario, benefitted by the high density of Motus stations in the landscape. Using the same automated telemetry system and continuous tracking, Bani Assadi et al. (2022) studied the early post-breeding movements of juveniles and adults Purple Martins (*Progne subita*), accurately tracking individuals during the nesting period until departure from the colony.

1.4. The Prairie Pothole Region and its dynamic hydrological and ecological complexity

The Prairie Pothole Region (PPR), where this study was conducted, is a unique region in the North American Great Plains that spans the Canadian provinces of Alberta, Saskatchewan, and Manitoba. The landscape of the PPR was shaped by the last glacial retreat and was historically dominated by vast areas of grasslands and high density of shallow depressional wetlands, commonly called “potholes”. (Doherty et al., 2018; Van der Valk, 1989). The relatively low precipitation, persistent winds, cold and long winters, frequent droughts, and high summer temperatures make the PPR a semi-arid region (Fang et al., 2007; McGinn, 2010).

The PPR in Canada is a major agricultural region, with the largest and most intensive grain, pulse, and canola crop production in the nation (Stats Canada, 2022). In the PPR, agricultural intensification and industrial development have dramatically affected habitat composition (Kissinger & Rees, 2009), with wetlands and grasslands becoming highly threatened ecosystems in this region. Since settlement, the PPR has experienced an estimated loss of 70% of native prairie, and 40 to 70% of the wetlands, largely due to anthropogenic activities primarily related to land use changes and industrial and urban development (Bartzen et al., 2010; McKenna et al., 2019; Watmough et al., 2017; Wiken et al., 2003). Transformations of the land use have increased the homogenization of the landscape (Benton et al., 2003), and caused the deterioration of wetland quality through contamination from pesticides and fertilizers (Main et al., 2014; Malaj et al., 2019), and high rates of sedimentation (Watmough et al., 2017). Collectively, these changes have important ecological effects on the maintenance of the biodiversity in the ecosystem, including impacts on terrestrial, aquatic and riparian food webs (Rowen et al., 2020; Wrubleski & Ross, 2011).

The remaining wetlands in the PPR have great ecological importance as they have essential functions in the hydrological balance and ecology of the region. They contribute to the storage of

surface waters, mitigate floods, and are a water source for the atmosphere (LaBaugh et al., 1998). The hydroecology of the PPR is exceptionally complex, and multiple interactions between biotic and abiotic processes contribute to its complexity. Extreme climate variation and the duration of seasonal dry-wet cycles cause high fluctuations in water levels, especially during dry years (Hayashi et al., 2016). Wetland water levels depend greatly on blown-snow redistribution and snowmelt runoff from the surrounding landscape, accounting for as much as 90% of the total surface runoff when soils are frozen (Hayashi et al., 2016). The shifts in wetlands hydroperiods not only act as drivers of change in the biochemistry of these aquatic ecosystems (i.e., salinity, isotopic composition) but also determine the biological composition and seasonal phenology of the wetland-dependent organisms (Bortolotti et al., 2013; Euliss et al., 2004). Wetlands, together with the grasslands, are therefore considered biodiversity hotspots, providing critical habitat for supporting great biological diversity, including several species of migratory waterfowl and other wetland-dependent species, including aerial insectivores.

1.5. Focal Study Species

Within the guild of aerial insectivores, swallows, swifts and nightjars are experiencing the steeper declines in population trends in North America (Smith et al., 2015). Swallows are associated with agroecosystems, for breeding, foraging, and roosting. Thus, they are an interesting and, relatively easier group to evaluate in terms of potential effects of agricultural intensification on components of fitness, such as reproductive success and other demographic rates.

Barn Swallows and Tree Swallows inhabit the Prairie Pothole Region of Saskatchewan but differ in key life-history strategies. Barn Swallows are a long-distance migrant that breeds across North America and winters in Central and South America (Brown & Brown, 2019; Hobson et al., 2015). This species can be double-brooded and nest semi-colonially using human structures such as barns, sheds, and abandoned buildings (Brown & Brown, 2019). Historically, Barn Swallows

nested in caves, but with the expansion of human settlements in North America, adapted to the use of homesteads and buildings. Tree Swallows, are short-medium distance migratory birds that winter in the southern United States and Mexico (Winkler et al., 2011) and usually raise one brood a year. They are secondary cavity nesters (Rendell & Robertson, 1989), but will also use artificial nest boxes provided by humans. This species relies heavily on aquatic-emergent insects (McCarty & Winkler, 1999a; Michelson et al., 2018) relative to Barn Swallows, which is known for being more generalist taking prey from a broad range of taxa, and from terrestrial and aquatic habitats (Kusack et al., 2022; McClenaghan et al., 2019a).

Population trends for these two species in North America have revealed different spatio-temporal patterns of decline. Based on the North American Breeding Bird Survey (BBS) data, Barn Swallows, which were listed as ‘threatened’ on the Species at Risk Act (COSEWIC, 2011), and designated Special Concern in 2021, declined by 69% between 1970 and 2019 in Canada (Smith et al., 2020). After a long period of negative trends, Barn Swallow populations in Canada have stabilized at low levels, with an average annual percent increase of 1.74% (2009 – 2019) in the PPR, most likely driven by a 3.1% increase in the Saskatchewan PPR (Smith et al., 2020). On the other hand, Tree Swallows have undergone a steep decline of 35% since 1970, with more drastic changes in northeastern North America (Shutler et al., 2012). In Ontario and Quebec, short-term trends (2009-2019) indicated 1.5 to 4% annual decreases, whereas in the PPR, Tree Swallows have maintained relatively stable populations, with a 1.6% annual increase (Smith et al., 2020).

1.6. Scope of thesis

The overarching goal of my thesis was to evaluate landscape-level effects of agricultural intensification on aspects of the diet, condition, and post-fledging survival in two sympatric swallow species in the Prairie Pothole Region of Saskatchewan. The study is presented in two

data chapters (Chapters 2 and 3).

In Chapter 2, my objectives were to examine the effects of agricultural intensity on the broad contribution of aquatic-emergent prey to the diet of nestlings, using $\delta^2\text{H}$ feather values as intrinsic markers of broad use of aquatic or terrestrial prey use. I assessed the effect of crop and water landscape features on body condition and growth of nestling Tree and Barn Swallows. I hypothesized that the two species would show differential reliance on aquatic-emergent prey and that aquatic or terrestrial-based diets would be associated with landscape composition around the nest. I predicted that 1) $\delta^2\text{H}$ feather values would be lower in Tree Swallow nestlings than in Barn Swallows (indicated by higher assimilation of aquatic prey by Tree Swallows), 2) $\delta^2\text{H}$ feather values for both Tree and Barn Swallow nestlings would decrease with greater extent of wetland area surrounding the natal colony because higher pond abundance may increase the availability of aquatic-emergent prey, and 3) nestling body condition and daily mass gain would be lower in Barn and Tree Swallow nestlings in natal colony sites with higher relative coverage of annual row crops and lower standing water coverage due to potential indirect and direct effects of agricultural practices on swallow prey abundance and quality.

In Chapter 3, I compared the early post-fledging movements and survival of Barn and Tree Swallows, using a local network of automated radio-telemetry stations. In this chapter, I used data from juvenile Barn and Tree Swallows tagged before they left the nest and tracked while still in the natal area for the following two weeks, to obtain insights into the timing and extent of local fledging movements and to estimate post-fledging survival. I assessed how intrinsic factors such as duration of nesting period, brood size, and body condition of nestlings could influence these estimates. Based on data from the literature and my knowledge of the local study system, I hypothesized post-fledging survival estimates for Barn and Tree Swallows would be similar given their comparable populations trends in the PPR. For both species, I predicted a general pattern of

lower apparent daily survival the first day(s) after leaving the nest, as this period has been identified as a common bottleneck in different species of songbirds, followed by increased survival as surviving juveniles gained mobility and experience. I predicted a positive relationship between apparent daily survival and body condition because nutritional conditions before leaving the nest could potentially buffer individuals from challenging environmental conditions or reduced provisioning rates that may occur after fledging. I also predicted a positive relationship between wing length or nestling period duration and apparent daily survival. I predicted that this relationship would be stronger for Tree Swallows because, unlike Barn Swallows, fledglings must be able to fly and catch prey independently and efficiently soon after leaving the nest, and Tree Swallows that had not fully developed would be more vulnerable to food shortages, predators or other challenging conditions. Regarding post-fledging movements, I predicted that Tree Swallows would depart from natal sites before Barn Swallows, given their species-specific differences in natural history including differences in their reliance on riparian habitats and adult breeding and post-breeding strategies.

CHAPTER 2. Landscape-level effects of agricultural intensity on diet source and condition of Barn and Tree Swallow nestlings

ABSTRACT

It is still unclear how landscape changes caused by intensification of agriculture have affected breeding aerial insectivores and more specifically the effects on the quality of nestlings and other key demographic drivers. In 2020 and 2021, I investigated the landscape-level effects of agricultural intensity on nestling diet source (terrestrial versus aquatic-emergent prey), and the body condition of two sympatric species of breeding aerial insectivores, Tree Swallows (*Tachycineta bicolor*) and Barn Swallows (*Hirundo rustica*), across a gradient of agricultural intensity in the Prairie Pothole Region. Using hydrogen stable isotope analyses ($\delta^2\text{H}$) of nestling feathers, local insect taxa, and wetland water, I investigated whether the intensity of agriculture, with buffer sizes determined by a scale of effect analysis, were associated with differential prey selection of terrestrial versus aquatic-emergent insects provisioned to nestlings. I also tested for differences in nestling quality (body condition and growth) across the gradient of agricultural intensity measured as area of cropland and open water cover around the nest. I found stable isotopic evidence that Barn Swallows used aquatic aerial prey resources to provision nestlings with more open water cover in the proximity to the nest (500 m), whereas in Tree Swallows the contribution of aquatic-emergent prey was high but not related to open water cover surrounding their natal site. Both wetland cover (1700 m) and row-crop cover (500 m) showed weak but negative effects on nestling body condition of Tree and Barn Swallows, respectively; however nestling quality was more strongly influenced by other variables such as nest and site. I speculate that parental care and foraging effort could be potential mechanisms used by aerial insectivores to mitigate effects of agricultural intensity on the diet composition and quality of young. This research contributes to the growing body of evidence that multiple species of aerial insectivores

can be differentially impacted by shifts in insect communities as a consequence of agricultural activities. My results highlight the importance of conservation of wetlands in the agricultural landscapes in the Prairie Pothole Region to mitigate range-wide declines in breeding populations of aerial insectivores.

2.1. INTRODUCTION

Early life-stages in altricial birds are among the most nutritionally and energetically demanding periods of their life cycle, and the quantity and quality of food provisioned by parents can influence nestling phenotype and subsequent fitness. Diet quality and composition depends on several factors including, but not limited to, foraging strategies of the adults (e.g., distance and height of foraging; Bumelis et al., 2022; Dreelin et al., 2018; Orłowski & Karg, 2013), nutritional demands of the young (Twining et al., 2021) and the spatiotemporal availability of high-quality or preferred prey determined by the landscape structure and the quality of the habitat (Génier et al., 2021). Even though adult birds can have some flexibility to respond to changes in available prey (Mallord et al., 2017; Naef-Daenzer et al., 2000), food quality and availability during the breeding season can be a strong determinant of nestling body condition, growth, and survival (Ardia, 2006; McCarty & Winkler, 1999b; Naef-Daenzer et al., 2011; Winkler et al., 2013).

In the last several decades, changes in agricultural practices in North America and globally are increasingly shifting towards high-input agriculture and the expansion of cropped areas (Matson et al., 1997), which has transformed and degraded aquatic and terrestrial natural habitats (Belanger & Grenier, 2002; Benton et al., 2002; Tschardt et al., 2005). Wetlands in agricultural lands are widely recognized for providing subsidies of nutrients for terrestrial and riparian consumers (Baxter et al., 2005; Fritz et al., 2017; Kowarik et al., 2021; Twining et al., 2019), but are becoming more sparse (Hayashi et al., 2016; McKenna et al., 2019), and their quality has been deteriorating (Bartzen et al., 2010; Main et al., 2014; Morrissey et al., 2015). At a global scale,

agricultural intensification, principally through land use change and chemical pollution, has played a major role in shaping the structure, diversity and phenology of aquatic and terrestrial arthropod communities (Campbell et al., 2009; Cavallaro et al., 2019; Euliss & Mushet, 1999; Morrissey et al., 2015; Raitif et al., 2019; Rowen et al., 2020; Sánchez-Bayo & Wyckhuys, 2019), potentially affecting the diet and fitness of consumers that use this resource in farmland habitats (Benton et al., 2002).

Aerial insectivores are a diverse guild of birds that rely almost exclusively on flying insects, including aquatic-emergent and terrestrial taxa (Bellavance et al., 2018; Bumelis et al., 2022; Kusack et al., 2020; McClenaghan et al., 2019a; Michelson et al., 2018). This guild has experienced severe and sustained declines in abundance in the last five decades in parts of their geographic ranges in North America (Sauer et al., 2017; Smith et al., 2015). Given the strong association of many aerial insectivore species with open habitats, agroecosystems and riparian features, a reduction in availability of high-quality prey caused by agricultural intensification and climate change have been recently hypothesized as major drivers of population declines of this guild (Spiller & Dettmers, 2019).

Aquatic-emergent insects represent a high-quality source of food for some consumers, relative to terrestrial insects (Twining et al., 2019), as they are richer in long chain polyunsaturated fatty acids (LCPUFA) (Twining et al., 2019). Omega-3 LCPUFAs are considered essential nutrients for animals to maintain important physiological processes and cannot be synthesized by many taxa (Twining et al., 2016a). Increased contribution of omega-3 LCPUFA-rich aquatic-emergent prey to the diet of nestlings improves body condition, growth and immunocompetence in different species of riparian songbirds, including Tree Swallows (Berzins et al., 2021; Dodson et al., 2016; Twining et al., 2016b, 2019). Habitat features can determine the availability of different types of insect prey in the landscape, and with that the quality and

composition of bird diets. For instance, in different species of aerial insectivores, such as Bank Swallows (*Riparia riparia*) and Tree Swallows, nestlings are provisioned with higher abundance of aquatic-emergent prey when this type of prey is more available indicating that their reliance on the aquatic-emergent prey can be dependent on the habitat of the natal sites and the surrounding landscape (Génier et al., 2021, 2022). In contrast, Barn Swallows appear to be less dependent on aquatic-emergent insects regardless of their natal habitat (Kusack et al., 2022; McClenaghan et al., 2019; Orłowski et al., 2014, Génier et al 2022). Given the diversity of life-history traits of the aerial insectivores, it is important to study their dietary composition and species-specific reliance on aquatic-emergent prey for provisioning nestlings as this may provide clues as to what factors are limiting population growth of the guild and could help direct conservation efforts. As large landscape-level changes can occur from the intensification of agricultural practices, the expansion of cropland and loss of wetlands may alter the availability of prey types consumed by aerial insectivores during the breeding season, which may be detectable through measurements of nestling body condition and growth of individual nestlings.

Hydrogen stable isotope analysis ($\delta^2\text{H}$) is a widely used tool to estimate the broad contribution of aquatic-emergent prey to the diet of birds and mammals (Bumelis et al., 2022; Génier et al., 2021, 2022; Voigt et al., 2015). Hydrogen atoms are incorporated into food webs from environmental waters to primary producers, and subsequently through all trophic levels (Fogel & Cifuentes, 1993; Hobson, 2007). In general, aquatic food webs from same locations tend to be more depleted in ^2H compared to terrestrial food webs due to differential evapotranspiration rates (Bortolotti et al., 2013; Doucett et al., 2007; Vander Zanden et al., 2016), and this distinction is transferred to higher levels of the food chain. Thus, differences in measurements of $\delta^2\text{H}$ in bird feathers can be compared among species from same locations. While several hydrological processes can introduce variation, these $\delta^2\text{H}$ values in insect consumers should reflect differences

in aquatic or terrestrial prey origin.

Declines of aerial insectivores in North America vary geographically and among species (Michel et al., 2016). Barn Swallows were recently designated as Special Concern after being listed as ‘threatened’ under Canada’s Species at Risk Act (COSEWIC, 2011), while sympatric Tree Swallows which similarly inhabit the agricultural landscapes have been declining in part of their distribution though not as precipitously. While populations in some other parts of Canada are still experiencing steep declines (Smith et al., 2020), in the Prairie Pothole Region (PPR), both species have maintained relatively stable populations with a ~1.5% positive annual change since 2009 (Smith et al., 2020). Throughout this geographic area most of the landscape is dominated by annual crops and intensive farming practices, with 70% of native prairie and more than half of the region’s wetlands having been lost mostly due to the conversion of native grasslands to agricultural lands and the extensive wetland drainage (Bartzen et al., 2010; Watmough et al., 2017). Therefore, the trends of stable or increasing populations for both Barn and Tree Swallows in the PPR remain unexplained considering the growing evidence that agricultural intensification causes shifts in abundance and composition of insect communities (Sánchez-Bayo & Wyckhuys, 2019; Wagner et al., 2021), which may indirectly reduce prey quality and availability for aerial insectivores.

Using a gradient of agricultural intensity in the Saskatchewan Prairies and nestling $\delta^2\text{H}$ feather ($\delta^2\text{H}_f$) values as intrinsic markers of broad use of aquatic or terrestrial diet (Génier et al., 2021, 2022; Vander Zanden et al., 2016; Voigt et al., 2015), my first objective was to test the hypothesis that Barn and Tree Swallows would differ in contributions of aquatic prey in their diet. Second, I tested the effect of agricultural intensity on nestling body condition and growth for both species. I predicted that more intensive agriculture (higher annual crop coverage and lower open water abundance) would influence the contribution of aquatic-emergent prey in their nestling’s

diet. Specifically, I predicted 1) lower $\delta^2\text{H}_f$ (more reliance on aquatic prey) in Tree Swallow nestlings than in those of Barn Swallows; 2) $\delta^2\text{H}_f$ for both Tree and Barn Swallow nestlings would decrease with greater extent of wetland area in the natal colony due to increased availability of ^2H -enriched aquatic-emergent prey, and 3) nestling body condition and daily mass gain would be lower in Barn and Tree Swallow nestlings in sites with higher relative coverage of annual row crops and lower open water due to potential effects of agricultural practices in lowering availability of high quality aquatic prey.

2.2. METHODS

2.2.1. Study site selection

Fieldwork was conducted at 16 sites in 2020 and 2021 within 70 km east and south of the city of Saskatoon, SK, in the vicinity of Dundurn (51.8096° N, 106.5076° W), Hanley (51.6280° N, 106.4395°W), Kenaston (51.5006° N, 106.2706° W) and Allan (51.8940° N, 106.0555° W). This area is characterized by mixed annual row crops (primarily canola, lentils, and wheat), natural grasslands and planted forages. Wetlands of varying size and permanency were abundant, especially in the Allan Hills area, east of Highway 11, but were increasingly rare towards the west. The Brightwater Reservoir and Blackstrap Lake are the main large permanent waterbodies located with 3-4 km from the closest study site (Figure 2.1).

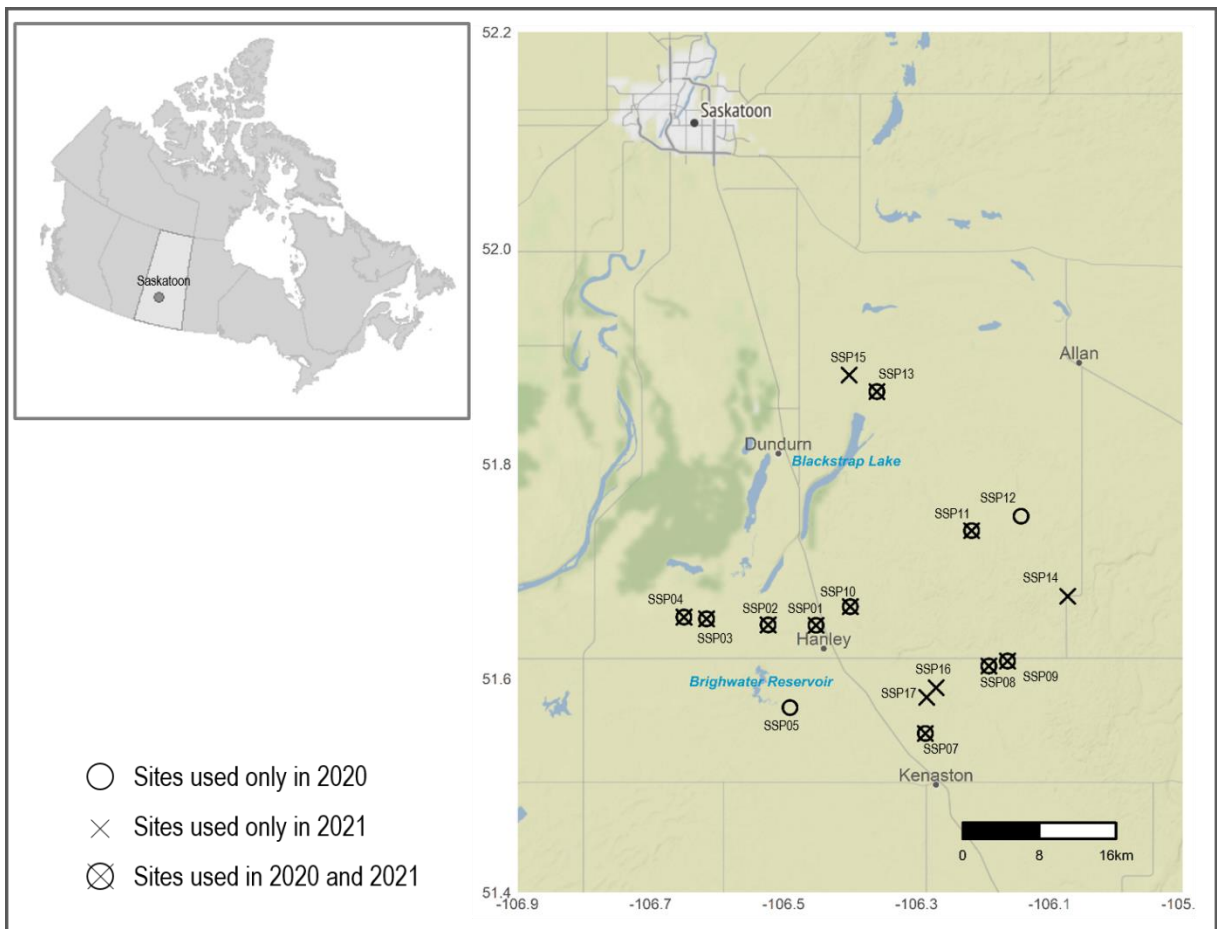


Figure 2.1. Location of the Barn and Tree Swallow study sites followed in 2020 (n=12) and 2021 (n=14). Sites were within 100km southeast of the city of Saskatoon in Central Saskatchewan.

Twelve colony sites were used 2020 and 14 in 2021. Three sites were only included in 2020 (SSP05, SSP06, SSP12) and dropped for the second season due to poor occupancy or high rates of predation. In 2021, four new sites were added to the study (SSP14, SSP15, SSP16, and SSP17). Site SSP17 was used exclusively for the study of Barn Swallows as it was added later in the season after Tree Swallows were already nesting in the area. SSP06 from 2020 was also excluded from all analyses because of high nest failure of both Barn and Tree Swallows due to rain events and high abundance of mites affecting nests in barns or due to competition of House Wrens (*Troglodytes aedon*) and House Sparrows (*Passer domesticus*) with box-nesting Tree Swallows.

Each site was selected based on the evidence of previous occupancy of Barn Swallow colonies in abandoned buildings, especially barns and sheds. Eight to ten Tree Swallow boxes were then installed within 100-200 m around each Barn Swallow colony spaced at least 30 m from each other. This study design allowed me to investigate nestling individuals of both species, breeding sympatrically and under the same environmental conditions.

My study colonies were located in a gradient of agriculture where crop coverage ranged between 0.25% and 94% in a 500 m radius from the nests (mean \pm SD = $40.0 \pm 27.3\%$), and was negatively correlated with the perennial grass cover which ranged between 0.24% and 88% ($41.7 \pm 22.1\%$). Open water area ranged between 0 and 13% ($3.0 \pm 3.4\%$; Figure 2.2, Table 2.1). Trees and urban areas were present in the landscape surrounding the nests, but did not represent a major component of the landscape, except for one site where tree coverage was relatively more abundant (SSP11, $14.3 \pm 3.4\%$).

2.2.2. Land use classification

The landscape surrounding each nest or building was classified by cover types: annual row crop, perennial forages (including natural grasslands and forage crops), and open water, urban and trees. Concentric buffers (n=20) spanning from 500 to 2000 m around each nest or colony were used to calculate the relative proportion of each land cover class at each scale and their values ranged from 0 to 100. Land cover types were classified using the 2020 Annual Crop Inventory spatial dataset (30 m resolution) available from Agriculture and Agri-food Canada (AAFC 2020). Cropland cover included area under canola, wheat, lentils, flaxseed, barley, and other crops which were combined into an annual row crop category (hereafter “crop”), which I used as a proxy of agricultural intensity from landscape simplification (Malaj & Morrissey, 2022). Pastureland and area under grasses, including lands seeded to perennial forages and hay, were combined into a

“perennial grasses” category. Despite the Annual Crop Inventory product having wetlands and open water as categories, the resolution of this product (30x30 m) was larger than desired and the accuracy for non-agricultural land cover in Saskatchewan is low (73%) compared with the accuracy for crop land-cover for the same region (92%). Therefore, the Canadian Wetland Inventory (Ducks Unlimited 2020) was used to obtain a more accurate classification of the open water (wetlands) relative coverage (10 m resolution), as it includes the shallow/open water category. Although, I recognized that marshes, which often include ephemeral wetlands, can be important refugia for insects, this type of wetlands were excluded from the classification due to higher evaporation prior to the breeding season and the difficulty of ground-truthing their presence with satellite imagery. Digitized land cover data were compared with Copernicus Satellite 2 imagery (European Space Agency, 2021) from 26 June 2020 and 01 July 2021, which also corresponded with the breeding peak for both the focal species during the years of the study. The Canadian Wetland Inventory has not been completed for the whole study area; therefore, where coverage was not available (n=5 sites), I used satellite imagery from Sentinel2, to delineate wetland areas on the sites that were not available in the CWI (n=5). I used maximum likelihood supervised classification as well as free hand delineation to delineate all wetlands with open water (hereafter “water”). Landscape data were analyzed using ESRI ArcMap 10.8.1.

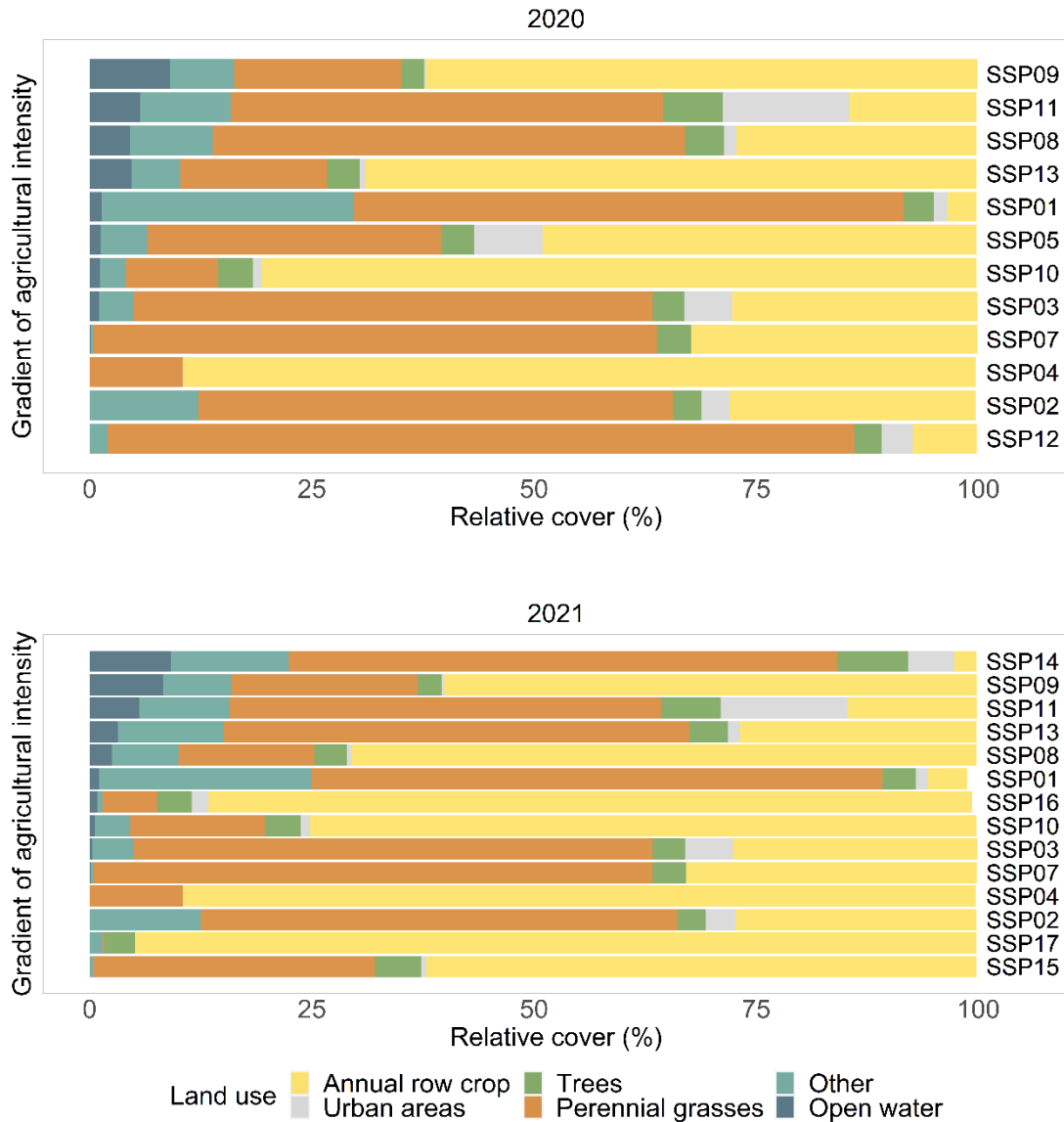


Figure 2.2 Agricultural intensity gradient measured across the study sites for each of the two study years (2020 and 2021). The plot shows % relative land use cover within 500 m radius from nest, extracted from the Annual Crop Inventory (Agriculture and Agri-Food Canada, 2020). The category of % open water was obtained from the Canadian Wetland Inventory and Sentinel2 Satellite imagery (European Space Agency, 2021). The category “Other” includes area of marshes and ephemeral wetlands, which were excluded from the analysis due to the high seasonal variability and difficulty to ground-truth.

Table 2.1 Summary of site-specific information on land use cover and colony size/nest box occupancy by year of the study. Shown are mean % and standard deviation of land use cover per site per year calculated from the land use relative cover surrounding Tree and Barn Swallow nests within a 500 m radius. This table also includes a summary of numbers of nestlings (nests) followed in 2020 and 2021, including nests that failed after laying at least one egg. For Tree Swallows, nest box occupancy (%) is also reported based on the percentage of boxes that were occupied. (*) indicates the only site where a Tree Swallow colony was previously established, and where the number of boxes available was >20.

Site	Year	Land use relative cover (500 m radius)			Barn Swallow	Tree Swallow	
		Open water (%)	Annual Row Crop (%)	Perennial Grasses (%)	Nestlings	Nestlings	Nest box Occupancy (%)
SSP01	2020	1.34 ± 0.16	3.28 ± 2.12	61.87 ± 4.81	23 (6)	25(4)	44
	2021	1.06 ± 0	4.40 ± 0	64.25 ± 0	-	5(1)	12
SSP02	2020	0.00 ± 0.01	27.68 ± 2.03	53.48 ± 0.94	34(7)	16(3)	33
	2021	0.01 ± 0.02	27.13 ± 2.89	53.62 ± 1.69	32(7)	41(8)	89
SSP03	2020	1.16 ± 0.02	27.57 ± 3.28	58.42 ± 3.51	31(6)	18(4)	70
	2021	0.29 ± 0.03	27.43 ± 4.33	58.44 ± 4.49	37(8)	53(10)	100
SSP04	2020	0.01 ± 0.03	89.24 ± 2.78	10.42 ± 2.76	32(8)	18(3)	44
	2021	0.02 ± 0.04	89.14 ± 2.92	10.41 ± 2.81	23(7)	11(2)	22
SSP05	2020	1.22 ± 0.05	48.84 ± 2.80	33.14 ± 2.31	16(5)	32(6)	68
	-	-	-	-	-	-	-
SSP07	2020	0.088 ± 0	32.18 ± 3.36	63.48 ± 3.41	23(5)	16(3)	56
	2021	0.088 ± 0	32.70 ± 4.38	62.91 ± 4.48	14(3)	40(7)	78
SSP08	2020	4.76 ± 0.55	68.76 ± 1.67	16.55 ± 1.49	24(5)	29(5)	100
	2021	2.49 ± 0.12	70.21 ± 3.25	15.32 ± 2.96	17(4)	14(3)	29
SSP09	2020	9.07 ± 0.26	62.01 ± 3.68	18.87 ± 3.82	43(9)	25(5)	56
	2021	8.27 ± 0.23	59.97 ± 4.95	20.99 ± 5.14	35(7)	54(9)	100
SSP10	2020	1.19 ± 0.14	80.45 ± 1.56	10.48 ± 0.70	12(3)	37(6)	67
	2021	0.63 ± 0.44	75.00 ± 16.46	15.19 ± 13.84	13(3)	39(8)	89
SSP11	2020	5.69 ± 0.85	14.31 ± 6.999	48.63 ± 5.59	26(6)	28(5)	89*
	2021	5.61 ± 0.85	14.59 ± 7.52	48.57 ± 5.44	28(6)	26(5)	40*
SSP12	2020	0 ± 0	7.22 ± 3.61	84.0 ± 3.88	7(2)	21(4)	75
	2021	-	-	-	-	-	-
SSP13	2020	4.56 ± 2.23	27.04 ± 3.65	53.18 ± 4.12	56(12)	45(8)	70
	2021	3.15 ± 1.99	26.60 ± 3.54	52.32 ± 6.74	36(8)	45(8)	80
SSP14	2020	-	-	-	-	-	-
	2021	9.14 ± 1.97	2.54 ± 0.57	61.66 ± 1.20	58(13)	33(6)	75
SSP15	2020	-	-	-	-	-	-
	2021	0 ± 0	61.92 ± 8.89	31.74 ± 8.68	11(3)	4(2)	12
SSP16	2020	-	-	-	-	-	-
	2021	0.84 ± 0	85.88 ± 0	6.12 ± 0	26(6)	-	-
SSP17	2020	-	-	-	-	-	-
	2021	0 ± 0	94.64 ± 0.18	0.24 ± 0	17(5)	21(4)	44
All		3.0 ± 3.4	41.6 ± 28.0	40.6 ± 21.9	25±12.9	25±13.9	61.7±27.1

2.2.3. Weather conditions

Weather conditions, especially in terms of maximum temperature and monthly precipitation, varied among the two years. In 2021, the mean monthly maximum temperatures for June and July were approximately 16-20 % higher, and monthly total precipitation was ~60% lower relative to 2020. On July 2, 2021, temperatures reached 40°C and maximum temperatures stayed above average and consistently within the range of 28 to 34°C for the rest of the month (Appendix A, Figure A.4, Table A.1).

2.2.4. Nest monitoring and Nestling measurements

Barn and Tree Swallow colonies were visited every 3 to 4 days starting May 15, to check for signs of occupancy and nesting activity (building or repairing) in the barns and in the nest boxes. To reduce disturbance to Barn Swallow adults and nestlings, I used a lighted mirror attached to an extension pole to check nests. It was not possible to follow every clutch attempt of all the females breeding in some sites, especially for Barn Swallows, because they were out of reach or because they were not found in time to follow their nest phenology. Nests were visited approximately every two days to estimate clutch initiation date, assuming that eggs were laid one per day until the penultimate egg, when the incubation period starts (Day 0). Time of hatching was predicted to be 12-17 days after incubation began, for Barn Swallows, and 13-14 days for Tree Swallows (Brown & Brown, 2019; Winkler et al., 2011). The day the first nestling hatched was considered Day 0 for the whole brood. If hatch day was not directly observed, age of brood was estimated based on a combination of different criteria: eggshell remains in the nest, number and size of nestlings hatched, and presence of wet feathers. When necessary, I also used an aging guide for Barn Swallow nestlings (Morales Fernaz et al., 2012) or Tree Swallow nestlings

(<http://www.treeswallowprojects.com/cgrowth.html>) based on size and feather tract development and feather shaft emergence.

Most nests were visited three times during the nestling period on Day 4 and Day 8 and the last check occurred on Day 12 for Tree Swallows and Day 15 for Barn Swallows. Day 12 and 15 were selected as they are the last days that nestling can be handled without risk of premature fledging (R. Clark and K. Hobson, pers. Comm). Every visit, nestlings were removed from the nest and covered to reduce stress and maintain warmth (also enhanced with hand warmers on coldest days). While nestlings were removed from the nest, a bag was placed in the entrance of the nest to avoid parental nest abandonment. On Day 4, 8 and 12 (Tree Swallows) or 15 (Barn Swallows) each nestling was individually marked, and morphometric measurements were taken. Nestlings were marked on Day 4 by trimming feather groups following an identification code to identify nestlings in the next visit. On Day 8, nestlings were banded using a size 1 Canadian Wildlife Service aluminum band. For each nestling, I measured unflattened right wing-chord, tarsus length, head-bill length, and body mass (nearest 0.1 g), in addition to the total length of the 9th primary and the portion of feather that had already emerged from the pin (hereafter “p9 pin”). P9 pin and head-bill were taken only on the last visit. Wings were measured using a wing ruler (nearest 1 mm), tarsus and bill lengths were measured with dial calipers (nearest 0.001mm) and body mass with a portable digital scale (nearest 0.1 g). All nestling were then returned immediately to the nest.

I calculated nestling body condition index (BCI) for each nestling as the residuals of a linear regression of mass and wing length, to account for variation in structural size (Labocha & Hayes, 2012). BCI was estimated for nestlings on Day 8, during the active growth phase (Appendix A Figure 2.2). Measurements from later in the nestling stage (day 12 and 15) were not used because they were not comparable and Barn and Tree Swallows experienced mass reduction several days prior to fledging (Moeller & Ritchison, 2019; Ricklefs, 1967; Wright et al., 2006; Zach & Mayoh,

1982). For Barn Swallows, mass and wing length, and mass and tarsus length on Day 15 were poorly correlated, violating the assumption of high correlation between mass and structural measurement needed to use this body condition index (Green, 2001) (Appendix A, Figure A.2, A.3). As a proxy for growth rate, I estimated the relative daily mass gain (Day 4 to Day 8) by dividing the mass difference on the number of days between measurements (g/day).

2.2.5. Blood and Feather sampling

On Day 12 or 15, three nestlings were randomly chosen from each nest to sample feathers and blood. I collected 5-6 body feathers and stored them in coin envelopes for future lab processing and analysis. Nestlings were sampled for blood by venipuncture of the brachial vein using 27-gauge needles and blood was collected into heparinized capillary tubes and then transferred to microcentrifuge tubes. Blood samples were used for a parallel study to quantify exposure to pesticides of nestlings in the same system. The previously described methods were used to follow first broods. However, in 2020 due to high nest failure rates caused by intense rain events and frequent predation events at Barn Swallow nests, some second attempts (i.e., a new clutch after the first nest or clutch failed) and second broods (i.e., new brood after successful fledgling) were used to increase sample size. When a Barn Swallow nest failed, adults would typically build or repair a nest located close to the failed nests. Similarly, as Barn Swallows can be double-brooded, adults would rarely use the same nest to start a second brood (Safran, 2006). However, adults would usually build or repair a nest near the first nest (A. Diaz, *pers.observ*). Accordingly, first broods and first attempts were categorized as “first” and late broods and/or second attempts were called “late”. I was not able to access every nest attempt in barns and not all adults were marked so there is uncertainty about whether clutches were second attempts or just late broods. Thus, I calculated the 5-95% quantile range of hatching date of a set of nests from 2021 that were known

as “true” first broods. All nests with a hatching date later than the 95% quantile (Barn Swallows, day 189- July 8; Tree Swallows, day 180-June 30) were then assigned to the “late” category (Appendix A, Figure A.1). Only early broods were included in analyses.

2.2.6. Terrestrial insect sampling

In 2020 and 2021, I collected insects to provide an isotopic baseline of the potential prey sourced and to characterize terrestrial versus aquatic-emergent insect isotope values among sites. I conducted standardized sweep-netting in each site, using conical insect nets (Ward’s Professional Insect Net, VWR International catalogue # 470018–488, Radnor, Pennsylvania, USA). Sweep netting was conducted every 10 to 15 days, from the last week of May until the first week of August, to cover the whole breeding period. At each site, sweep net transects were conducted within 500 m from the main Barn Swallow colony in four habitats: cropland, grassland, and field or road margin, and within 2 m from wetland shorelines, where available. Each transect was 50 m long. Samples were stored in zip-lock plastic bags, placed on ice in a dark cooler in the field and upon returning to the lab were stored at -20°C until later identification.

Samples were thawed and identified to Order, following a dichotomous key (Triplehorn et al., 2005); Diptera was further sorted to suborders Nematocera and Brachycera which reflect distinct aquatic and terrestrial life histories. After identification, samples were refrozen for 24 h at -80°C and subsequently freeze-dried for a minimum of 48 h.

For the stable isotope study, only Coleoptera (i.e., beetles), representing largely terrestrial prey, and Nematocera (i.e., chironomids, midges) representing aquatic-emergent prey, were analyzed for $\delta^2\text{H}$. Nematocera has been previously identified as one of the favoured prey groups for swallows and the order Coleoptera has been detected by DNA metabarcoding in nestling fecal DNA samples (Harris, 2023; McClenaghan et al., 2019a; Mengelkoch et al., 2004; Orłowski &

Karg, 2011).

2.2.7. Water sample collection

Seasonal and spatial variation occurs in environmental $\delta^2\text{H}$ waters in the PPR (Bam & Ireson, 2019; Bortolotti et al., 2013; Cavallaro et al., 2022), therefore water samples were collected in 2021 from at least one natural or artificial wetland at each site. Sampled ponds were located within 500-1000 m from the main swallow colony. Samples were collected from the nearest permanent wetland as some ephemeral and semi-permanents wetlands dry up by mid-July. In sites where wetlands were not present near the colony, we collected water samples from artificial ponds (i.e., dugouts). Water collection occurred two or three times during the breeding season (mid-May, mid-June, mid-July). Water was collected within 1m of the wetland edge and approximately 10cm below the surface. Samples were collected in 25 ml scintillation vials filled to exclude air space. Vials were capped tightly, covered with parafilm, and maintained cool in the field to subsequently refrigerate them at 4°C in the lab until analysis within one month.

2.2.8. Stable isotope analysis

Body feathers were soaked overnight in 2:1 chloroform:methanol, decanted, rinsed, and dried under a fume hood for 24 h, as described by Wassenaar and Hobson (2000). Then samples were analyzed for stable hydrogen isotope abundance by weighing subsamples (0.35mg) into silver capsules using exclusively the feather barbs (not rachis). Insect samples from 2020 were freeze-dried after insects were identified to order (suborder Nematocera for Diptera). Before encapsulation of insects, samples collected from June 11 to July 16, 2020, were homogenized by taxa and pooled to obtain the target mass necessary for isotopes analysis. Six pooled samples were encapsulated per site. Capsules were crushed and trays were sent for analysis to the LSIS-AFAR Stable Isotope facilities at the University of Western Ontario for $\delta^2\text{H}$ analysis. Samples were

loaded in a UNI-prep (Eurovector, Milan, Italy) heated carousel (60°C) coupled with an Eurovector elemental analyser and combusted on a glassy carbon reactor at 1350°C. The resultant H₂ gas was analyzed using a coupled Thermo Delta V Plus (Thermo Scientific®, Bremen, DEU) isotope-ratio mass spectrometer in continuous-flow mode via a Conflo interface.

Pre-calibrated in-house keratin standards (CBS; 197‰; KHS: -54.1‰) were used to derive the δ²H value of the non-exchangeable H fraction, according to the comparative equilibration technique described by Wassenaar and Hobson (2003). Results were expressed in the standard delta (δ) notation in parts per thousand (‰) deviation from the Vienna Standard Mean Ocean Water (VSMOW). Based on replicate measurements (n=5 for 38 unknowns) of each keratin standard, analytical error (SD) was estimated to be ± 2‰.

Water samples were analyzed for δ²H by off-axis Integrated Cavity Output Spectroscopy (OA-ICOS) using a Los Gatos Research DLT-100 lasers spectrometer in the Stable Isotope Lab at the National Hydrology Research Center (NHRC) in Saskatoon. To normalize raw delta values to the VSMOW–SLAP scale, two calibrated reference waters were used (INV1 δ²H = -217.7‰, δ¹⁸O = -28.5‰ and ROD3 δ²H = -3.9‰, δ¹⁸O = -1.0‰). To reduce carryover between samples, nine aliquots were analyzed from each sample, but only the last five were used to obtain the raw delta values (Koehler, 2019).

2.2.9. Statistical analyses

I used linear mixed-effect models (LMM) to test for differences in contributions of aquatic versus terrestrial prey to the diet of Barn and Tree Swallows, and the effects of land use on their diet source, juvenile body condition index (BCI) and daily mass gain. Before the analyses, I standardized all the continuous variables (mean=0, SD=1) (Grueber et al., 2011). I used the Akaike Information Criterion for small sample size (AICc) to determine the best-fitting model.

Unless a single best-fitting model could be determined and no other models had $\Delta\text{AICc} < 2$, the effects of individual variables were estimated via multi-model inference (Burnham & Anderson, 2002), and model predictions were calculated using conditional model averaging whereby parameters are only averaged over models in which they occur (Grueber et al., 2011). Explanatory variables with unconditional 95% CI overlapping zero were noted as uninformative (Arnold, 2010). I performed all statistical analyses using R (version 4.0.3) and RStudio (v. 1.3.1093, RStudio Team 2020). I used the R package “lme4” to fit LMMs (Bates et al, 2015) and package “MuMIn” to perform model selection, and model averaging (Barton, 2022). I assessed the collinearity between variables using the VIF function from the “car” package and the normality of residuals by normal Q-Q and residual plots. Subsequently, using the “performance” package in R, calculated marginal R^2 and conditional R^2 of top models ($\Delta\text{AICc} < 2$), to evaluate the variance explained by the fixed effects, and the variance explained by both fixed and random effects, respectively (Nakagawa & Schielzeth, 2013).

In order to test for differences in $\delta^2\text{H}$ values of water samples from different types of wetlands, I ran a LMM to compare the $\delta^2\text{H}$ in water values at each colony site accounting for the type of wetlands sampled. The type of wetland and collection date (May, June, or July) were fixed effects, and site was a random effect. Similarly, I ran a LMM to compare aquatic versus terrestrial prey $\delta^2\text{H}$ values, including insect $\delta^2\text{H}$ values as the response variable, insect taxa as a fixed effect and site as a random effect.

To evaluate the landscape effects of land use on my response variables, I used the relative coverage of annual crop and open water as proxies of agricultural intensification. I initially chose 500 m as an appropriate area of interest to evaluate the effect of annual row crop based on previous studies that have reported breeding swallows foraging range. Both species are central-place foragers, and forage mostly within the vicinity of the nests (McCarty & Winkler, 1999a).

This is also supported by the adult foraging data obtained with geolocators deployed in Tree and Barn Swallows during the rearing period in the same study system (Harris, 2023) and by previous work conducted with adult female Tree Swallows (Elgin et al., 2020) in Saskatchewan which confirmed that 75% of the foraging trips for both species occur within 500 m. However, given the evidence that Tree Swallows increase their selection for water when traveling further from the nest, I wanted to determine the optimal scale of effect at which open water could be influencing my response variables ($\delta^2\text{H}_f$, body condition). For each species, I used a scale-of-effect approach as in Kusack et al. (2019). I fitted a set of LMM for each response variable using a set of fixed factors (i.e., brood size, hatching date and year, crop at 500 m), and water coverage at each nested scale (500 to 2000 m radii, every 100 m). Based on likelihood tests among random intercept-only models, I found that the best random effect structure for my model included nest identity nested within site identity by year ($p < 0.001$; Zuur et al., 2009). Including site specific identity each year accounted for site-level differences among years such as local crop types and cropping specific practices that could have affected insect emergence and availability. The random effects structure also accounted for the non-independence of nestlings within nests. Scale-of-effect models were fitted using maximum likelihood. By using lower AICc values, I determined the model with the most appropriate scale for open water relative coverage.

I first tested for isotopic differences between species of swallows, without accounting for the land use effect. I used a LMM with $\delta^2\text{H}_f$ as a response variable and included species, year, brood size (number of young when sampling), and hatching date (day of year) as fixed effects. Hatching day was included to account for seasonal effects on $\delta^2\text{H}_f$. By including brood size as a covariate, I controlled for potential differences in parental selection of food sources or travel times dependent on the number of nestlings raised and the demands on provisioning (Ardia, 2007). I used the best random effect structure which included site identity by year and nest identity, following a nested

structure.

To test my prediction that the contribution of aquatic and terrestrial-emergent prey to the diet, body condition and daily mass gain of Barn and Tree Swallows is higher on landscapes with lower agricultural intensity (i.e., lower crop and higher water coverage), I used a set of pre-designed LMM candidate models for each species and for each response variable to compare with a null model (random intercept only model). All candidate models included hatching date, brood size, and year (biological model). The candidate set of models also included crop, water or water and year interaction. To evaluate the effect of open water cover around the nest on each response variable, open water cover was included in the models at the most appropriate scale based on the scale of effect analysis. All models included site identity and nest identity as random effects following a nested structure, as used in the scale-of-effect models.

2.3. RESULTS

Totals of 679 Barn Swallow and 711 Tree Swallow nestlings were followed during some stage of their life cycle; however, 10% of Tree Swallows and more than 15% of Barn Swallows died before fledgling due to predation, heat stress, rain events, or unknown causes. I studied an average of 6.0 ± 2.7 (mean \pm SD) Barn Swallow nests per site in 2020 and 2021. Tree Swallow occupancy was generally higher in 2021. Thus, the average number of Tree Swallow nests followed per site was 4.75 ± 1.4 in 2020 and 5.6 ± 2.9 in 2021.

2.3.1. Isotopic characterization of environmental water $\delta^2\text{H}$ in natural and artificial wetlands

Surface water $\delta^2\text{H}$ values collected in natural wetlands ranged between -57 and -129‰ and those from artificial wetlands ranged between -68 and -150‰. As expected, values of water $\delta^2\text{H}$ showed seasonal increases at most sites relative to May samples, with highest values in samples collected in July ($\beta_{\text{June}}=15.46 \pm \text{SE } 5.41$; 95% CI= 4.79 – 25.87, $\beta_{\text{July}}=26.02 \pm \text{SE } 5.23$; 95% CI=

15.55 - 36.02). Water collected from smaller artificial ponds was generally more depleted in ^2H than samples collected in natural wetlands ($\beta_{\text{natural}}=50.28 \pm \text{SE } 9.94$; 95% CI= 31.05 - 69.58) (Figure 2.3; Appendix A, Table A.2).

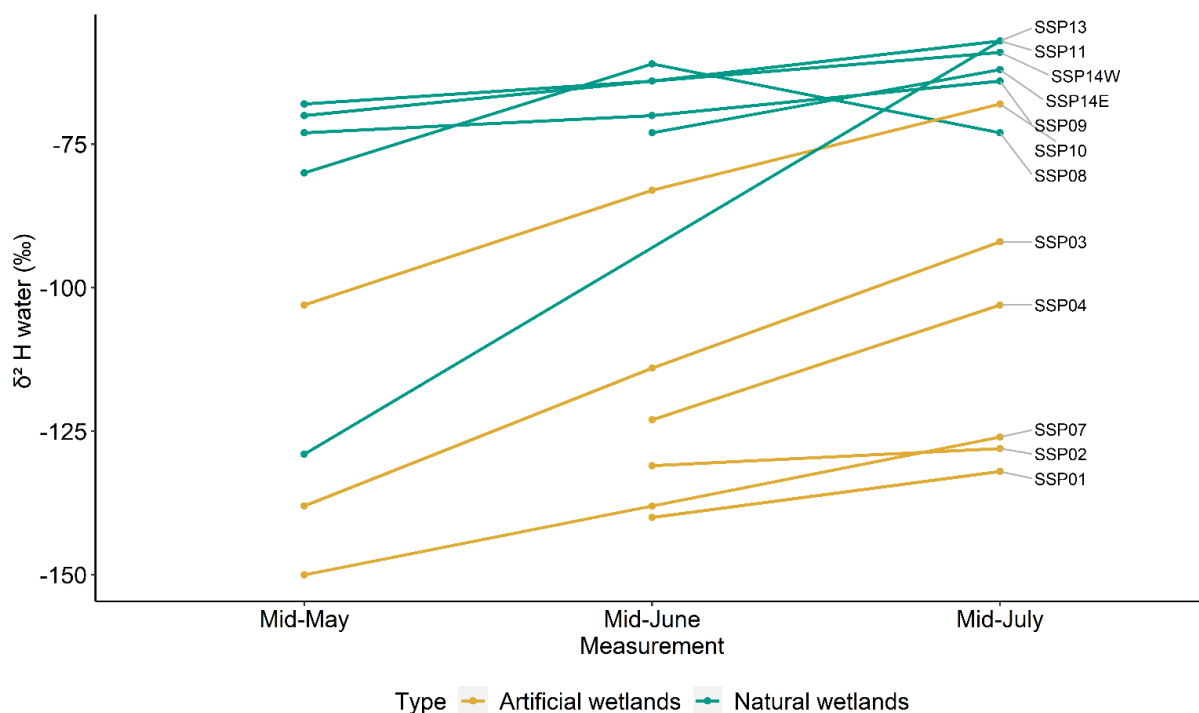


Figure 2.3. $\delta^2\text{H}$ values (‰) from water samples collected during three periods in the breeding season (Mid-May, Mid-June, Mid-July 2021). Samples were collected from artificial dugouts (yellow) and natural wetlands (green) based on availability at each of the 12 swallow study sites (SSP01-SSP14).

2.3.2. Isotopic differences in $\delta^2\text{H}$ of aquatic vs terrestrial prey.

Terrestrial insect (Coleoptera) $\delta^2\text{H}$ values in 2020 ranged between -161.2‰ and -223.2‰ and aquatic-emergent insect (Nematocera) values ranged between -152.50‰ and -248.3‰ (Figure 2.4, Appendix A, Table A.3). There were large inter-site differences in isotopic values and no clear patterns or statistical differences between Nematocera and Coleoptera $\delta^2\text{H}$ values after controlling for site ($\beta_{\text{Nematocera}}=-1.54 \pm \text{SE } 9.94$; 95% CI= -6.76 to 3.69 Figure 2.4).

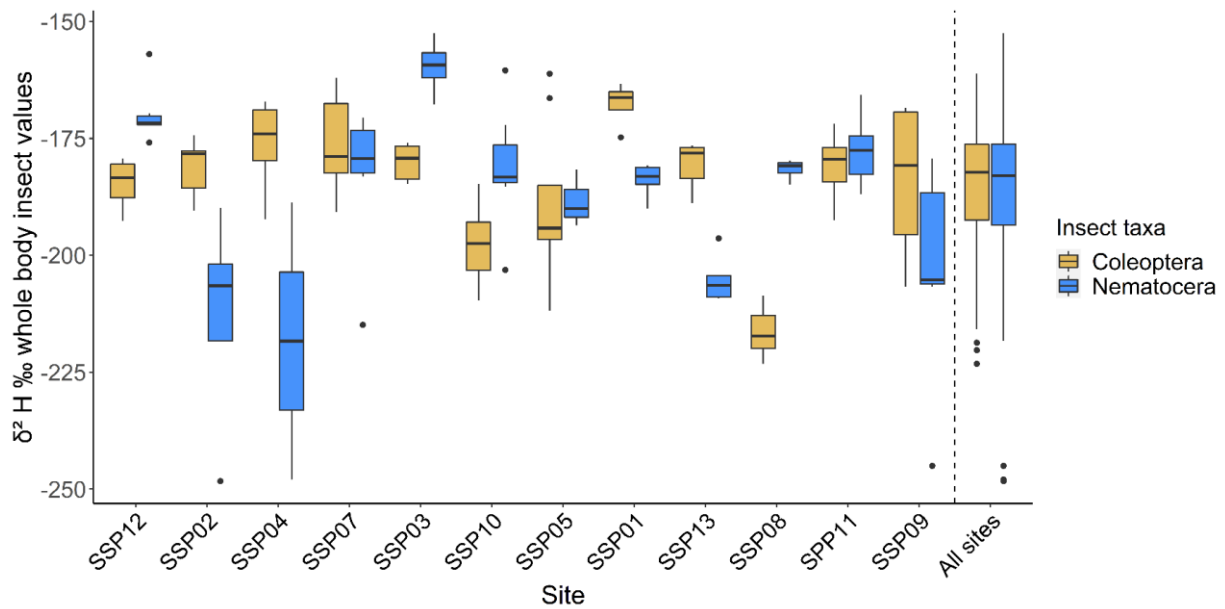


Figure 2.4 Comparative boxplot of whole insect $\delta^2\text{H}$ values for samples at each site. Coleoptera and Nematocera were collected only in 2020 across 12 sites. A total of 70 samples were analyzed for $\delta^2\text{H}$. Sites were ordered by increasing open water coverage from low (left) to high open water coverage (right).

2.3.3. Comparison of $\delta^2\text{H}_f$ values of nestling Tree and Barn Swallows

I sampled feathers from 360 Barn and 355 Tree Swallow nestlings from 133 and 124 nests, respectively. As late broods were removed from the analyses, I only used 258 Barn and 313 Tree Swallow nestling feathers to test the effect of agricultural intensity on aquatic-terrestrial source contributions of insect prey to the diet (Table 2.2). A detailed summary of feathers by site and year is provided in Appendix A, Table A.4.

Across sites and years, Barn Swallow $\delta^2\text{H}_f$ values were on average 3.8% higher than in Tree Swallows ($\beta_{\text{Barn}} = 5.82 \pm \text{SE } 0.91$, 95% CI= 4.02 - 7.62) and, for both species, $\delta^2\text{H}_f$ values were 11-13% more enriched in ^2H in 2021 relative to 2020 ($\beta_{2021} = 11.38 \pm \text{SE } 1.90$; 95% CI= 7.45 -15.31) (Figure 2.5; Appendix A, Table A.5).

Table 2.2 Summary of $\delta^2\text{H}_f$ values (mean \pm SD) for Barn and Tree Swallows collected in 17 sites in Saskatchewan, Canada, during the breeding seasons of 2020 and 2021.

Year	Species	First day of feather sampling	Last date of feather sampling	Mean \pm SD (‰)	nestlings	nests
2020	Barn Swallow	2020-06-26	2020-07-22	-143.71 \pm 12.41	102	36
2020	Tree Swallow	2020-06-23	2020-07-16	-149.73 \pm 10.24	127	58
2021	Barn Swallow	2021-07-02	2021-07-23	-132.20 \pm 6.74	156	44
2021	Tree Swallow	2021-06-19	2021-07-12	-136.96 \pm 5.80	186	65

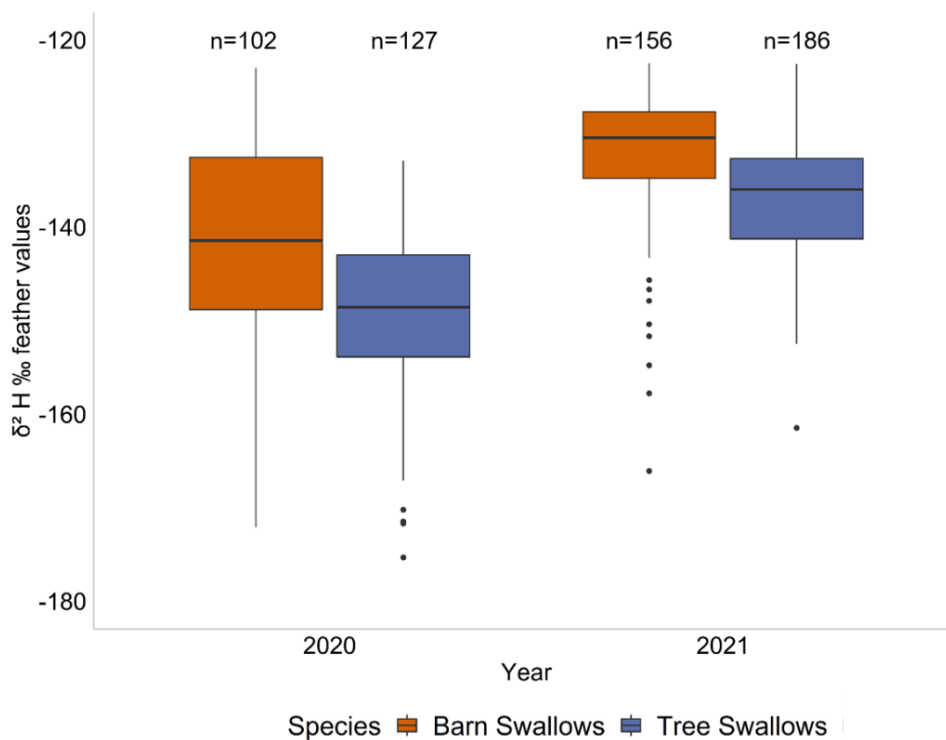


Figure 2.5 Boxplot of nestling Barn Swallow and Tree Swallow $\delta^2\text{H}$ feather values (‰) sampled in 2020 and 2021 from 16 agricultural study sites in central Saskatchewan.

2.3.4. Effect of land use on $\delta^2\text{H}_f$ values in Barn and Tree Swallows.

The scale-of-effect analysis indicated that the models with strongest support included water coverage within a buffer of 500 m for both species; however, for Tree Swallows, all scale of effect models were competitive ($\Delta\text{AICc} < 2$; Figure 2.6).

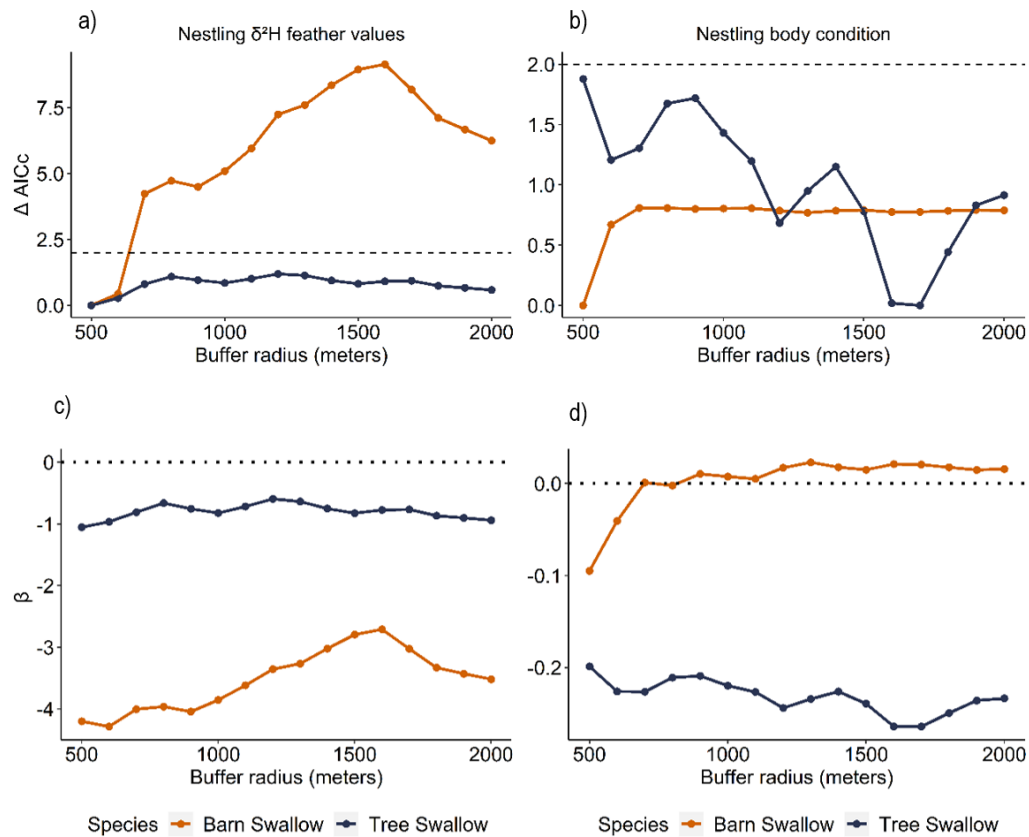


Figure 2.6 Scale of effect showing model fits for nestling $\delta^2\text{H}_f$ values (plots a and c) and nestling body condition (b and d) in Barn and Tree Swallows in response to increasing buffer sizes (m) for relative proportion of open water in the landscape around the nest site. The top plots (a and b) show ΔAICc values resulting from the linear mixed effect models at each nested scale (500 to 2000 m radii, every 100 m), and using crop cover at 500 m, year, hatching date, and brood as fixed effects and site ID and nest as random effects. The dashed lines in top plots (a and b) indicate the threshold of $\Delta < 2.0$ AICc used to identify competitive models. The bottom plots (c and d) show parameter estimates (β) from models.

When I tested the effects of crop and water cover at the most appropriate spatial scale, for Barn Swallow $\delta^2\text{H}_f$ values, three models had a $\Delta\text{AICc}<2$, and the models included crop, water, or both (Table 2.3). Model-averaged estimates indicated that $\delta^2\text{H}_f$ values were lower with relatively higher water cover around the nest ($\beta=-4.82 \pm \text{SE } 1.56$; 95% CI: -7.89 to -1.74), and were related to year, being higher in 2021 ($\beta=11.66 \pm \text{SE } 1.83$, 95% CI: 8.08 to 15.24) (Table 2.2, Figure 2.7). Although crop and the interaction of water and year were included in the top models, I considered these parameters non-informative given that the CI overlapped 0 (Table 2.6).

When evaluating the effect of land use on Tree Swallow $\delta^2\text{H}_f$ values, two models had $\Delta\text{AICc}<2$, but none of them included the crop cover variable (Table 2.3). Model-averaged estimates indicated that Tree Swallow $\delta^2\text{H}_f$ values had a positive relationship with year ($\beta=11.52 \pm \text{SE } 1.80$; 95% CI:7.97 to 15.06) and were lower in the wetter 2020 year than in 2021 (Table 2.2; Figure 2.6). Feather $\delta^2\text{H}$ values increased later in the season and decreased with brood size (Table 2.6). Water cover parameter was included in the averaged models; however, I considered it non-informative because the CI overlapped zero (Table 2.6).

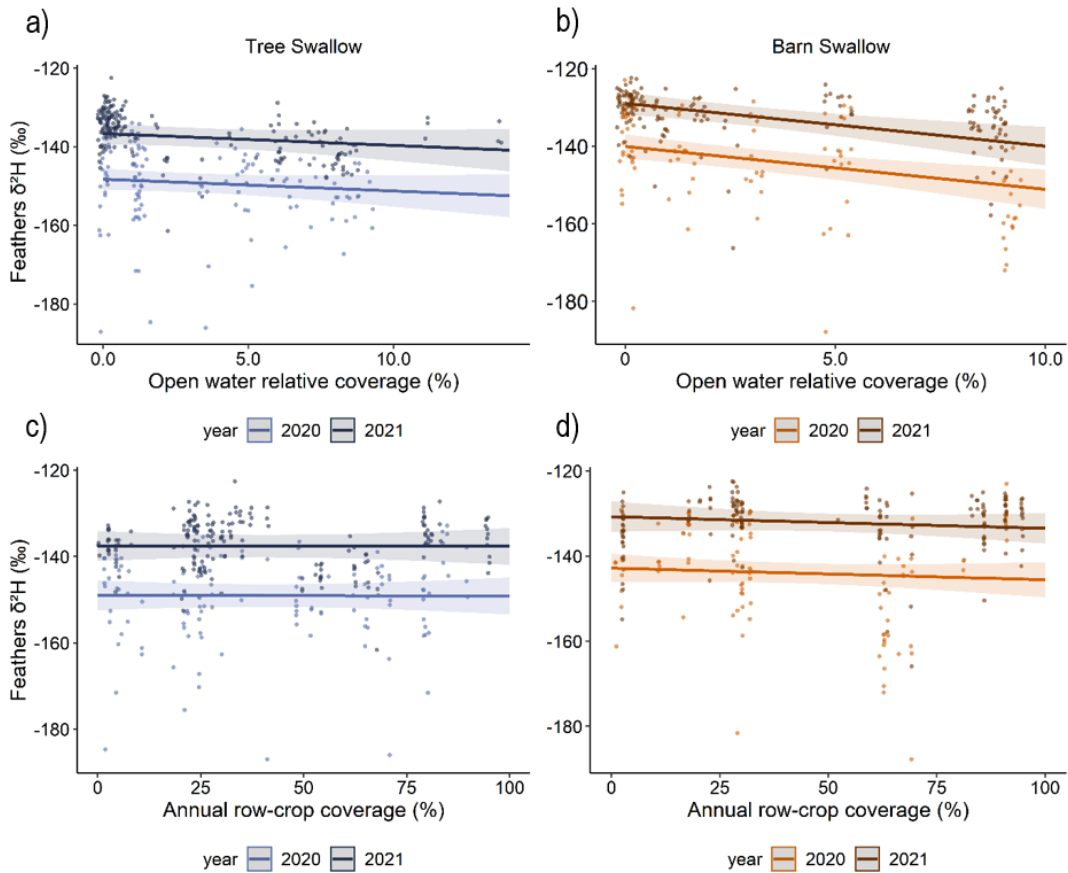


Figure 2.7 Model predicted δ^2H_f values for Tree Swallows (a and c) and Barn Swallows (b and d) nestlings and plotted against open water and annual row relative coverage at 500 m (%). Points represent individual feather data. The model predicted δ^2H_f values and 95% CIs are based on the most parsimonious model from the top models (lower ΔAIC_c), that include each of the land use variables (water or crop). δ^2H_f predicted values from 2020 are shown with light-colored lines and the darker lines are showing 2021 predicted values.

Table 2.3 Model selection table for linear mixed-effect models to evaluate effects of crop and water coverage (%) on $\delta^2\text{H}$ values from Tree and Barn Swallows nestling feathers. Includes six candidate models for each species, including the null model (intercept only) with only the random effect structure. All models included site ID and nest as random effects, following a nested structure. Bold indicates models with $\Delta\text{AICc} < 2$, and that were averaged (See Table 2.6).

<i>Response variable</i>	<i>Models</i>	<i>K</i>	<i>ΔAICc</i>	<i>Log Likelihood</i>	<i>weight</i>
Tree Swallow $\delta^2\text{H}_f$	year+ hatching date + brood size	7	0	-1054.68	0.41
	water + year + hatching date + brood size	8	0.56	-1053.91	0.31
	crop + year + hatching date + brood size	8	2.10	-1054.68	0.14
	crop + water + year + hatching date + brood size	9	2.63	-1053.88	0.11
	water*year + crop + hatching date + brood size	10	4.76	-1053.88	0.04
	(null model)	3	24.91	-1070.25	0
Barn Swallow $\delta^2\text{H}_f$	water*year + crop + hatching date + brood size	10	0	-908.80	0.37
	water + year + hatching date + brood size	8	0.29	-911.10	0.32
	water + crop + hatching date + brood size	9	0.48	-910.12	0.29
	year + hatching date + brood size	7	8.64	-916.34	0
	crop + year + hatching date + brood size	8	10.64	-916.27	0
	(null model)	4	19.53	-924.93	0

2.3.5. Effect of land use on Barn and Tree Swallow nestling body condition and daily mass gain

I included 481 Barn Swallows and 618 Tree Swallows after restricting the analysis to early broods (June 11 to July 8). Nestling body mass and body condition (BCI) on Day 8 in Barn Swallows ranged between 8.1 g and 25.4 g (BCI range: -4.29 to 6.24), and in Tree Swallows between 6.3 g and 24.6 g (BCI range: -3.50 to 6.96, Table 2.4).

Table 2.4 Summary statistics (mean \pm SD) for Barn and Tree Swallow body mass, wing length, body condition and daily mass gain from early broods. Number of nestlings included in each estimate are reported in brackets followed by the number of nests.

<i>Species</i>	<i>year</i>	<i>Mass (g)</i> <i>Day 8</i>	<i>Wing length (mm)</i> <i>(Day 8)</i>	<i>BCI</i> <i>(Day 8)</i>	<i>Daily mass gain</i> <i>(g/day)</i> <i>(Day 4 to Day 8)</i>
Barn Swallow	2020	16.90 \pm 1.73 (198, 43)	32.51 \pm 3.93	0.41 \pm 1.09	1.95 \pm 0.29
	2021	16.25 \pm 2.12 (283, 66)	32.65 \pm 4.41	-0.29 \pm 1.40	1.85 \pm 0.34
Tree Swallow	2020	18.3 \pm 2.75 (260, 46)	29.91 \pm 4.42	0.20 \pm 1.46	2.07 \pm 0.45
	2021	17.38 \pm 2.53 (358, 66)	28.73 \pm 4.65	-0.14 \pm 1.42	2.06 \pm 0.33

According to the scale-of-effect analysis, there was no significant scale of effect of water coverage on body condition in either of the two species, as all models were competitive ($\Delta\text{AICc} < 2$). However, the optimal scales differed for both species with strongest support for a buffer of 1700 m in Tree Swallows, while for Barn Swallow, the strongest model included a buffer of 500 m around the nest (Figure 2.6).

For Barn Swallow nestling body condition (BCI), three models had $\Delta\text{AICc} < 2$, and crop and water were included in the competitive models. In all three models, marginal R^2 ranged between 0.097 and 0.112, while the conditional R^2 ranged between 0.574 and 0.579. Model-averaged estimates showed that crop cover had a negative relationship with nestling BCI ($\beta = -0.22 \pm \text{SE}$ 0.10; 95% CI: -0.42 to -0.02); however area of water cover was considered uninformative (Figure 2.8, Table 2.6). In 2021, the drier year, Barn Swallow nestling body condition was lower than in 2020 (Table 2.6).

For Tree Swallow, four BCI models had a ΔAICc within 2 units, including the null model (Table 2.5). The marginal R^2 of the top models ranged between 0.029 and 0.058, except in the intercept-only model. The conditional R^2 of top models ranged between 0.428 and 0.429. Water

and crop cover around the nest were included in models with ΔAICc lower than 2 units, however only water cover within 1700 m had a weak negative effect on Tree Swallow (Figure 2.8a). In contrast, crop cover was considered non-informative. For year, brood size and hatching date, CIs overlapped zero indicating little evidence that these variables affected body condition of nestling Tree Swallows (Table 2.6)

The average daily mass gain for Tree Swallows during the early nesting period (Day 4 to Day 8) was slightly higher in Tree Swallows (2.09 ± 0.33 g/day) than in Barn Swallows (1.89 ± 0.33 g/day). Both in Barn and Tree Swallows, the null model had the lowest ΔAICc , however, the biological model in Barn Swallows (marginal R^2 : 0.032; conditional R^2 : 0.717) and the model that included water (marginal R^2 : 0.060; conditional R^2 : 0.637) in Tree Swallows were within 2AICc units of the null model (Table 2.5). For Tree Swallows, model-averaged estimates showed evidence of a weak negative relationship of daily mass gain with extent of water coverage within 1700 m. However, I did not find evidence that crop explained change in early growth rates in Tree Swallows. In Barn Swallows, despite inclusion of crop and water terms in the top models (ΔAICc), both variables were considered uninformative due to overlap of the 95% CIs with 0.

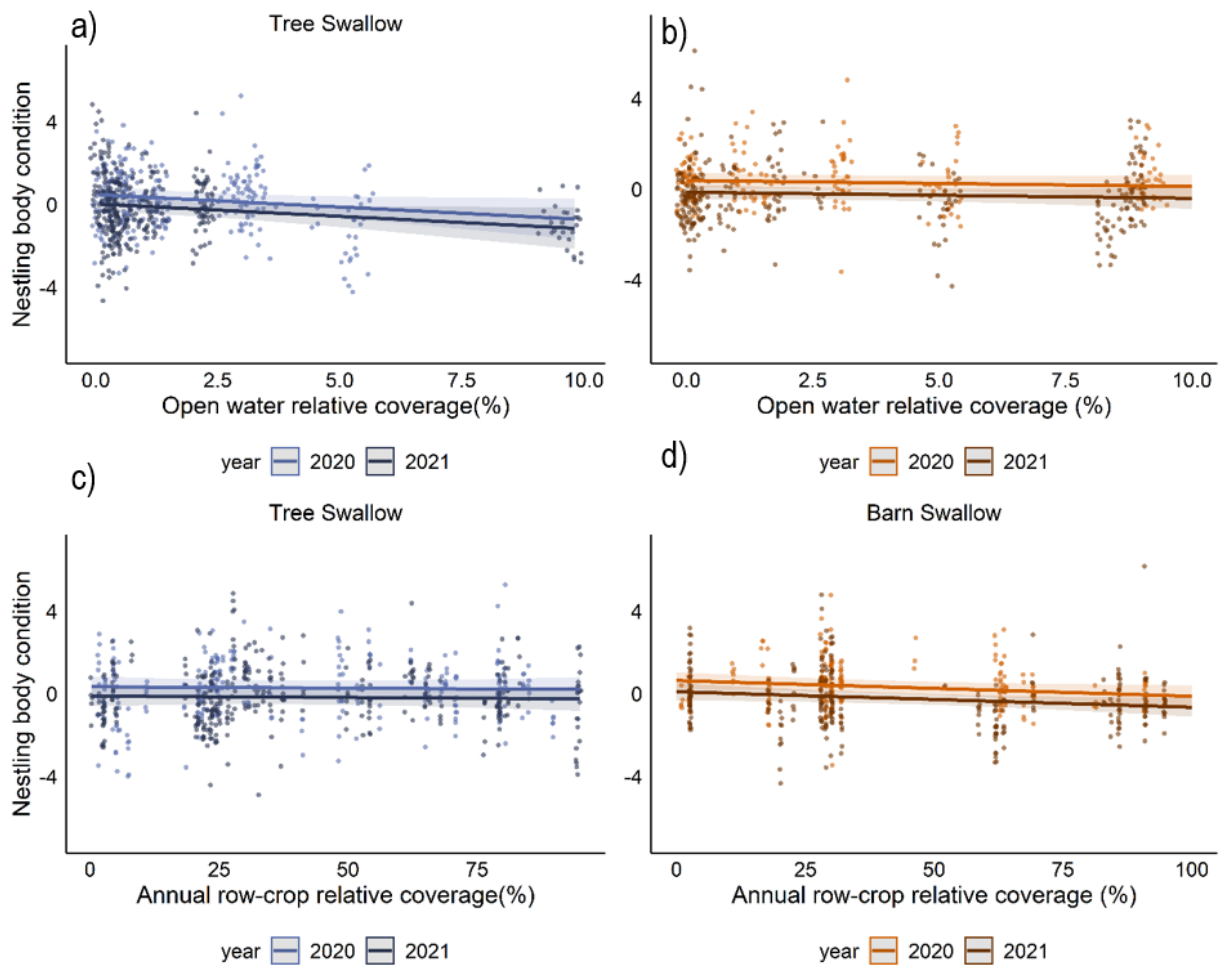


Figure 2.8 Model predicted nestling body condition (BCI) for Tree Swallows (a and c) and Barn Swallows (b and d) plotted against % open water or % annual row relative coverage, respectively. Based on the above scale of effect analysis, buffer sizes for water coverage were 1700 m for Tree swallows and 500m for Barn Swallows. Annual row-crop coverage for both species was a 500m buffer. The model predicted BCI values and 95% CI are based on the most parsimonious model (fewest parameters) from the top models (lower ΔAIC), that include each of the land use variables (water or crop). BCI predicted values from 2020 are shown with light-colored lines and the darker lines are showing 2021 predicted values. Points represent raw data.

Table 2.5 Model selection table for linear mixed effect models to evaluate effects of crop and water coverage (%) on Tree and Barn Swallow nestling body condition (BCI), and daily mass gain (from Day 4 to Day 8). Shown are six candidate models for each species. All models included site ID and nest as random effects, following a nested structure. Bold indicates models with $\Delta AICc < 2$ which estimates were averaged (See Table 2.6).

<i>Response variable</i>	<i>Models</i>	<i>K</i>	<i>$\Delta AICc$</i>	<i>weight</i>	<i>Log Likelihood</i>
Tree Swallow BCI	water + hatching date + brood size + year	8	0	0.36	-1015.89
	<i>Null model</i>	4	0.59	0.27	-1020.27
	hatching date + brood size + year	7	1.91	0.14	-1017.87
	water + crop + hatching date + brood size + year	9	1.96	0.14	-1015.84
	water*year + crop + hatching date + brood size + year	10	3.90	0.05	-1015.77
	Crop + hatching date + brood size + year	8	3.96	0.05	-1017.87
Barn Swallow BCI	crop + hatching date + brood size+ year	8	0	0.42	-705.43
	water + crop + hatching date + brood size+ year	9	1.27	0.22	-705.02
	hatching date + brood size + year	7	1.76	0.18	-707.34
	Water*year + crop + hatching date + brood size+ year	10	2.72	0.11	-704.70
	water + hatching date + brood size+ year + 1 nest	8	3.68	0.07	-707.27
	<i>Null model</i>	4	10.56	0.00	-714.82
Tree Swallow nestling daily mass gain	<i>Null model</i>	4	0	0.54	-94.52
	water + brood size + hatching date + year	8	1.70	0.22	-91.32
	water + crop + brood size + hatching date + year	9	3.03	0.12	-90.92
	water*year+ brood size + hatching date	10	3.05	0.12	-89.89
	brood size + hatching date + year	7	4.61	0.051	-93.76
Barn Swallow nestling daily mass gain	<i>Null model</i>	4	0	0.51	16.392
	brood size + hatching date + year	7	1.85	0.20	18.543
	crop + brood size + hatching date + year	8	3.16	0.10	18.921
	water + brood size + hatching date + year	8	3.34	0.95	18.835
	crop + water + brood size + hatching date + year	9	4.20	0.06	19.443
	water*year + brood size + hatching date	10	5.50	0.03	19.835

Table 2.6 Averaged model coefficients with adjusted SE and unconditional 95% confidence intervals (CI) from the best-fit models ($\Delta AICc \leq 2$ units) for Barn and Tree Swallow nestling δ^2H_f , body condition and daily mass gain. (-) indicates that explanatory variables were not included in the model averaging.

Response variable	Explanatory variables	Tree Swallows			Barn Swallows		
		Estimate	Adjusted SE	Uncond. 95% CI	Estimate	Adjusted SE	Uncond. 95% CI
δ^2H_f feathers	Intercept	-149.09	1.29	-151.61 - -146.57	-143.88	1.34	-146.50 - -141.25
	water cover	-1.02	0.75	-2.51 - 0.46	-4.82	1.56	-7.89 - -1.74
	crop cover	-	-	-	-1.07	0.96	-2.96 - 0.80
	2021	11.52	1.80	7.97 - 15.06	11.66	1.83	8.08 - 15.24
	hatching date	1.01	0.46	0.10 - 1.92	-0.97	0.62	-2.19 - 0.22
	brood size	-0.99	0.42	-1.83 - -0.14	0.423	0.6	-0.77 - 1.62
	water cover*year	-	-	-	3.35	1.91	-0.40 - 7.12
Nestling body condition	Intercept	0.22	0.20	-0.17 - 0.61	0.32	0.16	0.00 - 0.64
	water cover	-0.26	0.13	-0.50 - -0.01	-0.09	0.10	-0.30 - 0.11
	crop cover	-0.04	0.12	-0.27 - 0.20	-0.22	0.10	-0.42 - -0.02
	2021	-0.44	0.26	-0.95 - 0.06	-0.54	0.22	-0.97 - -0.12
	hatching date	-0.10	0.09	-0.28 - 0.08	-0.15	0.10	-0.35 - 0.03
	brood size	-0.10	0.09	-0.27 - 0.07	-0.26	0.09	-0.44 - 0.08
Daily mass gain	Intercept	2.07	0.05	1.98 - 2.17	1.91	0.04	1.83 - 1.98
	water cover	-0.08	0.04	-0.16 - -0.01	-	-	-
	crop cover	-	-	-	-	-	-
	2021	-0.05	0.03	-0.20 - 0.10	-0.07	0.06	-0.20 - 0.05
	hatching date	-0.03	0.03	-0.08 - 0.02	-0.03	0.03	-0.08 - 0.02
	brood size	-0.01	0.03	-0.06 - 0.04	-0.03	0.02	-0.08 - 0.02

2.4. DISCUSSION

Using nestling δ^2H_f measurements, I found evidence that when Barn and Tree Swallows breed sympatrically in the agricultural landscapes of the SK, Tree Swallows used aquatic-emergent prey more than Barn Swallows. These results are interesting given that shifts in availability of high-quality prey caused by agricultural intensification and climate have been proposed as a shared driver for different species of aerial insectivore population declines (Spiller & Dettmers, 2019).

My results suggest that Barn and Tree Swallows in the PPR may be affected differently by shifts

in the composition of invertebrate communities caused by anthropogenic activities in the agricultural landscapes. I found species-specific effects of land use on the proportion of aquatic-emergent prey in the diet, most likely driven by differences on their reliance on riparian habitats, diet preferences, and parental care strategies. However, the relationship of nestling body condition and daily mass gain with annual row crop and open water was not as strong as predicted. These results could have been partially explained by the effects of other extrinsic factors at brood and site levels that affect nestling quality (e.g., weather, predators, ectoparasites, exposure to agrochemicals), as well as the parental care and their ability to compensate for changes in prey availability.

2.4.1. Environmental water and insect stable isotopes in the PPR

The variation of $\delta^2\text{H}$ of water among wetlands over time in my study area reflected the complex hydro-ecology of the PPR. Natural wetlands, which were permanent, showed lower $\delta^2\text{H}$ values and less seasonal variability relative to artificial wetlands, which were usually smaller and shallower. Variation in water $\delta^2\text{H}$ among different types of wetlands with different seasonal standing water levels had already been reported by other studies in the PPR (Bam & Ireson, 2019; Bortolotti et al., 2013; Cavallaro et al., 2022). In the PPR, while permanent ponds retain water from previous years, smaller semi-permanent and ephemeral wetlands, as the artificial wetlands I sampled, usually dry up by the end of the summer. Therefore, spring snowmelt runoff, depleted in ^2H , is the primary source of water of shallower wetlands and would determine their isotopic composition compared to permanent wetlands. Water $\delta^2\text{H}$ values from wetlands also followed seasonal predictable patterns related to snowmelt and evapotranspiration (Clark & Fritz, 1997). Given their size and depth, smaller non-permanent artificial wetlands undoubtedly involved greater overall effects of evapotranspiration rates across the season than permanent wetlands

(Bam & Ireson, 2019; Hayashi et al., 2016). The year 2021 was characterized by little precipitation from mid-May to the beginning of August, low relative humidity, and high temperatures. These environmental conditions likely contributed the higher evaporation of surface waters, causing seasonal ^2H enrichment of pond water (Dansgaard, 1964).

Aquatic food webs from the same area tend to be more depleted in ^2H compared to terrestrial food webs (Doucett et al., 2007). Thus, I expected lower $\delta^2\text{H}$ values for aquatic insects relative to terrestrial insects by the site. Contrary to what I predicted, and to what other studies in less hydrologically dynamic areas have reported (Génier et al., 2022), I found no consistent significant differences but high variability among $\delta^2\text{H}$ values of insects, within taxa, and depending on site (Figure 2.4). These data based on a single isotope measurement were therefore uninformative to characterize general patterns of aquatic and terrestrial sources based on $\delta^2\text{H}$ alone. Different factors could have driven this variation, and they are likely not mutually exclusive. In aquatic insects, the chitinous tissues represent the isotopic composition of the aquatic larval stages, which are influenced by isotopic composition of the waterbody they emerged from. Thus, the high variability of wetland water in the study area may have influenced the variation in the isotopic composition of aquatically derived taxa. Additionally, flying insects are highly mobile organisms associated with further dispersal (Muehlbauer et al., 2014), therefore, doubt remains whether insects sampled at a single point in time reflect those used by swallows as insects may have emerged at different times and potentially, moved across open landscapes or carried in some cases long distances by the wind.

Life-history traits, habitats, and physiology, including trophic position, use of drinking water and evaporative water loss are other possible factors that could have contributed to the variation in $\delta^2\text{H}$ in the sampled insects (Vander Zanden et al., 2016). For instance, even though many adult aquatic-emergent insects do not feed as adults, the natal environment isotopic signature of

terrestrial and aquatic insects that feed as adult flying insects could be replaced over time by dietary or drinking water sources (Myers et al., 2012). Numerous families of Coleoptera are predaceous (e.g., Carabidae, Cicindelidae and Gyrinidae). For example, the Carabidae family is riparian and feed mainly on aquatic insects, obtaining food by preying on adult aquatic insects or scavenging on dead insects (Paetzold et al., 2005). As some of the Coleopterans were collected in the vicinity of the shoreline, some individuals might have preyed on aquatic insects, thus integrating isotopic signals from aquatic sources.

The high variability in $\delta^2\text{H}$ among terrestrial insects may also be a result of analyzing whole-body insects for stable isotopes instead of using only chitinous inert tissues (e.g., wings, legs). The composition of soft tissues may contribute to variation in $\delta^2\text{H}$ values. For example, lipids have more negative $\delta^2\text{H}$ values than proteins and carbohydrates, due to differences in water-tissue isotopic fractionation during their synthesis or metabolic processes (Hobson et al., 1999; Inger & Bearhop, 2008; Sessions et al., 1999). However, birds are consuming whole insects in their diet and digestion efficiencies will vary widely.

2.4.2. Effects of agricultural intensity on differential parental selection of aquatic-emergent prey by Barn and Tree Swallows

For aerial insectivores, $\delta^2\text{H}_f$ values should broadly reflect the isotopic composition of their insect prey (Hobson et al., 1999). Consistent with predictions, Tree Swallow $\delta^2\text{H}_f$ values were lower than in Barn Swallows, and that relationship holds throughout the two years of the study, which suggests that Tree Swallows consume more aquatic-emergent prey whereas Barn Swallows are less reliant on this diet source. Similarly, in Ontario, Tree and Cliff Swallow nestling $\delta^2\text{H}_f$ values were lower relative to Barn Swallow feathers, indicating dietary segregation on sympatric species of swallows, and different reliance on the aquatic prey (Bumelis et al., 2022). Previous studies have found that the majority of Tree Swallow diet consists of aquatic-emergent prey

(Michelson et al., 2018), with a high contribution of aquatic Diptera to the diet (McCarty & Winkler, 1999a; Winkler et al., 2011). Barn Swallows, instead, have been reported to have greater dietary flexibility (McClenaghan et al., 2019b).

Across the gradient of agriculture intensity, I found species-specific effects of land use on the proportion of aquatic-emergent prey in the diet. Barn Swallow nestling $\delta^2\text{H}_f$ values were lower when the open water relative area increased in the landscape. These results contradict a study conducted in Ontario, in which Barn Swallow nestling $\delta^2\text{H}_f$ did not differ between inland and lakeshore locations and appeared to maintain a predominantly terrestrial diet independent of the surrounding nesting habitat (Génier et al., 2022). If higher wetland cover in agricultural lands increases the availability of aquatic-emergent prey in the landscape (Lewis-Phillips et al., 2020), my results suggest that Barn Swallows consume more aquatic-emergent insects opportunistically in this study system, but may not be as dependent on the resource. Barn Swallows commonly forage nearer their nest site, and select large actively flying Diptera, but adjust the provisioning depending on availability even at the expense of larger or preferred prey (Brown & Brown, 2019; Turner, 1982). It is unclear whether aquatic-emergent insects represent a nutritional benefit for Barn Swallows, or if the increased use of aquatically derived prey simply reflects their relative abundance. Linking these results to measures of prey availability and nutritional value (i.e., fatty acids) may help better understand the role of aquatic-prey resource dependence for Barn Swallows.

None of the land use measurements evaluated as a proxy of agricultural intensity were related to the $\delta^2\text{H}$ values in Tree Swallows. Tree Swallows maintained high reliance on aquatic-emergent prey regardless of cropland extension and wetland abundance in the landscape. Previous studies in the PPR did not find clear evidence of differences in apparent diet composition between Tree Swallows nesting at cropland and grassland sites (Michelson et al., 2018), suggesting that in this

region, cropland area alone might not be a good predictor of diet composition for Tree Swallows. However, there is increasing evidence that abundance and area of wetlands plays a disproportionately large role in the diet and foraging ecology of Tree Swallows, as subsidies of high quality insect prey (Berzins et al., 2022; Elgin et al., 2020), and in turn on their reproductive success and survival (Clark et al., 2018; Twining et al., 2018b). Previous research in the PPR found that Tree Swallows preferentially select wetlands for foraging relative to terrestrial habitats (Elgin et al., 2020), and that dependence rises with the increasing distance to wetlands. Although, in other systems, Tree Swallow diet quality increased with proximity to waterbodies with presumably higher abundance of aquatic prey (Génier et al., 2022), Tree Swallows in the PPR may have sufficient access to wetlands such that their availability was not limiting (at least at larger scales) (Berzins et al. 2022). Some potential mechanisms to mitigate the effect of agricultural intensity on nestling's diet might involve changing parental care strategies by increasing feeding rates (Garrett et al., 2022b), travelling farther to find high-quality food (Elgin et al., 2020; Harris, 2023), adjusting foraging rates or increasing the time away from the nest to forage for preferred prey (Stanton et al., 2016). This trade off has been shown to represent a potential cost to the body condition or fitness of parents (Ardia, 2005; Clark et al., 2018; Harrison et al., 2011; Saino et al., 1999; Stanton et al., 2017).

Moreover, PPR wetlands have different sizes and hydrologic regimes (i.e., permanent, semi-permanent and ephemeral), as well as diverse biotic and abiotic characteristics which enhance the habitat heterogeneity and contribute to asynchronous emergences of aquatic insects (Euliss & Mushet, 1999; Mantyka-Pringle et al., 2019; Mclean et al., 2022; Wrubleski & Ross, 2011). Aquatic emergent insects' phenology can also change seasonally, even daily, depending on the species, and depending on factors such as local weather (Euliss 2004), causing short-term and local shifts in the insect community composition and structure (Wrubleski & Ross, 2011). Thus, I

speculate that in the PPR, the remaining wetlands in the landscape, the asynchrony of the peaks of insect emergence during the early summer, and the highly mobile condition of aerial insects could favour the constant flow and diffusion of aquatic-emergent prey into terrestrial and riparian environments and may also help offset lower insect availability associated with a lower local abundance of wetlands and more intense agricultural practices in the PPR. These results contribute to the growing body of evidence that wetlands in the agricultural landscapes of the PPR are critical for supporting breeding populations of some aerial insectivores as sources of high prey quality (Berzins et al., 2021, 2022; Michelson et al., 2018).

The use of $\delta^2\text{H}$ as a tracer of diet and the interpretation of results based on this metric requires important considerations, especially in highly seasonal environments like the Canadian Prairies. Hydrogen isotopic composition of tissues reflects the variability in diet and environmental water from where tissues were synthesized (Hobson et al., 1999; Soto et al., 2013). In food webs, $\delta^2\text{H}$ values depend on biotic and environmental factors such as habitat and other life history traits of organisms (Hobson et al., 2012; Jardine et al., 2009; Reese et al., 2018; Vander Zanden et al., 2016), as well as climate and hydrological processes that can influence the ^2H of environmental waters (i.e., temperature, evaporation, groundwater inputs) (Bortolotti et al., 2013; Bowen et al., 2005; Clark et al., 2021). For example, previous studies conducted in Saskatchewan have found that the type and characteristics of wetlands used by Mallards could represent a significant source of variation in $\delta^2\text{H}$ feather values in the prairie ecosystems (Coulton et al., 2009). Using only $\delta^2\text{H}$ in feathers as a tracer of the contribution of aquatic-emergent prey create challenges given the strong link of stable hydrogen isotopes with the hydrological cycle and ambient temperatures, especially in a hydrologically dynamic region as the PPR. Future studies using multiple dietary tracers in concert (e.g. ^{13}C stable isotopes, eDNA, fatty acids) could help address the shortcomings identified here (Hoenig et al., 2022b, 2022a).

2.4.3. Effects of agricultural intensity on nestling body condition and daily mass gain

Based on presumed higher nutritional value of aquatic insects relative to terrestrial insects (Parmar et al., 2022; Twining et al., 2019), I predicted that higher abundance of open water cover would improve body condition and daily mass gain in both species through higher availability of aquatic-emergent prey (Parmar et al., 2022; Twining et al., 2019). However, I did not find strong evidence that local water relative abundance affects body condition in Barn Swallows, despite the apparent higher broad contribution of aquatic-emergent prey to the diet of nestlings as water cover increased at their natal sites. Depending on the foraging flexibility of the consumers and their capacity to synthesize essential nutrients (Twining et al., 2021), benefits from the high nutritional value of aquatic-emergent prey will be reflected in the consumers' health and fitness. For example, aquatic-emergent prey rich in omega-3 LCPUFAs has been identified as a strong predictor of Tree Swallows fledging success and nestling growth (Twining et al., 2016b, 2018b) given their poor efficiency in synthesizing omega-3 LCPUFAs from their precursor molecules and the need to find these nutrients readily available in the diet. However, recent research suggested that Barn Swallows may be able to synthesize omega-3 LCPUFAs from their precursor molecules (Génier et al., 2022), without depending on them as a nutritional source. Further research is needed to confirm Barn Swallow's ability to synthesize omega-3 LCPUFA to meet their physiological needs and to investigate their conversion efficiency (Twining et al., 2018a). This information would help understand better the reliance of this species on aquatic-emergent prey and the potential effect of changes in the availability of this prey on their body condition and health.

Cropland had negative effects on Barn Swallow nestling body condition. This relationship, even if weak, may be explained by reductions in prey availability in cultivated areas (Attwood et al., 2008; Evans et al., 2007; Spiller & Dettmers, 2019; but see Imlay et al. 2017). Such prey

reductions may result from lower heterogeneity in the landscape (Benton et al., 2003), intensive practices that disturb soil (Rowen et al., 2020), or the effects of intensive use of pesticides and other agrochemicals on non-target species (Sánchez-Bayo & Wyckhuys, 2019). I did not investigate the effects of grassland coverage around the nest on the condition of the nestlings because of the high negative correlation with row crop area. However, at the less intensively cropped sites (<50% row crop), forage grasses were dominant in the landscape, and some had an intermittent presence of livestock near the barn. The presence of livestock in and surrounding the colony buildings has been associated with higher abundance, survival and, reproductive success in Barn Swallows, likely because of an increase in insects (Evans et al., 2007; Gruebler et al., 2010; Møller, 2001, but see Ambrosini et al. 2006). Even if only two of the colony barns or buildings were temporarily used for cattle farming during the period of this study, the presence of livestock, hayfields and manure heaps within the foraging range from the nest in low agricultural intensity sites may have enhanced availability of preferred type and size of prey for Barn Swallows (Orłowski & Karg, 2013) and provided a higher-quality habitat for this species relative to cropland, especially during adverse weather conditions (Evans et al., 2007; Gruebler et al., 2008; Rioux Paquette et al., 2013). My results contrast with studies in other populations in Canada where croplands in the vicinity of the nests had neutral or weakly positive effects on Barn Swallow nestling body condition (Boynton et al., 2020; Kusack et al., 2020). Boynton et al. (2020) reported neutral effects of croplands area on nestling body condition, however effects were assessed for nestlings on Day 15, and therefore results may reflect pre-fledge mass loss in preparation for fledging (Ricklefs, 1967) rather than a land use effect. Positive effects of cropland area within 100 m of the nest reported by Kusack et al., (2020) suggest that some cropped agroecosystems could be of higher quality for Barn Swallows. However, the PPR is the most intensively farmed region in Canada, in terms of crop area and agrochemical use (Malaj et al.,

2020).

While crop coverage was not a good predictor of body condition or daily mass gain of Tree Swallows, and contrary to my predictions, my results suggested a weak but negative effect of water cover in these two measures of nestling Tree Swallows quality. In contrast, recent studies have reported that an increasing abundance of wetlands in agricultural landscapes can offset the negative effects of cropland on the quality of Tree Swallow nestlings (Berzins et al., 2021, 2022; Gómez et al., 2021). These effects were attributed to the role of wetland ponds as buffers of negative effects of agriculture, presumably through a higher abundance of high-aquatic-emergent prey. Although my findings did not support my predictions, given that this is a short-term study, the relationships between land use variables and body condition, and daily mass gain should be interpreted with caution. Low marginal R^2 (<0.15) and relatively high conditional R^2 (>0.45), were evidence of poor model power and indicated that most of the variance of the models is explained by other variables such as site and nest, and that were not the focus of this study.

Nestling body condition and growth can be a result of complex interactions of multiple environmental and ecological circumstances during ontogeny, beyond the extension of each land use alone (Metcalf & Monaghan, 2001). On one hand, the wide ranges of variation in mass and size among and within nests suggest there might be multiple mechanisms leading to brood-specific and most likely, site-specific variation. High intra-brood variation in size was observed in both species, potentially related to their hierarchical position within the brood as a consequence of the asynchronous hatching, and which in some cases persisted during the nestling period (Magrath, 1990; Mainwaring et al., 2009; Saino et al., 2012). Other plausible drivers of nestling quality variation could be: adult female quality and age (De Steven, 1978; Pigeault et al., 2020), local weather (Cox et al., 2018, 2019; Mitchell et al., 2022), foraging effort of adults (Elgin et al., 2020; Stanton et al., 2016), microclimate (Dawson et al., 2005; Winkler, 1993), or parasite

infestation (Clark & Russell Mason, 1988; Hoogland & Sherman, 1976).

At a site level, the spatio-temporal variation in agricultural practices across natal areas (seeding, tillage, and pesticide application), as well as the configuration of wetlands in the landscape and the physical and chemical characteristics specific to the individual wetlands (e.g. size, type, hydroperiod, salinity), beyond the extent of open water, may impact or benefit emergence of insects and, with that, the nutritional quality of aerial insectivores. For instance, water chemistry measurements, like higher salinity or pH, have been associated with abundance and emergence of aquatic insects from wetlands (Kraus et al., 2021). Meanwhile, agrochemicals and other toxicants can directly impact the health of the birds or reduce the insect emergence, potentially affecting abundance of prey for aerial insectivores (Cavallaro et al., 2019; Kraus et al., 2021; Morrissey et al., 2015). To understand the potential landscape level impacts of agriculture on aquatic-emergent prey use and the fitness and demography of Barn and Tree Swallows and other riparian species that rely on this resource and breed in agricultural environments, further research should directly evaluate the abundance and availability of aquatic emergent prey, seasonal emergence from different types of wetlands, as well as investigating the nutritional quality and their potential role as a vector of exposure to toxicants for consumers (Kraus et al. 2021).

2.4.4. Conclusions

The main conclusion of my study is that Barn and Tree Swallows have different reliance on aquatic-emergent prey when provisioning nestlings in the PPR. Barn Swallows, as a generalist species, opportunistically use aquatic aerial prey resources when they are available, while Tree Swallows have higher reliance in aquatic-emergent prey. Those differences may occur as a result of different nutritional requirements of nestlings but also as a mechanism of partitioning of

resources that can benefit the coexistence of sympatric species. This intraspecific differences on their reliance on aquatically derived prey are of interest because different species of aerial insectivores may be dissimilarly impacted by shifts in insect communities as a consequence of agricultural activities. My results also indicate that nestling quality in this agroecosystem may be a result of complex interactions among ecological and environmental factors such as quality and abundance of food, adult female quality, nest temperature, local weather conditions, differential parental care strategies and other site-specific environmental stressors, but need to be further investigated.

Similar to other work conducted in PPR, my research highlights how $\delta^2\text{H}$ values in the food web are highly influenced by the hydrological cycle and the effect of environmental conditions on $\delta^2\text{H}_f$, adding additional complexity and uncertainty to the interpretation of $\delta^2\text{H}$ for the estimation of prey origin (Bortolotti et al., 2013; Jardine et al., 2009). The comparative nature of this research includes the variance in the system by studying two species simultaneously under same environmental conditions. However, my results underscore the importance of documenting the fluctuating isotopic composition of potential dietary and water sources during the growth period of the consumer's tissues, which can act as a baseline to reliably use $\delta^2\text{H}$ as an intrinsic marker for diet composition and water-to-land linkages (Clark et al., 2021; Vander Zanden et al., 2016). Moreover, the use of multiple diet tracers could help avoid biases in the interpretation of results from isotopic methods of diet characterization and to have greater insight into the spatio-temporal shifts in diet (Hoenig et al., 2022b, 2022a; Nielsen et al., 2018) .

With the increasing evidence of shifts in composition, abundance and phenology of aquatic insect communities at a global scale (Campbell et al., 2009; Cavallaro et al., 2019; Euliss & Mushet, 1999; Gladyshev & Sushchik, 2019; Morrissey et al., 2015; Stenroth et al., 2015), an important source of highly nutritious food may also become limited, especially for species with

more specialized diet, such as Tree Swallows. For Barn Swallows, however, high-quality terrestrial prey (i.e., larger size) may play a more important role, but they do use the aquatic-emergent prey when available; even if apparent effects on the nestling body condition are undetectable. Conserving and protecting the remaining wetlands and natural habitats in the Prairie Pothole Region appears to be a key strategy to support aerial insectivores and other farmland birds before they start experiencing similar negative population trends, as has been reported for other parts of Canada and North America.

This study emphasizes the utility of studying multiple sympatric species under identical environmental conditions and using the same methods as a valuable way to understand how different species of aerial insectivores respond to the environmental conditions of the breeding grounds and how they may be similarly or differentially using their environment when rearing young. Moreover, it highlights the need for further investigation to disentangle the complex mechanisms driving nestling body condition and health and that could have long-lasting consequences in reproductive success and other life stages of the annual cycle of aerial insectivores, such as the post-fledging period.

CHAPTER 3. Using automated radio telemetry to study early post-fledging survival and movement of Barn and Tree Swallows in Central Saskatchewan

ABSTRACT

The post-fledging stage is a relatively short transition period, in which juveniles must rapidly learn how to fly, maneuver and forage under varying conditions and challenging environments before undertaking their southward migration. For many species of songbirds, and particularly the declining guild of aerial insectivores, this life stage remains poorly characterized. In 2020 and 2021, using the Motus automated telemetry system, I conducted a comparative study to gain insights into post-fledging survival and early movement ecology of Barn Swallows (*Hirundo rustica*) and Tree Swallows (*Tachycineta bicolor*) breeding in Saskatchewan crop-land dominated agroecosystems. I found that nest survival from tagging to fledging was 91.75% but within only seven days after fledging, apparent daily survival of fledged Tree and Barn Swallows declined to 60%. Cumulative apparent survival rates over a 14-day period declined to 28% (95%CI 14.2 – 42.2) for Tree Swallows and 23% (95%CI 12.3 – 37.0), for Barn Swallows in 2020, and in 2021 rates were slightly higher for both species, with estimates of 32% (95%CI 18.2 – 49.4) and 29% (95%CI 1.6 – 38.5), respectively. Even though survival in both species was not related to individual traits in the nest (body condition, wing length on day 12 or 15), shorter development time in the nest was an important factor involved in lower survival in Barn Swallows. I also found significant differences in latency to depart from the natal site between species. Tree Swallow fledglings moved away from their natal colonies within 3.7 ± 2.9 days after leaving the nest, presumably to look for more suitable habitats like wetlands and marshes while Barn Swallows stayed significantly longer in their natal colonies, on average 7.6 ± 4.8 days potentially due to differential life-history traits such as reliance on barns or other structures for roosting, and the

multi-brooded strategy of the adults. This research contributes to the growing evidence that survival in the post-fledging period can be a critical population demographic driver in the annual cycle of aerial insectivores. Additionally, it highlights the utility of using Motus to study the poorly studied post-fledging movements, behaviours, and survival rates of aerial insectivores. This information is critical to understand their spatial and population ecology. Future work studying the relationship between juvenile habitat use and causes of mortality would help clarify how changes in the biotic and abiotic environment influences population demographics of swallows.

3.1. INTRODUCTION

Departure from the nest by inexperienced fledglings to the wider natural environment is a critical transition in the life cycle of altricial songbirds, and involves rapid changes in behaviour and lifestyle (Cox et al., 2014). Consequently, the post-fledging period, described as the time since birds leave the nest until migration, dispersal or independence, is a high mortality stage of the annual cycle, that might represent a population bottleneck (Jones & Ward, 2020; Martin et al., 2018; Naef-Daenzer & Gruebler, 2016). In fact, survival in the early the post-fledging period has been identified as an important driver of population dynamics, as fledging mortality has been implicated in subsequent low recruitment to the breeding population (Anders & Marshall, 2005; Cox et al., 2014; Naef-Daenzer, 2007; Naef-Daenzer et al., 2001; Naef-Daenzer & Gruebler, 2016). Despite the importance of this life-stage, the post-fledging period has often been one of the least studied periods of the avian life cycle, likely due to the challenges and technological limitations when following juvenile birds after they have left the nest (Anders et al., 1997; Cox et al., 2014; Rush & Stutchbury, 2008; Vitz & Rodewald, 2011). Recently, the use of novel automated radio telemetry technologies, such as the Motus Wildlife Tracking system, has

expanded our abilities to study this period in greater detail and in smaller but also more mobile species (Brown & Taylor, 2015; Evans et al., 2019; Fischer et al., 2022; Jones et al., 2018; Mitchell et al., 2011).

Developmental traits, such as nestling body condition and wing length, as well as the length of the nestling period have been suggested as important determinants of post-fledging survival in songbirds (Cox et al., 2014; Evans et al., 2019; Gruebler & Naef-Daenzer, 2010b; Jones et al., 2017; Naef-Daenzer et al., 2001; Vitz & Rodewald, 2011). The quality of parental care and the environmental conditions during the nesting period (e.g. prey availability, habitat quality, predation pressure) can result in differences in developmental traits (Johnson & Lombardo, 2000) that can carry over to improve or reduce the probability of survival of fledglings prior to and after independence in preparation for migration (Evans et al., 2019; Jones et al., 2017; Mitchell et al., 2011; Naef-Daenzer et al., 2011; Vitz & Rodewald, 2011). Moreover, given that the primary source of fledging mortality during the first weeks is thought to be predation (Martin, 2014), the length of time that nestlings spend developing in the nest, can determine the ability of nestlings to fly, forage, and ultimately survive (Cox et al., 2014; Martin, 2014).

Automated radiotelemetry systems, such as the Motus Automated Tracking Technology, have been widely used to study broad-scale movements in migratory animals (e.g. Bayly et al., 2012; Gómez et al., 2014). However, these systems also offer a tractable approach to study the post-fledging period in aerial insectivorous birds, including their movement and survival, especially when working with species that disperse rapidly in the landscape during the post-fledging stage and prior to migration. If receivers are located in strategic areas (i.e. natal sites), automated telemetry systems allow researchers to collect continuous data with high spatial resolution on birds prior to the fledging stage and over extended periods post-fledging and they can also inform on fine-scale movements and behaviours such as departure decisions (Morbey et al., 2020;

Schofield et al., 2018). Moreover, with these tracking systems, it is possible to monitor multiple tagged individuals simultaneously documenting their spatial movements for as long the tags are active and as long as tags are within the range of detection of the antennas (Jones et al., 2018). For instance, using the advantages of an extended Motus automated telemetry array in Ontario, Evans et al., (2019) provided insight for the first time in North America into the post-fledging survival of Barn Swallows (*Hirundo rustica*), from fledging until the departure for fall migration.

Since the 1980s, the guild of aerial insectivorous birds started experiencing declining populations across their breeding distribution in North America (Smith et al., 2015), with population trajectories varying geographically among and within species (Michel et al., 2016). Interest in understanding the causes of these declines has led to research investigating factors affecting demographic drivers. Most emphasis has been on reproductive success (i.e. nesting and fledging success) and annual survival across the breeding distribution with special attention on swallows (Family Hirundinidae) (e.g. Ghilain & Belisle, 2008; Imlay et al., 2019; Kusack et al., 2020; Rendell & Robertson, 1989). However, survival during the brief post-fledging period can also influence lifetime reproductive success and recruitment, and can limit population growth, even when nestling and fledgling success is high (Streby et al., 2014). As in other species of songbirds, due to the inconspicuous nature of juveniles and their highly mobile behaviour, the post-fledging stage of aerial insectivores has been studied only rarely in some species of swallows and only in some geographic areas of North America (Boynton et al., 2020; Evans et al., 2019; Pegan et al., 2018). There is an increasing need to investigate what factors may be influencing post-fledging survival of aerial insectivores to understand whether low juvenile survival could be contributing to species-specific regional population trajectories.

Tree Swallows (*Tachycineta bicolor*) and Barn Swallows are two of the species that have been experiencing differential population trajectories across their range (Michel et al., 2016; Smith et

al., 2015). Barn Swallows have undergone severe population declines that resulted in their listing as ‘threatened’ under Canada’s Species at Risk Act (COSEWIC, 2011). Tree Swallows have been declining in part of their geographic distribution, though not as precipitously (Smith et al., 2020). In the Prairie Pothole Region (PPR), both species have maintained relatively stable populations with a ~1.5 % annual increase between 2009 and 2019 (Smith et al., 2020), while population trajectories in other parts of Canada are still experiencing steep declines (Smith et al., 2020). Although little is still known about their post-fledging ecology, Barn and Tree Swallows vary considerably in other life history traits (i.e., nesting strategies, diet preferences, post-fledging parental care, and migratory strategies). Such differences may determine juvenile survival and post-fledging movement (Baker, 1993; Şahin-Arslan & Martin, 2021; Schoener, 1968; Vega Rivera et al., 2000).

I used automated telemetry to explore the early post-fledging survival and local movements in Barn Swallows and Tree Swallows inhabiting the agricultural landscapes in the Prairie Pothole Region of Saskatchewan. The primary objectives of this study were to 1) compare early post-fledging survival for the first two weeks after leaving the nest when most birds could still be successfully tracked, 2) assess the effect of intrinsic factors (age, nestling period duration, nestling condition and wing chord length) on apparent survival, and 3) compare latency of departure from the natal site in the two species as an indicator of early fledgling movement behaviour. I hypothesized that Barn and Tree Swallows would have similar post-fledging survival given their similar populations trends experienced in the PPR, but different early movement patterns associated with differential life-history traits and post-fledging ecology. For both species, I predicted a general pattern of lower apparent daily survival the first day after leaving the nest as it has been identified as a common post-fledging bottleneck in different species of songbirds (Jones & Ward, 2020) followed by an increased survival when juveniles gained mobility and experience.

I predicted higher apparent daily survival of juveniles that had higher body condition in the nest because nutritional conditions before leaving the nest could potentially buffer individuals from challenging environmental conditions or reduced provision rates that may occur after fledging. I also predicted lower apparent daily survival in juvenile with shorter wing length and shorter nestling duration, using these two traits as indicators of state of development. I predicted that the relationship between wing length and duration of nestling period would be stronger for Tree Swallows because, unlike Barn Swallows, Tree swallow fledglings must be able to fly and catch prey independently and efficiently soon after leaving the nest, such that birds that had not fully developed would be susceptible to food shortage, predators, or other challenging abiotic conditions. I predicted that Tree Swallows would have shorter post-fledging latency to the first departure from the natal site than Barn Swallows given the differences in reliance in riparian habitats or barns for roosting and adult breeding strategies (multi-brooded versus single-brooded).

3.2. METHODS

3.2.1. Study sites and species

Fieldwork was conducted at 16 sites in 2020 and 2021 within 70 km east and south of the city of Saskatoon, SK, in the vicinity of Dundurn (51.8096° N, 106.5076° W), Hanley (51.6280° N, 106.4395°W), Kenaston (51.5006° N, 106.2706° W) and Allan (51.8940° N, 106.0555° W). This area is characterized by mixed annual row crops (primarily canola, lentils, and wheat), natural grasslands and planted forage. Wetlands of varying size and permanency were abundant, especially in the Allan Hills area, east of Highway 11, but were increasingly rare towards the west. The Brightwater reservoir and Blackstrap lakes are main large permanent waterbodies located with 3-4 km from the closest study site (Figure 3.1).

Survival was studied at 10 of 16 sites in both years, however, one colony (SSP05) was dropped

for the second season 2021 due to high predation rates and a new site was added (SSP14). Sites were selected based on the evidence of previous occupancy of Barn Swallow colonies in abandoned buildings, especially barns and sheds. Eight to ten Tree Swallow boxes were installed in early 2020 within 100-200 meters around each Barn Swallow colony spaced at least 30 m from each other. This study design allowed us to study nesting individuals of both species, breeding simultaneously and under the same environmental conditions. Nest boxes had an average occupancy rate of 64.4% in 2020 and 59.3% in 2021.

Most of the barns and buildings were not actively used and had little to no human visits, although four of them were being actively used and presence of humans and/or cattle were regular but did not appear to affect adult provisioning.

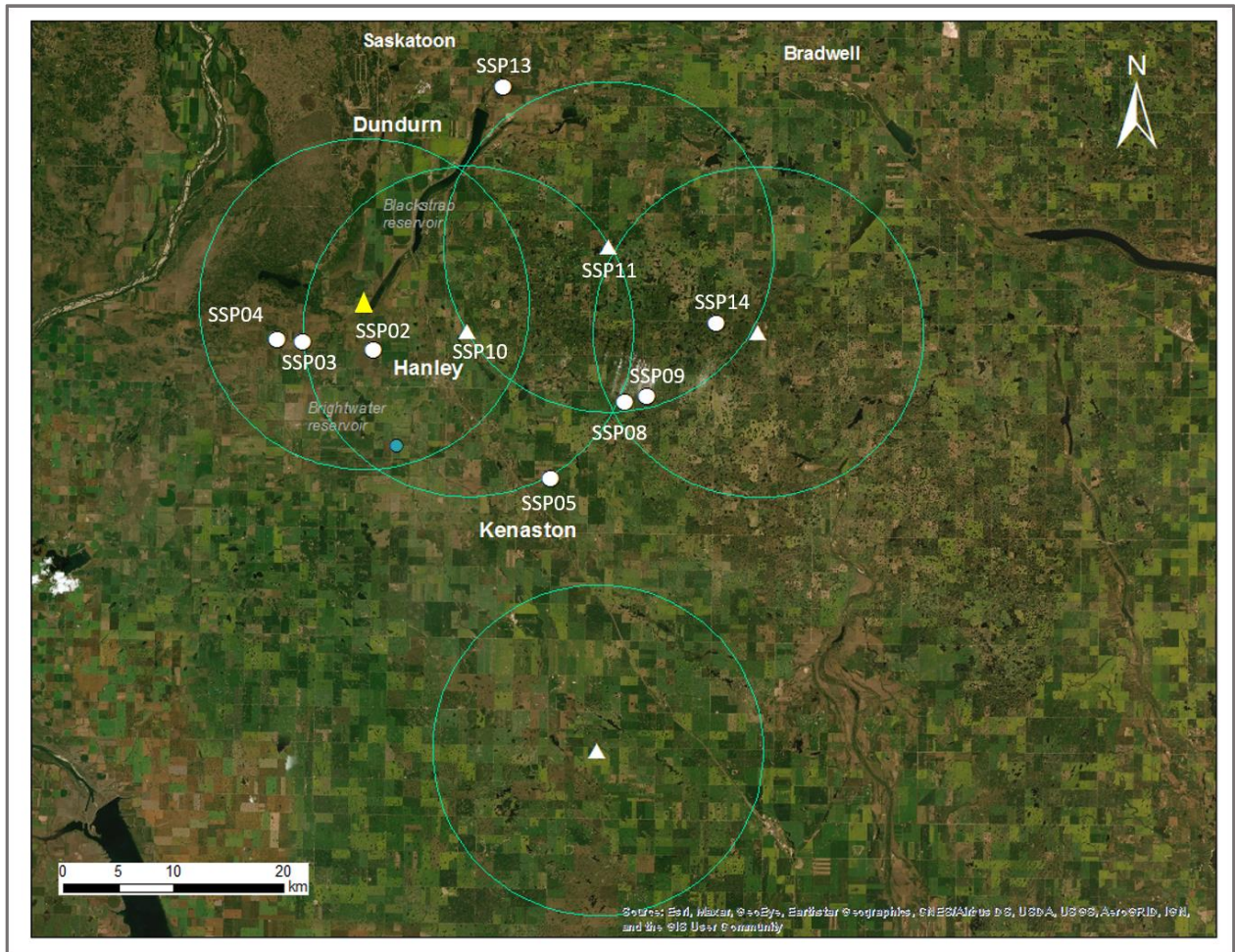


Figure 3.1 Map of location of Barn and Tree Swallow colonies in central Saskatchewan. White circles represent colonies equipped with omnidirectional antennas. The blue circle indicates a site used in 2020 but removed in 2021. White triangles represent colonies equipped with 3 9-element yagi antenna stations. Yellow triangles indicate the location of additional stations with 3 9-element yagi antennas to complement the Motus telemetry network array in 2020 and 2021. Red triangles indicate new stations added to the telemetry array in 2021. Green larger circles are the expected range of detection of stations with 9-element yagi antennas (~15 km).

3.2.2. Nest monitoring and Nestling measurements

Barn and Tree Swallow colonies were visited every three to four days starting May 15, to check for signs of occupancy and nesting activity (building or repairing) in the barns and in the nest boxes. To reduce disturbance to Barn Swallow adults and nestlings, I used a lighted mirror

attached to an extension pole to check nests. It was not possible to follow every clutch attempt of all the females breeding in some sites, especially for Barn Swallows, because they were out of reach or because they were not found in time to follow their nest phenology. Nests were visited approximately every two days to estimate clutch initiation date, assuming that eggs were laid one per day until the penultimate egg, when the incubation period starts (Day 0). Time of hatching was predicted to be 12-17 days after incubation started, for Barn Swallows, and 13-14 days after incubation started, for Tree Swallows (Brown & Brown, 2019; Winkler et al., 2011). The day the first nestling hatched was considered Day 0 for the whole brood, but some eggs did not hatch until the day after. If hatch day was not directly measured, age of brood was estimated based on a combination of different criteria: eggshell remains in the nest, number and size of nestlings hatched, and presence of wet feathers. When necessary, I also used an aging guide for Barn Swallow nestlings (Morales Fernaz et al., 2012) or Tree Swallow nestlings (<http://www.treeswallowprojects.com/cgrowth.html>) based on size and feather tract development and feather shaft emergence.

Although the study was focused primarily on first broods, due to intense rain events and frequent predation events that caused failure of the Barn Swallow nest in 2020, some second attempts (a new clutch after first clutch failed) and second broods (new brood after successful fledging) were used to increase the sample size. When a Barn Swallow nest failed, adults would typically build or repair a nest close to the failed nests (A. Diaz, pers. obs.). Accordingly, first broods and first attempts were categorized as “first” and late broods and/or second attempts were included in a category called “late”. I was not able to follow every clutch attempt in barns and not all adults were marked so there is uncertainty on what clutches were second attempts or just late broods. Thus, I calculated the 5-95% quantile range of hatching date of a set of nests from 2021 that were known as “true” first broods. All nests with a hatching date outside the 95% quantile

(Barn Swallows, day 189- July 8; Tree Swallows, day 180-June 30) were assigned to the “late” category.

Most nests were visited three times during the nestling growth period on Day 4 and Day 8 and the last check occurred on Day 12 for Tree Swallows and Day 15 for Barn Swallows. Day 12 and Day 15 were selected as they are the last days that nestlings can be handled without risk of premature fledging (R. Clark and K. Hobson, pers. comm). Every visit, nestlings were removed from the nest and covered to reduce stress and maintain warmth (also enhanced with hand warmers on coldest days). While nestlings were removed from the nest, a bag was placed in the entrance of the nest to avoid parental nest abandonment. On Day 4, 8 and 12 (Tree Swallows) or 15 (Barn Swallows) each nestling was individually marked, and morphometric measurements were taken. Nestlings were marked on Day 4 by trimming body feather groups following an identification code to identify nestlings in the next visit when they could be uniquely banded. On Day 8, nestlings were banded using a size 1 Canadian Wildlife Service aluminum band. For each nestling, I measured un-flattened right-wing chord (nearest 1 mm), tarsus length, head-bill length, and body mass (nearest 0.1 g), in addition to the total length of the 9th primary and the portion of feather that had already emerged from the pin (hereafter “p9 pin”). P9 pin and head-bill were taken only on the last visit. Wings were measured using a ruler, tarsus and bill lengths were measured with dial calipers (nearest 0.001 mm) and body mass with a portable digital scale (nearest 0.1 g). All nestlings were returned to the nest immediately after measurements.

3.2.3. Nestling tagging

On Day 12 or 15, in a subset of nests, one nestling was randomly chosen and fitted with a digitally coded VHF radiotransmitter (model NTQB2-2, 0.34g; Lotek, New Market, ON, Canada), using the leg-loop backpack harness method (Rappole & Tipton, 1991). Each tag weighs ~0.32 g,

which equals 1.6% of the average weight of a juvenile swallow before fledging, and it is much lower than the 5.0% recommended cut-off. Harnesses were made of elastic thread, flexible enough to allow for growth, and eventual breakdown. This harness and thread technique has been used in similar studies in aerial insectivores with successful tag retention (Bumelis, 2020; Evans et al., 2019). Tags were set on a standard frequency of 166.38 MHz, emitting a unique signal on 13 sec or 19 sec burst intervals resulting in a 145 or 200-day average lifespan, respectively. After tagging, a bird bag or piece of cloth was used to cover the Barn Swallow nestlings for up to 5 min after returning them to the nest to avoid premature fledging (Ardia, 2006; Gruebler & Naef-Daenzer, 2008b).

3.2.4. Automated telemetry array

I set up Motus radio-telemetry stations with two different receiver antennas to look at local and larger scale movements. I installed an array of telemetry stations at a local farm scale, using an elevated omnidirectional antenna at 8 of 10 natal sites (hereafter “omni stations”), attached to the barn or a tall pole, and connected to a data-logging receiver (homemade SensorGnome - www.sensor gnome.org, following Birds Canada protocol). Each omni station had an estimated range of detection of 500-1000 m, depending on height of antenna and local topography. At two of the colonies, Motus stations with 3 9-element Yagi antennas (hereafter “yagi stations”), were installed and connected to the data-logging receiver. An additional array of two (2020) or three (2021) yagi stations was set up in the study area, to complement the pre-existing network of Motus telemetry stations in SK (Figure 3.1). These stations were installed in strategic high elevation points within proximity of the natal sites to detect juveniles outside the immediate surrounding of the colony, as previous studies have found that fledglings can forage long distances away from their colonies (>20 km) within the first three weeks after fledging (Boynton

et al., 2020). These yagi stations can have a range of detection up to 15 km, depending on topography and foraging habits (e.g., altitude when flying) of the birds tagged (Taylor et al., 2017). Each station was constantly detecting the presence or absence of tagged birds within the range of detection of the antennas. These detections were used to estimate apparent daily survival and timing of fledging of tagged Barn and Tree Swallows. When a tagged individual moves, the orientation or position of the tag antenna changes, while the receiver in each station detects those movements as a change in signal strength between subsequent detections. Those signal patterns helped to differentiate among birds that were still alive versus dead birds or lost tags which, if detected, had a constant signal strength between detections. Signal pattern differences permitted estimation of the date and approximate time of fledging.

3.2.5. Manual detections

Mobile manual tracking was used to complement automated detections to track birds outside of the range of detection of the receiver deployed at each site. Birds were tracked using a LOTEK SRX800 Receiver connected to an omni-antenna attached to a vehicle. Manual tracking surveys were conducted only once every seven to ten days in 2020 due to logistical constraints. In 2021, I conducted manual telemetry every two or three days and for at least 20 days after nestlings fledged, starting from the focal barn and expanding outwards driving on grid roads as far as 5 to 7 km from the colonies. Standardization of routes was not possible due to limited access to roads during wet periods in the summer, and especially during 2020. Due to high mobility of swallows, I conducted mobile telemetry when travelling among colonies, and by visiting potential wetlands or areas where big congregations of swallows have been observed, even if further than 10 km from any of the colonies. When mortality was suspected due to static tag signal during multiple visits, intensive efforts were made to find the tag and to discern the bird's fate.

3.2.6. Estimation of fledging date via change-point analysis

To estimate fledging date, I used signal strength changes using change-point analysis with “changept” R package. Nestlings were constantly detected while in the nest by each colony’s Motus station. Therefore, changes in the pattern of the signal strength allowed me to estimate when birds left the nest. When a Motus station detects a tag registered in the system, it records the time stamp and the maximum and standard deviation of the raw signal strength (dB) among the four pulses that characterize each tag. Changes in signal strength at different time intervals can give information of movement at different scales. In this study, I adapted the Morbey et al., (2020) protocol to estimate fledging day from changes in signal patterns between an 8 to 10-days interval after swallows were tagged. This method provided an estimate of fledging age, with the advantage of limiting the number of visits to the nests. The pre-fledging period is critical, and any disturbance can cause premature fledging, which can reduce survival probability when juveniles are not yet fully developed and may not be prepared to avoid predators and other threats.

For the identification of the fledging date, I used only the range of detection between Day 1 and Day 9 post-tagging for Barn Swallows. For Tree Swallows I used the range between Day 3 and Day 13. This way, I accounted for the potential disturbance of tagging and avoided the identification of earlier change-points as a result of increasing activity rate of nestlings in the nest. When birds died before that range of days ended, I only included detections while birds were alive.

To remove major signal differences among antennas driven by distance from the nest or the juvenile to the antenna, I de-trended the signal strength variable d by calculating signal strength differences between consecutive detections from the same antenna using the equation

$$d = sig_t - sig_{t-1} \text{ Eq.1}$$

I then calculated the squared root of absolute d values ($\sqrt{|d|}$) which, for most nests, showed

higher distinctive mean values during nesting and post-fledging activity. Changes in the mean and variance of the $\sqrt{|d|}$ were used to identify the transition between nestling and fledgling period (Figure 3.2). False change points, which usually corresponded to changes in signal strength early in the nesting period, were disregarded. For those birds, day of fledging was assigned manually by inspecting daily detections and detection plots. For a subset of Barn Swallows from the 2021 season, I was able to confirm and verify fledging events using recorded video with trail-cameras located in the proximity of nests (Appendix B, Figure B.1).

3.2.7. Mark-recapture models and building encounter histories

Prior to formatting detection data for analysis in a mark recapture framework, I inspected and filtered the Motus data to eliminate false positives and noise detections (Birds Canada, 2022). I also removed birds whose tags or carcass were not found after tags stopped being detected abruptly before the expected fledging date (Day 19 post-hatch). In this case, tagged birds were assumed to have been preyed upon in the nest and were excluded from the post-fledging survival analysis. If a bird's signal changed before the anticipated age of fledging, but were still detected alive for at least several hours after the event, they were retained in the analysis.

Once data were cleaned, detections were used to create daily encounter histories for each tagged juvenile Barn and Tree Swallow. Encounter histories consist of strings of binary variables (1 when bird was detected across each sub-period of the day and 0 when it was not detected). For all individuals, the encounter history started the day of fledging (day of fledging = first encounter) until 14 days post-fledging. Less than 27% of swallows were detected 15 days after fledging and at least one Tree Swallow was detected 400 km away from the colony 17 days weeks post-fledging; therefore the survival analysis was limited to only 14 days after birds have fledged as detection probabilities declined rapidly after that.

3.2.8. Statistical analysis

3.2.8.1. Post-fledging apparent daily survival analysis

Survival analyses were conducted using Program MARK (White & Burnham, 2009). Automated telemetry produced detection data at two different temporal periods (daily and hourly), following a robust design. Robust designs distinguish between primary periods and secondary sessions. Primary periods are separated from each other by enough time that gains and losses to the population are expected to occur. Each primary period includes multiple secondary sessions during which populations are considered closed to gains and losses. Data from secondary sessions allows the estimation of detection probability with higher accuracy, especially in the presence of temporary emigration (Kendall et al., 1997). I used a Huggins robust analysis that does not include abundance as a model parameter (Huggins, 1989). The parameters estimated by my model were apparent survival (Φ ; apparent because mortality cannot be separated from permanent emigration), the probability of temporary emigration (γ ; the probability that a bird was not available for a detection on a specific day, and would stay unavailable for consecutive days) and recapture probability within days, and across secondary sessions (p). For every model, I fixed the probability of capture (p) and recapture (c) to be equal ($p=c$), given that individuals were captured passively and that there should not be any effect of trap. The estimation of temporary emigration under a robust approach involves two parameters: Temporary emigration (γ''_t) that denotes the probability that a bird moved out of the study area and was not available to be detected in the area of study at time $t-1$ and temporary immigration (γ'_t) that indicates the probability of a bird that was unavailable for detection to be detected at time $t-1$ remained unavailable for capture at time t . I kept the probability of temporary emigration and temporary immigration equal to each other ($\gamma'' = \gamma'$) and constant over time.

The analysis was performed in two stages (Lebreton et al., 1992) in which I modeled detection

probability (p), and apparent survival probability (Φ) individually. I modeled each of these parameters as a function of age (A), using different structures: linear effect of age (A), polynomial relation of age to the second order ($A+A^2$) and to the third order ($A+A^2+A^3$). I first modelled probability of detection, keeping temporary emigration and immigration and apparent survival constant. I built a set of candidate models and employed an information theoretic approach to select best-approximating models, ranking them by Akaike's Information Criterion corrected for small sample size (AICc) (Burnham & Anderson, 2002). Models with a Δ AICc below 2 from the top model were considered plausible. When more than one model was equally supported, differed by one parameter, and that parameter's 95% confidence interval included 0, the model with the lower number of terms was considered to have higher support (Burnham & Anderson, 2002) and the top model was retained for the next stage of the analysis.

When modelling probability of detection, I first tested different structures of secondary sessions: 1) 6 x 4-hour secondary sessions (04:00 to 07:59, 08:00 to 11:59, 12:00 to 15:59, 16:00 to 19:59, 20:00 to 23:59), 2) 3 x 8-hour secondary sessions (04:00h to 11:59h, 12:00h to 19:59, 20:00h to 03:59) and 3) 2 x 12-hour secondary sessions (04:00 to 15:59h and 16:00h to 03:59), keeping the rest of the parameters constant. This way, I accounted for times of the day when birds would move away from the natal site or far from the range of detection of the telemetry network, either for roosting, foraging, or exploring. Once I found the best secondary session structure, I added it to my models as an additive term to the different age structures. In a preliminary analysis, I included brood type (early vs late) to account for differences in detection probability later in the season due to potential differences in juvenile Barn Swallow pre-migratory behaviors. I did not test for the effect of brood type in Tree Swallows detection probability as only one tagged individual hatched after the cut-off date for defining first broods. As no effect of brood was found in 2020 or 2021 for Barn Swallows, this variable was excluded from the analysis (results are not

shown here). In its place, the type of station installed in the natal site (yagi station or omni station) was included as a grouping variable, to account for the potential effect that antenna type could have on the probability of detection of nestlings.

During the second stage of the analysis, I first evaluated the best age structure for describing apparent daily survival. Next, I built a set of candidate models using the best age structure to assess the relation of intrinsic factors (nestling period duration, nestling body condition, wing length and brood size) on apparent survival. I tested the effect of duration of the nesting period, as a proxy of relative structural development, given that survival of fledglings can be related to the length of time spent developing in the nest (Cox et al., 2014). I also tested the effect of body condition index and wing length since both variables have been proposed as important predictors of post-fledging survival in songbirds (Cox et al., 2014; Evans et al., 2019; Gruebler & Naef-Daenzer, 2010b; Martin et al., 2018; Naef-Daenzer et al., 2001; Remeš & Matysioková, 2016) and are known to be highly influenced by the quality of the habitat and the parental care in the nest. Nestling body condition (Day 8) was used as a proxy of nutritional condition of the juveniles and was calculated as the residuals of a linear regression between mass and wing length to control for structural size. Pre-fledging wing chord was used as an indicator of the locomotor performance of nestlings at the moment of fledging (Jones & Ward, 2020). All covariates included in the models were z -transformed before analysis. I calculated cumulative survival probabilities by multiplying daily survival estimates derived for the period of 14 days after fledging. I use bootstrapping in MARK program to resample my study population ($n=500$) to further estimate the approximate confidence interval of cumulative survival.

3.2.8.2. Post-fledging movement

Using the constant detection of birds by the telemetry stations located in the natal sites and

following a similar approach to Pegan et al. (2013), I estimated the post fledging latency of departure of Barn and Tree Swallows. Departure latency was defined as the number of days between the date of fledging and the first day that a bird was not detected by the local station. I used this estimation as a proxy of post-fledging early movements, assuming that when a bird was missed by the natal station for one day or more it would be due to the individual having moved beyond the range of detection of the antenna. Young birds have been observed to expand their natal range size by following adults on foraging excursions to other habitats (van Overveld et al., 2011; White & Faaborg, 2008), presumably higher quality ones in preparation for moult and migration, or as exploratory movements.

To assess differences in post-fledging departure latency between Barn Swallow and Tree Swallows I used a two-way ANOVA that included species and the type of station to control for differences in the range of detection among different types of antennas at each site. Omni station detections would capture departure of young from the immediate natal area as defined by the 500-1000 m detection range whereas Yagi stations, given their much wider range of detection, would inform about larger scale movements of juveniles relative to their natal site. I removed from the analysis two individual Barn Swallows for which I could not confirm death on the day of fledging in their natal sites. My measure of post-fledging latency of departure was only apparent as, without confirming death, it was not possible to discern if birds that stopped being detected in the local station had left the natal site permanently or were dead.

3.3. RESULTS

3.3.1. Nestling and fledging survival

In 2020 and 2021, 97 nestling Barn Swallows and 77 Tree Swallows were tagged, and of these,

85 tagged Barn Swallows (88%) and 72 tagged Tree Swallows (95.5%) survived until fledging. Main causes of nest failure were predation, extreme weather (rain, high temperatures) and ectoparasite infestations (mainly mites). Principal predators of nestlings were Raccoons (*Procyon lotor*), Great-horned Owls (*Bubo virginianus*), with some events of predation from domestic cats (*Felis catus*). Long-tailed Weasels (*Mustela frenata*) occurred in the area and were also a potential, but unconfirmed, predator of Tree Swallows. House Sparrows also killed tagged Tree Swallows nestlings, but nest failure attributed to sparrows principally occurred when adults were building nests or starting to lay eggs.

3.3.2. Apparent daily survival

I confirmed fledging of 82 Barn and 68 Tree Swallows. Duration of nesting period ranged between 16 and 22 days in Barn Swallows, and between 17 and 22 days in Tree Swallows. Individual Tree Swallow nesting period (mean \pm SD: 19.5 \pm 1.05 days, n=68) was slightly shorter on average than in Barn Swallows (20.0 \pm 1.4 days, n=82) (ANOVA: $F_1=6.21$, $p<0.01$; n=150; Figure 3.2) and did not vary between years (ANOVA: $F_1=0.27$, $p=0.6$). It was not possible to estimate fledging date or fate of three tagged Barn Swallow and three Tree Swallow nestlings, due to the malfunction of the local station or the intermittency of the signal. Three Barn Swallow and one Tree Swallow nestlings were removed from the survival analysis due to lack of morphometric measurements from Day 8 to estimate body condition (Table 3.1).

During the two-year study, I could only confirm location and cause of death of three Tree Swallow and four Barn Swallow fledglings. Because of the location, the condition of the tags and the remnants of birds found, I suspect all deaths were caused by birds of prey. Recoveries were found from 500 m to 4.5 km from the nest.

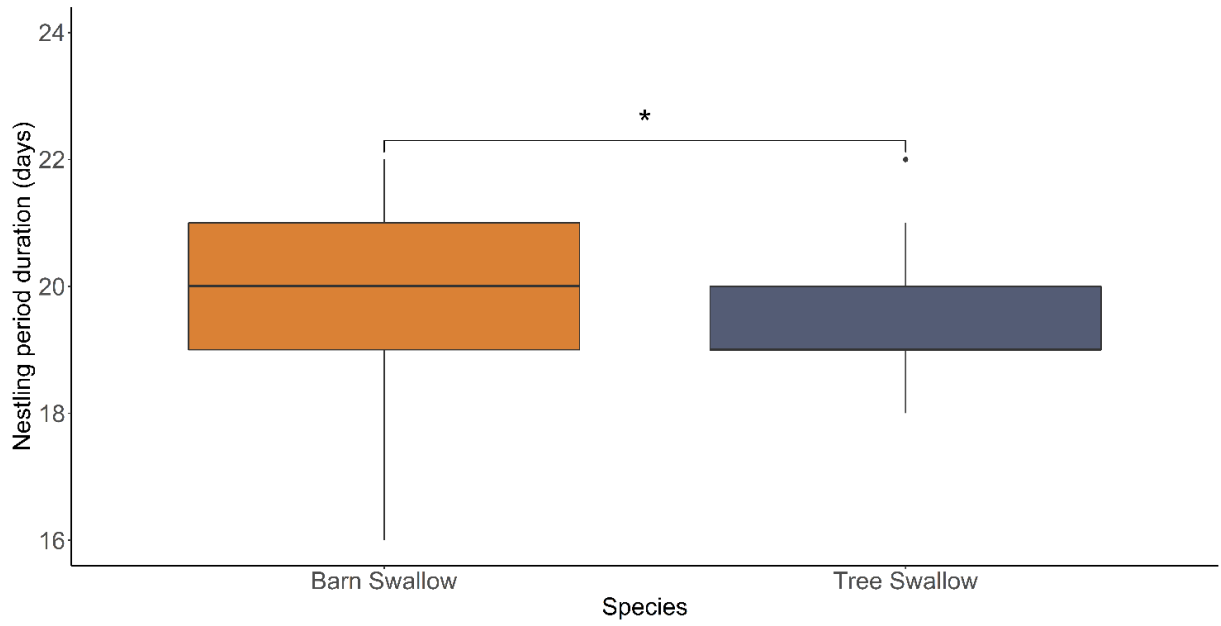


Figure 3.2 Boxplot showing difference in duration of nesting period between Tree Swallows (n=68) and Barn Swallows (n=82).

Table 3.1 Summary statistics (mean \pm SD) of Motus nanotagged nestlings. These factors were used to evaluate potential effects on apparent survival of Tree and Barn Swallow fledglings, in 2020 and 2021. Samples sizes are included in parentheses.

	Tree Swallows		Barn Swallow	
	2020 (30)	2021 (37)	2020 (41)	2021 (38)
Nestling period duration (days)	19.3 \pm 1.09	19.6 \pm 0.98	20.0 \pm 1.37	20.0 \pm 1.44
Brood size	5.3 \pm 1.26	5.24 \pm 1.26	4.27 \pm 0.98	4.21 \pm 0.99
Body condition	0.68 \pm 1.37	0.28 \pm 1.56	0.43 \pm 1.23	0.69 \pm 1.64
Wing length (mm)	54.4 \pm 3.26	54.4 \pm 3.40	70.4 \pm 2.74	71.6 \pm 2.15

Both years, the best supported models for probability of apparent survival of Barn Swallows suggest a quadratic relationship of survival and age post-fledging, while for Tree Swallows the relationship was polynomial to the third-degree. Probability of survival for both species one day after fledging was lowest and increased as fledglings grew older. When juvenile Barn Swallows reached 10 days post-fledging, apparent survival estimates then decreased. In Tree Swallows, probability of survival was stable or increased initially but was characterized by a dip after 5 days in 2020 and 8 days in 2021 and peaked again after Day 12 to be close to 100% by the end of the 2-week period (Figure 3.3).

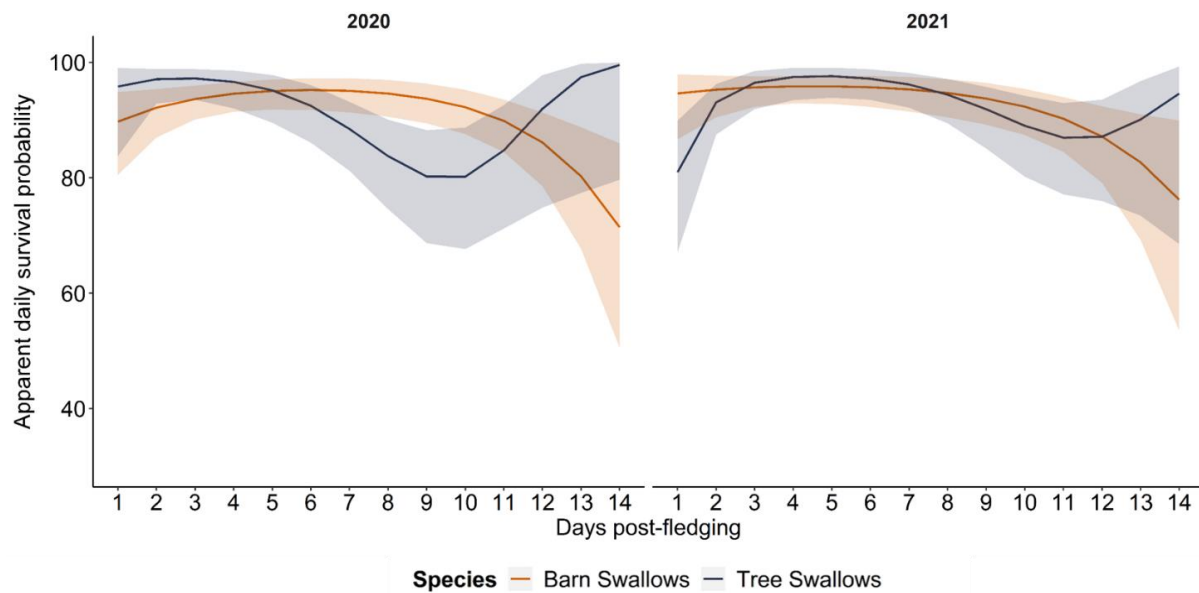


Figure 3.3 Comparative plot of predicted post-fledging apparent daily survival probability estimates for Tree Swallows (blue) and Barn Swallows (orange), in 2020 and 2021. The estimates of daily apparent survival (solid lines) were obtained from the top model (See Table 3.2). In total 41 Barn Swallow and 30 Tree Swallow fledglings were included in the analysis of apparent survival in 2020, and 38 Barn Swallow and 37 Tree Swallow fledglings were included in 2021. The shaded areas represent 95% confidence intervals.

The best-approximating models at explaining survival excluded covariates and only included the age trend, except for the Barn Swallows in 2021 where I found considerable support for nestling period duration influencing apparent survival. Barn Swallows fledged between Day 16 and Day 22 post-hatching, and I found evidence that longer nesting period improved the apparent daily probability of post-fledging ($\beta_{\text{Nest}} = 0.31$, 95% CI: 0.07 – 0.55, Table 3.3, Figure B.2). Even though the Tree Swallow models that included brood size, wing length and nest duration in 2020 and 2021 had $\Delta\text{AICc} < 2$, these covariates were considered non-informative as their confidence intervals overlapped 0 (Table 3.3, Appendix B, Figure B.2). For Barn Swallows in 2020, nest duration and body condition were included in models with $\Delta\text{AICc} < 2$ but were also uninformative (Table 3.3, Appendix B, Figure B.2).

Table 3.2 Results from the most parsimonious Huggins Robust design survival models. The reported estimates of early apparent daily post-fledging survival (ϕ), temporary migration (γ), and recapture or detection probability (p) are shown for Barn Swallows (top) and Tree Swallows (bottom) in 2020 and 2021. Beta estimates (β), Standard Error (SE) and 95% confidence intervals (CI) are reported in the logit scale. Dashes (-) indicate effects were not included in the best model.

Barn Swallows 2020				Barn Swallows 2021				
Effect	β	SE	95% CI	β	SE	95% CI		
ϕ :intercept	1.382	0.698	0.015	2.749	-3.447	2.466	-8.280	1.386
Age	0.458	0.208	0.051	0.866	0.201	0.215	-0.220	0.623
Age ²	-0.033	0.012	-0.057	-0.008	-0.022	0.014	-0.050	0.006
Nest duration	-	-	-	-	0.306	0.122	0.066	0.547
BCI	-	-	-	-	-	-	-	-
Wing chord	-	-	-	-	-	-	-	-
Brood size	-	-	-	-	-	-	-	-
γ	-2.398	0.197	-2.783	-2.012	-2.745	0.227	-3.190	-2.299
p :intercept	4.722	0.378	3.980	5.463	3.849	0.360	3.143	4.555
Station: Omni	-1.830	0.211	-2.245	-1.416	-0.894	0.195	-1.277	-0.512
Age	-0.243	0.149	-0.534	0.048	-0.318	0.144	-0.601	-0.035
Age ²	0.021	0.022	-0.022	0.064	0.031	0.021	-0.010	0.072
Age ³	-0.001	0.001	-0.003	0.001	-0.002	0.001	-0.003	0.000
8:00 - 11:59h	-0.046	0.215	-0.467	0.375	0.097	0.197	-0.289	0.482
12:00 - 15:59h	-0.605	0.200	-0.998	-0.212	-0.263	0.188	-0.631	0.105
16:00 - 19:59h	-0.431	0.204	-0.831	-0.031	-0.466	0.184	-0.827	-0.106
20:00 - 23:59h	-0.703	0.199	-1.093	-0.314	-0.639	0.181	-0.994	-0.284
00:00 - 03:59h	-1.572	0.190	-1.944	-1.200	-1.759	0.175	-2.101	-1.417
Tree Swallows 2020				Tree Swallows 2021				
Effect	β	SE	95% CI	β	SE	95% CI		
ϕ :intercept	1.062	2.310	-3.465	5.590	-2.452	1.531	-5.452	0.549
Age	1.527	1.130	-0.688	3.741	2.556	0.871	0.849	4.263
Age ²	-0.249	0.143	-0.529	0.031	-0.327	0.123	-0.568	-0.086
Age ³	0.014	0.007	0.000	0.027	0.012	0.005	0.002	0.022
Nest duration	-	-	-	-	-	-	-	-
BCI	-	-	-	-	-	-	-	-
Wing chord	-	-	-	-	-	-	-	-
Brood size	-	-	-	-	-	-	-	-
γ	-1.171	0.148	-1.462	-0.881	-1.465	0.152	-1.762	-1.168
p :intercept	3.957	0.298	3.372	4.542	2.550	0.313	1.936	3.164
Station: Omni	-0.746	0.158	-1.057	-0.436	-0.472	0.150	-0.766	-0.178
Age	-0.647	0.063	-0.770	-0.524	0.191	0.142	-0.086	0.469
Age ²	0.028	0.004	0.020	0.036	-0.055	0.022	-0.098	-0.013
Age ³	-	-	-	-	0.002	0.001	0.000	0.004
8:00 - 11:59h	0.686	0.213	0.269	1.104	-0.162	0.202	-0.558	0.233
12:00 - 15:59h	0.102	0.202	-0.294	0.498	-0.493	0.196	-0.878	-0.108
16:00 - 19:59h	0.249	0.204	-0.151	0.650	-0.629	0.195	-1.010	-0.247
20:00 - 23:59h	-0.353	0.199	-0.742	0.036	-1.245	0.191	-1.619	-0.872
00:00 - 03:59h	-1.712	0.207	-2.117	-1.306	-2.459	0.197	-2.845	-2.072

Table 3.3. Model predictors evaluated on apparent post-fledging survival of Barn Swallows and Tree Swallows in 2020 and 2021, with estimates and 95% confidence intervals. Estimates were derived from the model with best age structure and each of the predictor variables. Significant effects (95% CI non-overlapping 0) are highlighted in bold.

Species	Year	Model predictor variable	Estimate	SE	95% CI	
Tree Swallows	2020	Nestling period duration(days)	-0.07	0.16	-0.38	0.24
		Body condition index	-0.12	0.17	-0.45	0.20
		Wing chord length (mm)	0.08	0.06	-0.02	0.19
		Brood size	-0.32	0.19	-0.70	0.05
	2021	Nestling period duration(days)	-0.05	0.21	-0.47	0.36
		Body condition index	0.01	0.14	-0.26	0.29
		Wing chord length (mm)	0.00	0.06	-0.12	0.12
		Brood size	0.00	0.17	-0.34	0.34
Barn Swallows	2020	Nestling period duration(days)	-0.21	0.13	-0.47	0.04
		Body condition index	-0.15	0.14	-0.43	0.13
		Wing chord length (mm)	0.01	0.07	-0.12	0.14
		Brood size	0.01	0.21	-0.40	0.41
	2021	Nest duration (days)	0.31	0.12	0.06	0.54
		Body condition index	-0.18	0.13	-0.45	0.08
		Wing chord length (mm)	-0.08	0.10	-0.28	0.11
		Brood size	-0.16	0.21	-0.57	0.25

Cumulative survival probabilities for the first week post-fledging (1-8 days after fledging) were similar between both species, resulting in a cumulative survival in 2020 of 57.0% (95%CI 41.1 – 70.7) for Tree Swallow and 59.7% (95%CI 48.5 – 71.9) in Barn Swallows. In 2021, estimates of cumulative survival for Tree and Barn Swallows were 61.1% (95%CI 50.1 – 79.0) and 68.5% (95%CI 33.3 – 75.6) respectively. The total cumulative survival over the two-week post-fledging period for Tree Swallows and Barn Swallows in 2020 were 28% (95%CI 14.2 – 42.2) and 23% (95%CI 12.3 – 37.0), respectively, whereas in 2021 estimates were 32% (95%CI 18.2 – 49.4) for Tree Swallows and 29% (95%CI 1.6 – 38.5) for Barn Swallows (Figure 3.4).

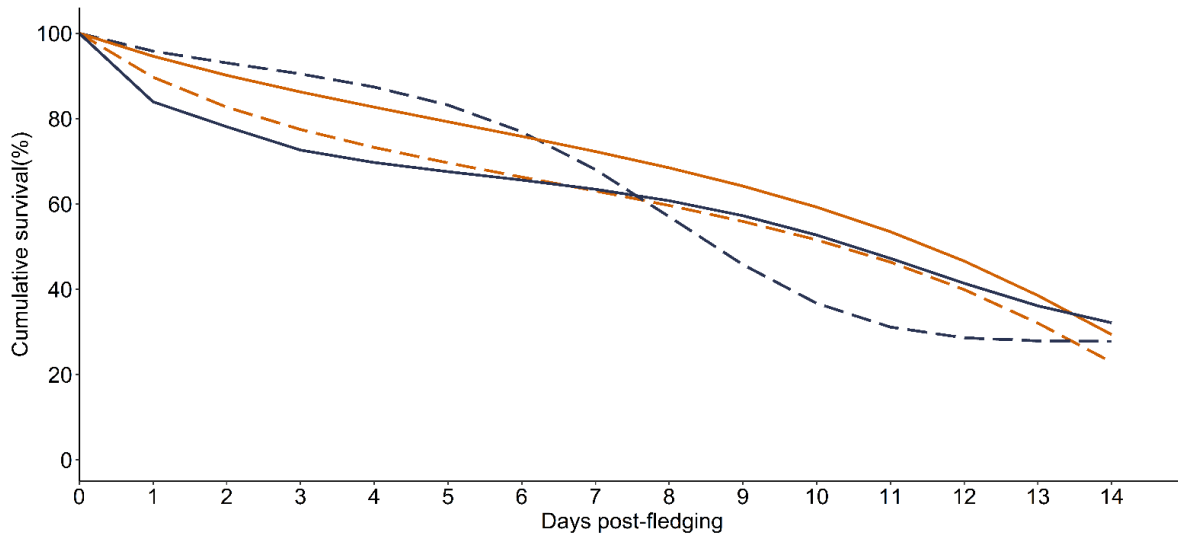


Figure 3.4 Predicted cumulative survival for Barn Swallows (orange) and Tree Swallows (Blue), in Central Saskatchewan during the post-fledging period of 2020 (dashed line) and 2021 (solid line). Day 0 corresponds to the day of fledging. Survival estimates were derived from the best candidate model (See Table 3.2)

3.3.3. Detection probability

Top models for daily detection probability had all strong support in 2020 and 2021 ($w_i > 0.95$, Appendix B, Tables B.1, B.2). The best-supported structure for detection probability in both species indicated a third-degree polynomial relationship with age for both species, except for Barn Swallows in 2021 when the relationship of probability of detection and age was quadratic. Daily detection probability also showed significant differences among secondary sessions, generally with lower probabilities between 00:00 and 04:00h and higher after sunrise, and for the rest of the morning between 04:00 and 11:59h (Figure 3.5, Table 3.3).

During the period of higher detection, detection probability of both Barn and Tree Swallows for the first few days post-fledging was close to 1 but for Tree Swallows it then declined rapidly with age after fledging in 2020. In 2021, probability of detection for the first five days after fledging was similar between both Barn and Tree Swallows; however, after six days post-fledging

it declined considerably for Tree Swallows while it remained relatively stable in Barn Swallows until Day 10 when it steeply declined. Station type was a significant predictor of detection probability, and juveniles originating from colonies with omni stations had on average a 12% lower probability of been detected than young from yagi station colonies, and that probability decreased with age (Figure 3.5, Table 3.3).

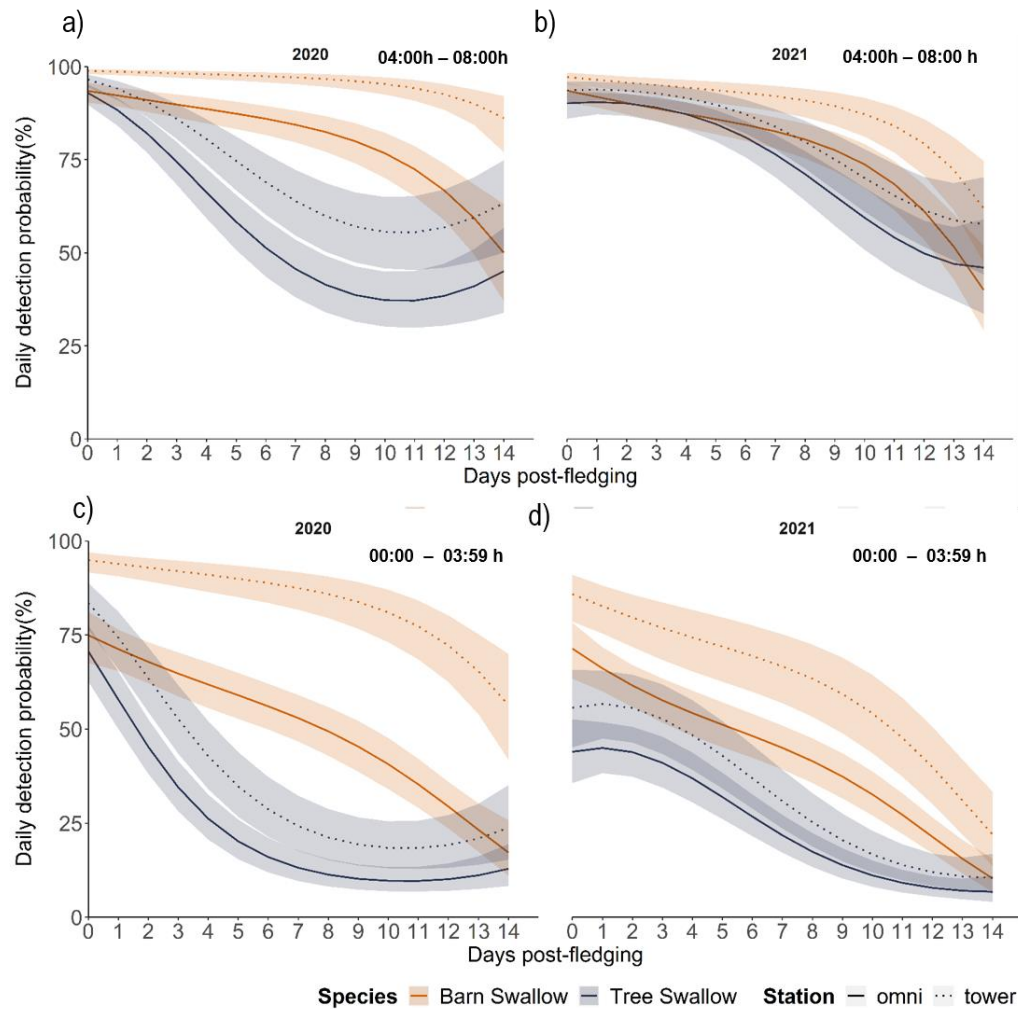


Figure 3.5. Comparative plot of predicted daily detection probability for Tree Swallows (blue) and Barn Swallows (orange) over time (days post-fledging), for 2020 and 2021. The two lines within the coloured area represent the two different Motus station types. The plot shows the estimates of detection probability in the early morning (04:00 – 08:00h) where probability of detection was generally higher (a and b), and at night (00:00 – 03:59h) when birds were usually roosting (c and d). The estimates of daily detection probabilities were obtained from the top-ranked model. Shaded areas represent 95% confidence intervals.

3.3.4. Patterns of early post-fledging movement

Barn Swallow juveniles were detected for up to 38 days after leaving the nest (mean \pm SD = 12.8 ± 9.4 days), while Tree Swallows were detected for up to 25 days post-fledging in 2020 and 39 days in 2021 (mean \pm SD = 10.8 ± 7.46 days) (Table 3.4).

Tree Swallow first departure (latency) from the natal site occurred sooner (mean $3.69 \pm$ SD 2.93 days $n=68$) than in Barn Swallows (7.60 ± 4.79 days, $n=80$), inferred using detections on the local station before being absent for an entire day (ANOVA: $F_1=38.74$, $p<0.001$). Station type had a significant effect on the first departure from natal sites as Barn and Tree Swallows from yagi station colonies were detected longer in their natal sites, compared to birds from omni stations, before they stopped being detected by the local stations for at least one day (ANOVA: $F_1=19.70$, $p<0.001$; Figure 3.6).

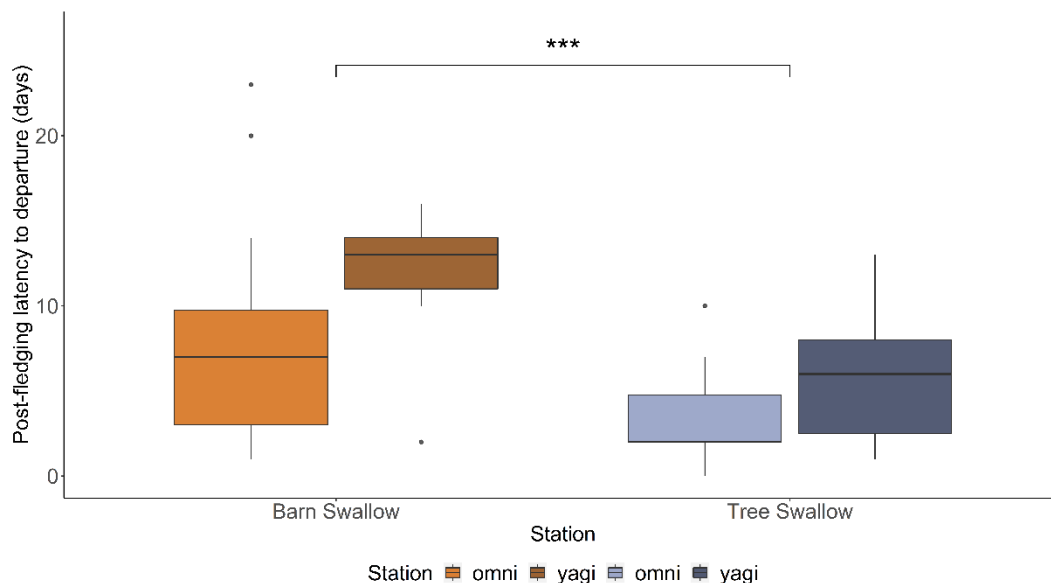


Figure 3.6 Comparison between Tree Swallows ($n=68$) and Barn Swallows ($n=80$) showing variation in post-fledging latency to first departure from the natal site. Post-fledging latency was estimated as the number of days before fledglings stopped being detected for a whole day without being detected by the local station. Omni stations had smaller range of detection (0.5 – 1 km) than yagi stations (up to 15 km). Eight of the study colonies had omni stations while only two colonies had yagi stations.

Table 3.4. Summary statistics of Barn and Tree Swallow post-fledging detections reported as the mean and standard deviation (mean \pm SD). Mean age of fledging, total number of days that bird were detected in the local telemetry network after fledging, including mobile telemetry detections, number of sites where birds were detected during the summer, post-fledging latency of departure, and the maximum distance that young birds were detected by mobile telemetry on day 15. Fledging dates include minimum and maximum date of fledging of birds included in survival analysis. Maximum distance from nest was estimated based on mobile telemetry detections. Samples sizes (number of birds) are included in brackets.

	Barn Swallow (n= 82)	Tree Swallow (n=68)
Nesting period duration	20 \pm 1.39 days	19.5 \pm 1.05 days
Post-fledging detections	12.8 \pm 9.42 days	10.8 \pm 7.49 days
No. sites where juvenile birds were detected	2.68 \pm 1.70	3.07 \pm 1.89
Latency of departure in site (days)	omni: 7.00 \pm 4.62 days (80) yagi: 11.80 \pm 3.91 days	omni: 3.00 \pm 2.21 days yagi: 6.07 \pm 4.07 days
Maximum distance from nest	16 km	33 km

Between July 17th to July 23rd, 2021, within a week after leaving their nests, Tree Swallows from different colonies were found foraging and resting in one of the bigger wetlands in the area (Salt Lake: 51.618662, -106.325321), which is located at least 8 -10 km away from their natal sites. Some of those individuals stayed in the area for up to 5 subsequent days. Tree Swallow fledglings were also detected at least 5 km from their natal site, foraging at the Brightwater reservoir (51.618287, -106.548788), and over a seasonal stream located close to the reservoir.

Barn Swallows and Tree Swallows were detected up to 16 and 33 km away from the colony site two weeks after fledging (Figure 3.4). No Barn Swallows were detected outside the local Motus Network installed for the project, after breeding or during migration. However, in 2021, a Motus station south of Oak Lake, Manitoba, detected two Tree Swallows more than 400 km away from their natal colonies and only 17 and 24 days after birds have fledged from the nest, and 3 and 6 days after the last detection in the local network (Appendix B, Figure B.5).

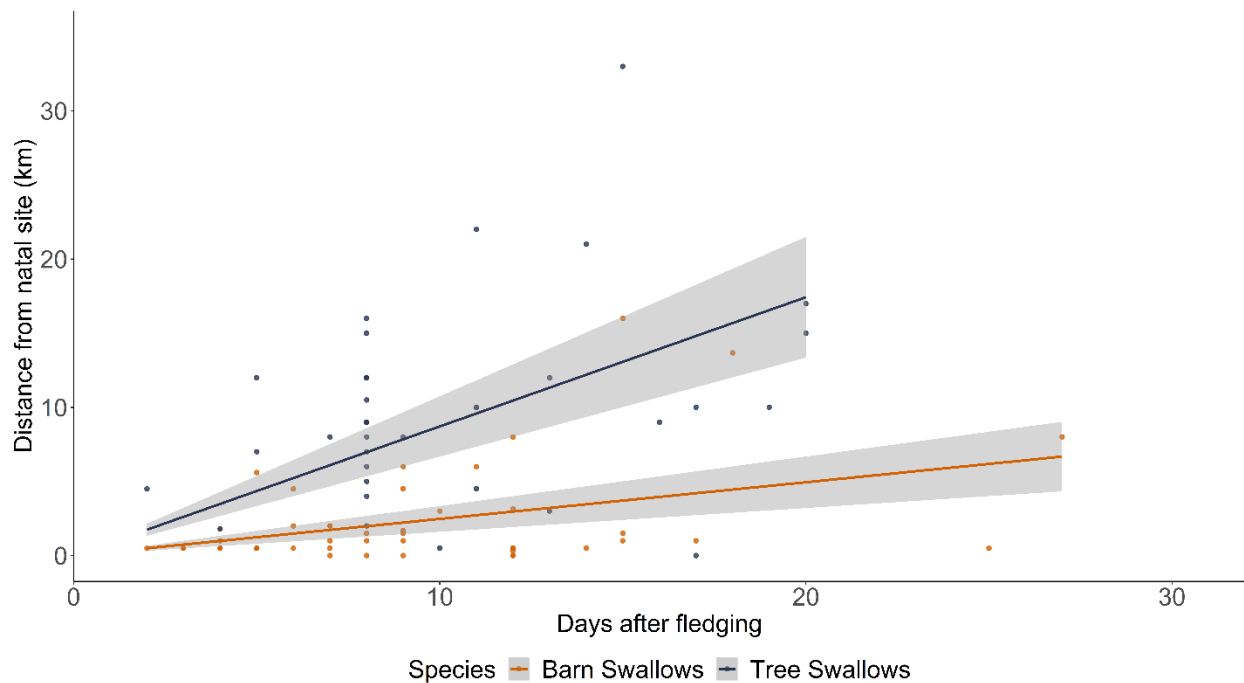


Figure 3.7 Scatter plot of distance from the nest travelled by Barn and Tree Swallows (km) in relation to days after fledging. Distances were estimated based on detection data from manual or vehicle mounted mobile telemetry, using an omni-directional antenna with a 500~1000 m range of detection.

3.4. DISCUSSION

Using automated telemetry and following a comparative interspecies approach, I was able to characterize early post-fledging survival and movement patterns for Barn and Tree Swallows utilizing cropped landscapes in the Prairie Pothole Region. Although I was not able to track the juveniles from fledging to migration as previous studies in areas with higher density of Motus automated telemetry towers (Evans et al., 2019), this approach allowed me to compare post-fledging survival and early-movement on two species of swallows with contrasting life-histories and different population trends in North America. Here I provided the first estimates of post-fledging apparent survival of Barn and Tree Swallows in the region, for the first two weeks after fledging when the highest mortality rates occur (Cox et al., 2014). Seven days after fledging,

survival of fledging Tree and Barn Swallows had declines to an average of 60%, with similar cumulative apparent survival estimates for both species over a two-week period in 2020 and 2021. Contrary to my predictions, I found little effect of individual factors (body condition, wing length, brood size) on Barn or Tree Swallow apparent daily survival after fledging, but I obtained some evidence that nestling period duration may be an important predictor of post-fledging survival in Barn Swallows. I also found that differential life-history traits between both species of swallows may determine departure from the natal and post-fledging early movements patterns; Tree Swallow fledglings stayed for shorter periods in their natal sites than those of Barn Swallows and moved away from their natal areas soon after fledging, towards riparian areas.

3.4.1. Factors influencing apparent daily survival.

In line with my predictions, I found that apparent daily post-fledging survival changed with the age of fledglings and showed different patterns in Barn and Tree Swallows. As in other altricial birds, low juvenile apparent survival in Barn and Tree Swallows occurred during the first days after fledging (Cox et al., 2014). These results suggest that the transition to a new environment outside the nest can be especially costly for the young because birds can depend on parental care, have limited mobility to escape from predators, or lack of experience identifying potential risks (Anders et al., 1997; Kershner et al., 2004; Martin et al., 2018; Naef-Daenzer et al., 2001; Vitz & Rodewald, 2011).

Apparent daily survival in both species slightly increased a few days after fledging and plateaued until what I presume was the transition to independence, when it declined again. For Barn Swallows, the start of a decline in apparent daily survival coincided with the end of parental care (9-10 days after fledging; Gruebler & Naef-Daenzer, 2010) and persisted until the end of the study period. Meanwhile, in Tree Swallows, the decline occurred sooner, however I speculate it

was also related to the transition to independence. There is a large knowledge gap of the post-fledging period in Tree Swallows, and it is not clear when fledglings reach independence or if adults continue their parental efforts away from the nest (Winkler et al., 2011). There is some evidence that the parental care stage in Tree Swallows is shorter and that some young may be able to take on long flights and acquire food independently, soon after leaving the nest (Michaud & Leonard, 2000; Winkler et al., 2011). Therefore, consistent with other studies in songbirds, my results suggest that the end of parental care may also be a precarious survival transition period for young Barn and Tree Swallow, given increasing exposure to threats and potential challenges when navigating new environments, as they still lack experience in maneuvering and foraging (Anders et al., 1997; Gruebler & Naef-Daenzer, 2010b; Sullivan, 1989; but see Evans et al, 2019).

In Tree Swallows, post-fledging survival probability on day 14 reached almost 100% which suggests that the costs of independence may only be temporary. It is also possible that my estimates of apparent post-fledging survival after eight days post-fledging are biased by low detection rates after independence, when young may take longer exploratory or foraging trips outside the detection area. Further research is needed to better understand the spatial ecology of the post-fledging period and the patterns of post-breeding habitat use of Tree Swallow fledglings.

The timing of fledging may be determined by the stage when birds have achieved a threshold state of development (Santema et al., 2021). However, multiple factors beyond development may be involved in the occurrence of this transition (e.g., hatching asynchrony, parent/offspring conflict, food availability, nest predation risk), and those factors may vary among species (Johnson et al., 2004, 2013). Regardless, fledging before achieving optimal development could be a disadvantage at the moment of leaving the nest, making it harder to fly and avoid predators (Gosler et al., 1995; Martins, 1997), and therefore will likely influence the exposure of juvenile to threats (Jones & Ward, 2020). For example, even though Tree Swallows can often take on long

first flights upon leaving the nest (Winkler et al., 2011), their foraging and flying skills may depend on their development time in the nest. Contrary to my predictions, I did not find evidence that duration of nestling period was related to Tree Swallow apparent daily survival, suggesting that locomotor ability may not be affected in birds that fledge past Day 18. On the contrary, a shorter nestling period in Barn Swallow showed negative effects on apparent daily survival. This relationship might have been driven by premature fledging (<17 post-hatching), when nestlings were capable of flight, but lacked capacity for sustained flight for long distances, due to incomplete wing feather development. In 2020, the relationship between nestling period length and apparent daily survival showed the opposite trend, although non-significant, indicating that other environmental or biological factors may have influenced post-fledging survival.

Better nutrient reserves associated with higher body condition may assist juveniles by conferring better endurance during periods of low food availability, adverse weather conditions or other challenges during transition to independence. Birds in lower condition may beg more and become more conspicuous (Naef-Daenzer et al., 2001; but see Gosler et al 1995). Similarly, shorter wings may affect the ability to escape from predators. Contrary to previous research on Barn Swallow populations in Ontario from Evans et al., (2020), I found no evidence that individual nestling body condition and wing length, at the stage they were measured, had any effect on post-fledging survival. These results may have been driven by lack of variability in morphometric measurements among the tagged birds, over the growth period. During this study, nestlings showed similar growth rates that resulted in individuals reaching similar relative pre-fledging mass (Day 12 and Day 15 in Tree and Barn Swallows) (Appendix B, Figure B.3). Moreover, the estimates of nestling body condition during the active growth period (Day 8) for this study, may not be fully representative of the health and energy reserves at the time of fledging, which occurred 10 to 14 days later, or of the condition of the bird at independence when

facing high energy demands. However, evaluating the effect of nestling body condition later in the nestling period (Day 12 or Day 15) on post-fledging survival, could lead to misinterpretation of effects since Tree and Barn Swallows, as in other aerial insectivores, experience mass reductions prior to fledging (Mauck & Ricklefs, 2005; Moeller & Ritchison, 2019; Wright et al., 2006) that can be unrelated to their condition, lean mass development or fat deposition rates. After a certain age threshold, it becomes difficult to document nestling condition and development using morphometric measurements for some species of birds (Anthony & Ely, 1976; but see Streby et al., 2013). Similarly, it is challenging to catch fledglings once they have left the nest to assess their condition and growth. Therefore, estimating the nestling period duration as accurately as possible may be an alternative to account for the state of development of fledglings when studying survival and to avoid misleading results based on only morphometric measurements.

One of the biggest knowledge gaps when studying the post-fledging survival of highly mobile birds, like swallows, is determining causes of specific mortality to better understand the mechanisms acting on post-fledging survival. Although high predation is suspected in this system based on the tags that were found, given the challenges of finding carcasses or tags once birds stop being detected, it is not clear what influenced swallow survival in this region.

The average cumulative estimates of post-fledging survival over a two-week period for Barn Swallows in the Saskatchewan Prairies (26%) were slightly lower than for Tree Swallows (30%), across the two years. Barn and Tree Swallow estimates in my study system were lower than what has been reported for swallows and martins studied in North America using radiotelemetry (Boynton et al., 2020; Evans et al., 2019; Tarof et al., 2011). However, those studies used different approaches and techniques, which together with the characteristics of the landscapes, and differences in life history traits among species make the comparison of survival rates across studies difficult. In my study, the 14-day post-fledging cumulative survival may be biased by

lower detectability due to the highly mobile behaviour of Barn and Tree Swallows in the Prairies, especially once birds reach independence, and the insufficient local automated telemetry array to capture those movements. Further research involving extensive automated telemetry in the surroundings of breeding sites would be valuable to determine if the low probability of detection is a factor of high rates of mortality or early post-breeding dispersal in these species.

Even though this research indicates that probability of survival for Barn and Tree Swallows is low in the study area and that it can certainly be a population bottleneck for both species, I did not find strong evidence that in my study area survival of fledglings may be differentially contributing to the increase in population trajectories of both species. These results are consistent with the similar annual population trends reported by the analysis of Breeding Bird surveys, which show that populations of Barn and Tree Swallows in the PPR have been more stable than in other regions of Canada, and that have been even experiencing subtle increasing trajectories in the last decades (2009-2019) (Smith et al., 2020). Further comparative research is needed on this period, in areas where aerial insectivore species are experiencing population declines to investigate if such declines may be at least partially explained by low post-fledging survival.

Although I tested several individual variables (i.e., body condition, wing length, nestling period duration) that could be a result of the conditions in the nest (i.e., environmental conditions, habitat quality, availability of food, parental care) and that have often been linked with post-fledging survival (Dunn et al., 2016; Evans et al., 2019; Green & Cockburn, 2001; Jones & Ward, 2020; Suedkamp Wells et al., 2007, but see Anders et al., 1997), I did not evaluate the effects of post-fledging habitat in the natal sites on survival, given the unequal spatial distribution and density of telemetry stations throughout the study area.

3.4.2. Early movements in Barn and Tree Swallows

Telemetry data of Barn and Tree Swallow juveniles after fledging revealed some evidence of differences between both species' early post-fledging behaviours and movements. After leaving the nest, Barn Swallow fledglings stayed in the immediate natal area (500-1000m) longer relative to Tree Swallows. Tree Swallows spent, on average, half the time Barn Swallows spent in the natal sites before moving further. Similarly, Tree Swallows from sites equipped with Yagi stations moved outside the range of detection sooner than Barn Swallows. These findings suggest Tree Swallows travelled and stayed away from the general breeding area, expanding their natal range sooner than Barn Swallows. Bumelis (2020) reported no difference in approximate residence time for fledged Barn and Tree Swallows in Ontario; however, that study estimated residency based on the number of days after fledging before birds were detected in a tower outside the natal site, without accounting for differences in detection probability. In my study, I estimated the number of days before a bird stopped being detected from the local station for an entire day, with an assumption of 100% probability of detection when birds were in their natal areas (500-1000m). I recognize that this measure of residency or latency to departure was only apparent as, it was not possible to discern if birds that stopped being detected in the local station had left the natal site permanently or were dead.

Contrasting life-histories, specifically post-breeding movement in adults, may partially explain the differences I encountered in early post-fledging movements between Tree and Barn Swallows. Tree Swallow adults usually raise one brood a year (Winkler et al., 2011), after which leave the natal area soon after the nestlings fledge (Pegan et al., 2018) moving to areas with high food abundance (i.e., wetlands, marshes), where they start moulting before migration (De Steven, 1978). There is increasing evidence that Tree Swallows rely heavily on adult stages of aquatic-emergent insects (McCarty & Winkler, 1999a; Michelson et al., 2018), which are essential to

fulfill their physiological needs (Twining et al., 2016b, 2019). Therefore, Tree Swallow fledglings may follow adults' post-breeding movements to riparian habitats potentially richer in preferred food than the natal sites, where young birds can continue their development of locomotor traits and growing feathers (Schoener, 1968). Following adults might also help young birds learn cues for foraging and avoiding predators. In contrast, Barn Swallow adults rely on barns or other structures and often extend their breeding period to produce multiple broods in one season (Brown & Brown, 2019) and, in my study area, can stay in the breeding sites until late August or later (Ana Diaz, *pers. observ.*). Therefore, during the dependent period, Barn Swallow fledglings may stay in their natal site longer, likely taking advantage of an extended parental care, and start exploring farther from their natal sites presumably when adults start new clutches, and provisioning rates reduce (Grüebler & Naef-Daenzer, 2008a).

Previous work in Ontario reported that Tree Swallows and Barn Swallows appeared to be using open water habitats after leaving the natal area (Bumelis, 2020). Although I did not measure resource availability or habitat use by fledging, by using fine-scale mobile telemetry, I obtained some anecdotal evidence that Tree Swallow juveniles, move to wetlands and riparian habitats soon after leaving the nest. In these areas they were seen congregating with other adult and young conspecifics. I speculate that Tree Swallow juveniles may travel from their nesting areas, to find suitable habitats that could have higher food abundance and where they can find better shelter than in natal sites. Similar movements have been reported outside the breeding season in adult Tree Swallows, who during migration, appear to also move considerable distances tracking resource availability to counteract the effects of poor habitat conditions (Knight et al., 2019).

Generally, nestling songbirds fledge before achieving full development. As fledglings age, their locomotor traits (i.e., wings, feathers, muscles) continue developing; which increases their ability to maneuver and sustain flight (Jones et al., 2018; McCarty, 2001). Therefore, in different

species of songbirds, including Swallows, the distance travelled from the natal sites increases with age after fledging. In Ovenbirds (*Seiurus aurocapila*) and Worm-eating Warblers (*Helmitheros vermivorum*), the average cumulative distance from the nest travelled by a juvenile leaving the nest does not exceed 500m before 21 days after fledging (Vitz & Rodewald, 2010). Similarly, Eastern Bluebirds (*Sialia sialis*) only moved further than 200m when they were older than 30 days post-fledging (Jackson et al., 2011). After fledging, Barn and Tree Swallows quickly increased the distance they move from the nest. Barn Swallow juveniles were detected ~15 km from the nest only 15 days after fledging, consistent with Boynton et al. (2020) who reported Barn Swallows moving 19 km away from the colony only 16 days after fledging. Bumelis (2020) also reported a cumulative flight distance greater than 350 km from fledging to migration. Tree Swallows increase their travelling distance even faster with age and were detected farther than 20 km away from their colony in only four days. Moreover, the probability of detection of Tree Swallows dropped with age compared to Barn Swallows, indicating their earlier dispersal.

Some Barn Swallows travelled > 500 m soon after fledging, which was confirmed through manual and mobile telemetry. However, they often returned to the natal colony in the evening to roost (inside the barn or the surrounding vegetation), which suggests these are exploratory movements (White & Faaborg, 2008). In contrast, the steep decline in the probability of detection of Tree Swallows at night (00:00h and 03:59h) compared to early morning (04:00 – 08:00h) suggested that this species, soon after they fledge, might move to other suitable habitats different than the natal sites to roost. The low probability of detection estimates before sunset (20:00 – 23:59), when birds generally forage actively or travel towards their roosting areas, builds on the evidence that availability of roosting sites may be an important determinant of post fledging movements. Tree Swallow habitat preferences post-breeding and during migration have been presumed to be similar to those for breeding individuals (Winkler et al., 2020), for which wetlands

and riparian habitats play an important role in providing nutritious food and shelter. More research is needed on the post-breeding behaviour and ecology of fledgling Barn and Tree Swallows once they have left the natal site, to understand the relationship between post-fledging use of habitat and potential movement and survival linkages associated with resource availability.

I obtained evidence that juveniles moved southeast less than three weeks before fledging in what appeared to be already pre-migratory trips. Two individuals were detected by two telemetry towers in Manitoba, located more than 400 km from their natal site and only 2-3 weeks after fledging. These findings are consistent with descriptions of adult swallow movement from the Saskatchewan Prairies towards wetlands and lakes in southern Manitoba and North Dakota (Knight et al., 2018). Adult Tree Swallows depart from the breeding areas and start migration within 1-2 week after nestlings fledge (around mid-July) (Knight et al., 2018). However, during their southward-bound trips to the non-breeding grounds, Tree Swallows use multiple areas presumably with high abundance of prey (i.e., wetlands, marshes) as stopover sites to complete their moult before arriving at their wintering areas (Stutchbury & Rohwer, 2011; Winkler, 2006).

3.4.3. Study limitations

One of the main limitations of the current study was the reduced ability to follow fledglings once they become more mobile and quickly expanded their home range. Despite the intense effort to compensate for the sparse Motus telemetry station array in the area by doing mobile telemetry, especially in 2021, swallows in the Prairies travelled far from the natal sites, and the extensive layout of the sites challenged my ability to follow the fledglings after leaving the immediate natal area to determine their location, and to document additional information such as habitat use. In addition, after two weeks, some young birds were detected already 400 km away from their natal colony, therefore it is possible that permanent emigration from this study was confounded with

mortality.

Using a robust analysis in a mark-recapture context, only apparent survival can be estimated. These parameters are usually underestimated compared to real survival because mortality cannot be separated from permanent emigration. The Huggins robust analysis addresses part of the challenges of other approaches at modelling temporary emigration among secondary sessions, in this case the time of the day, to account for different probabilities of detection among secondary periods in which birds are alive but are not within the range of detection of an antenna. This approach is useful when studying highly mobile individuals that can be missed from the study area temporarily, to reduce the bias between permanent and temporary emigration. However, given the sample size of this study, I kept temporary emigration and temporary immigration equivalent and constant over time. Thus, apparent survival estimates in this study are likely still biased. A larger sample size over multiple years with high and comparable detection effort (i.e., larger telemetry network array and fine-scale mobile telemetry) may allow the incorporation of the variation of temporary migration and emigration with age in the models and may improve the estimates of survival using the advantages of the Huggins robust model.

3.4.4. Conclusion

Aerial insectivores are a diverse group of birds that depend on aerial insects. However, as a group, they have a wide variety of breeding strategies and life-histories that influence how they interact with the environment during the post-fledging period, which may condition the challenges and risks that juveniles face once they transition to new environments outside the nest. I obtained evidence that post-fledging is a critical period for different species of swallows regardless of their different life histories. I also found that Barn Swallows stay close to the natal site for extended periods, probably encouraged by extended parental care and the shelter provided by barns, against

predators and inclement weather. Meanwhile, Tree Swallows, in this study, left the natal site soon after fledging, and the need for higher-quality habitats may have partially driven those early movements. These findings contribute to the growing evidence that wetlands have an important role sustaining aerial insectivores' populations during the breeding and pre-migratory periods. Further research involving extensive automated telemetry to study aerial insectivores post-fledging ecology, although logistically challenging, would be valuable to learn more about their movement and habitat requirements to fill gaps in the knowledge of their ecology throughout the full annual cycle, which is critical to guide conservation efforts for declining populations of aerial insectivores.

CHAPTER 4. General discussion

4.1. SUMMARY OF FINDINGS

The overall aim of my thesis was to evaluate landscape-level effects of an agricultural gradient of intensification on aspects of the diet and condition of nestlings Barn and Tree Swallows in the Prairie Pothole Region of Saskatchewan and to investigate differences in post-fledging movement and apparent daily survival between both species.

In Chapter 2, using $\delta^2\text{H}$ as tracers of diet source, I assessed differences in parental use of aquatic-emergent prey to provision nestlings, and the landscape-level effects of agricultural intensity (i.e. relative coverage area in row-crop and water) on their contribution to this type of prey in the diet. In addition, I evaluated the effects of agricultural intensity (% crop and % wetland cover) on nestling body condition and daily mass gain in Barn and Tree Swallows. I did not find strong evidence that Barn Swallows and Tree Swallows in intensively cropped areas changed the relative contribution of aquatic-emergent prey to the diet of their nestlings; however, the amount of water cover on the vicinity of the nest (500m from the nest) appeared to influence Barn Swallow use of aquatic prey. These results also suggested that Barn Swallows may be more flexible in their use of aquatic-emergent prey as source of essential nutrients, whereas Tree Swallows are more specialized (Twining et al., 2018b, 2021). I found little evidence to suggest that Tree and Barn Swallow nestling condition or growth were influenced by agricultural intensification, at least in the gradient evaluated in in my study system. However, other ecological and environmental factors at a brood- and site- level, such as parental care, weather, and predation pressure, may be involved in the development and growth of aerial insectivores during their early-life stages.

In Chapter 3, using Motus automated telemetry data and miniature radiotags (nanotags), I investigated differences in the early post-fledging apparent daily survival and movement of

juvenile Barn and Tree Swallows. The post-fledging survival analysis indicated that by day 8, cumulative survival was similar between both species, resulting in a cumulative survival of 59.0% for Tree Swallow and 64.1% in Barn Swallows. The total cumulative survival over the two-week post-fledging period for Tree Swallows and Barn Swallows decline to 30% and 26%, respectively. I found evidence of differential latency to departure from the natal site between the two species, most likely explained by their different life histories, such as reliance of different roosting sites. My research also found evidence of important habitats for Tree Swallow fledglings. With the use of manual and mobile telemetry, I confirmed that Tree Swallows used wetlands embedded in the agricultural landscapes of the Canadian Prairies and that juveniles can travel relatively long distances (>5 km) within days or weeks after fledging where they congregate with conspecifics. Congregation of swallows at roosts near open water have been already documented for some species of aerial insectivores, especially during the migratory period (Winkler, 2006); however little is still known about the use of these habitats by fledglings.

This study underscores the importance of studying multiple sympatric species under identical environmental conditions and using the same methods as a valuable way to understand how different species of aerial insectivores may respond differently to environmental characteristics at different spatial scales. Depending on their nutritional or ecological needs, such requirements may vary throughout different stages of the breeding period (i.e., nestling period, post-fledging period). Moreover, this study highlights the need for further investigation to disentangle the complex mechanisms driving nestling body condition and growth that may have lasting consequences on survival and other life stages of the annual cycle, including the post-fledging and migratory period.

4.2. IMPLICATIONS FOR CONSERVATION

Agriculture has been globally recognized as one of the major threats to biodiversity (Green et

al., 2005) and has been associated with the decline of farmland bird populations (Newton, 2004, Donald et al., 2001), including aerial insectivores. Recent research indicates that population declines vary geographically (Nebel et al., 2010) and among species (Michel et al., 2016), which suggests that different populations and species are possibly being exposed to complex stressors. Several species of swallows inhabit the agricultural landscapes of the Canadian Prairies, which contains one of the most intensive agricultural practices nationwide (Stats Canada 2022). The results presented in Chapter 2 showed evidence that at least in my study system, the intensively cropped areas may not be affecting contributed aquatic emergent prey to maintain nestling diet, condition, and growth of Tree Swallows. Although further study is needed, it is possible that adult Tree Swallows trade-off their own fitness to travel further in search of high-quality aquatically derived prey to ensure offspring success. Therefore, it remains critical to maintain and protect wetlands in the agricultural landscapes of the PPR to sustain Tree Swallow populations, and other aerial insect consumers before they start experiencing similar negative population trends, as has been reported for other parts of Canada and North America.

My results showed some evidence, although weak, that intensive cropping around barns (500m) may be detrimental for nestlings condition, likely by affecting the quality and abundance of preferred prey (Evans et al., 2007; Tschardt et al., 2005). Although I lack insect abundance and biomass data from my study system to link to my results, previous research has found a positive influence of natural grasslands, hay land, and livestock as having high sources of insect prey for Barn Swallows (Ambrosini et al., 2012; Gruebler et al., 2010). Preserving semi-natural grasses and livestock around farmsteads in agricultural landscapes, as well as maintaining habitat heterogeneity, may contribute to the improvement of nesting habitat quality for breeding Barn Swallows.

This research has highlighted that aerial insectivore, as many other species of migratory

songbirds, use wetlands and semi-natural habitats as sources of food, shelter, resting and social interaction during different stages of the life-cycle. Therefore, the conservation of these habitat features should be prioritized in view of the ongoing rates of degradation and loss of natural grasslands and wetlands that has occurred in the PPR in the last 50 years with the intensification of agricultural practices (Watmough et al., 2017; Wiken et al., 2003), and that may be exacerbated by more extreme climate variation of dry-wet cycles caused by climate change (Hayashi et al., 2016).

Conservation of avian species is more effective with increased understanding of the full annual cycle (Anders & Marshall, 2005). However, in aerial insectivores the post-fledging period remains understudied because soon after leaving the nest, juveniles are cryptic and highly mobile. This research contributes to the understanding of the post-fledging period of two species of swallows that have been declining in North America. Although this study does not present potential mechanisms of reduced post-fledging survival, it presents opportunities for using novel automated technology when studying the post-fledging period of small bodied aerial insectivores, where tag weight is limiting. In addition, it contributes to the large knowledge gap around survival during the post-fledging life-stage of swallows, which can aid to future conservation efforts.

4.3. STUDY LIMITATIONS

Finding Barn Swallow nesting locations around which to erect Tree Swallow nest-boxes was essential to the study's design. One of the main limitations of this research was finding nesting sites that represented a gradient of agricultural intensity, specifically row-crop and wetland cover, both at a small and large spatial scale. One of the consequences of agricultural expansion and intensification in the PPR is the removal or abandonment of old homesteads and rural wood-style barn structures, which are frequently used by Barn Swallows as nesting sites and are generally ideal to study this species. Given the challenges on locating this type of building in intensively

cropped areas, most of the sites in this study were surrounded, at a large scale (>2km), by a heterogeneous matrix of natural grasses, forage, and row crops. Even though these sites represented more diverse agricultural land use at a small scale, landscape composition at larger spatial scales was more uniform and did not reflect the extremes of the gradient of agricultural intensity that exists in the Prairies which varies from semi-natural areas with pasture and forage crops and a high abundance of water, to the highly cultivated areas with complete absence of water.

Organisms can respond to their surroundings at different scales depending on their nutritional or ecological needs, which can also vary throughout their life cycle (e.g., nesting period, post-fledging dependent period, post-fledging independent period). Performing this type of study in a larger representative gradient of agriculture, covering both small and larger spatial scales, would have allowed me to evaluate the extremes of landscape level effects of agricultural intensity on my response variables with greater resolution. Previous studies that have evaluated the landscape level effects of agriculture on reproductive success in aerial insectivores, have reported a positive effect of extensive (pastoral) agriculture surrounding nests on some breeding activities, that were sometimes strongest at spatial scales of 4-5 km around the nest (Ghilain & Belisle, 2008). These results suggest that land cover at larger spatial scales than the one used for foraging can have effects on diet, or reproductive success, likely through large scale effects on insect abundance. Similarly, previous work in the Prairies, evaluating the effects of pond abundance and cropland/grassland on condition of Tree Swallow nestlings have found positive effects of wetland (pond) area. That study obtained data from a wider wetland gradient that ranged between 0-30% pond cover within 500m around the nests (Berzins et al., 2022). In my study area, the open water relative proportion around nests ranged between 0 and 13% (at 500 m), and the majority of the

nests, except for some nest in two sites, were surrounded by < 9% of open water cover.

Although extent of cropland (annual row crop) was considered one single category, used as a proxy agricultural intensity from landscape simplification, the type of crop and the spatio-temporal variation in agricultural practices (seeding, tillage, and pesticide application rates), may be more important to consider in future analysis to understand the impacts of changes in land use on important measures of prey availability and condition of aerial insectivores and other farmland birds. I acknowledge that given the scale of my study, which characterizes the land use at least 2km around the breeding sites, getting this specific data may be challenging, and is highly dependent on the willingness of landowners to share that information as well as available land cover datasets with high resolution of field level cropping practices.

I recognize that it is possible that negative effects of extent of cropped area and wetlands on diet, condition or growth of aerial insectivores, can be exacerbated by weather events or climatic conditions through changes in prey availability or changes in the nestlings' energy requirements (Cox et al., 2019). Despite the contrasting weather conditions between 2020 and 2021, this study was conducted during two relatively dry years, which could have impacted the abundance of wetlands in the landscape, and with that, the abundance of aquatic-emergent prey. Therefore, there is uncertainty in whether these are generalizable to the future and under wetter conditions. Long term studies could be beneficial to have more robust estimates of the effects of loss of natural areas (i.e. grass, wetlands) and breeding habitat on the breeding ecology of declining species, especially in an areas where hydrology is highly dynamic and varies with extreme dry-wet cycles.

In other systems, using $\delta^2\text{H}$ measurements have proved to be useful in tracing aquatic diet sources in different taxa (*birds*: Bumelis et al., 2022; Génier et al., 2022; *bats*: Voigt et al., 2015). However, the strong link of stable hydrogen isotopes in animal tissues with the hydrological cycle and ambient temperatures adds additional complexity and uncertainty to the interpretation of $\delta^2\text{H}$

for the estimation of prey origin, especially in highly seasonal areas like the Canadian Prairies (Bortolotti et al., 2013; Jardine et al., 2009). In my study, aquatic-emergent insects for analysis of stable isotopes were collected through insect sweeps; however, aquatic-emergent insects emerge as local seasonal pulses after which they are rarely evenly distributed in the landscape, therefore insect sweeps often fail at trapping this kind of prey. More intense and standardized water sampling throughout the season, paired to sampling of early and late emergence of aquatic insects in the sampled wetlands, ideally using emergence traps, would be valuable to link $\delta^2\text{H}$ values in water, local aquatic-emergent insects, and diet of aerial insectivores. In addition, using $\delta^2\text{H}$ with other tools to study diet (e.g. fatty acids, mixing models, fecal eDNA) could also help overcome the uncertainty of only using $\delta^2\text{H}$ values to infer diet and to study causes of spatio-temporal variation.

The post-fledging movements and apparent survival analyses of this study had several limitations that must be considering when interpreting the results. First, the sample size of tagged nestlings was small, which may have influenced my power to detect any effect of the intrinsic measures on apparent daily survival. Secondly, the array of Motus telemetry stations with long-range of detection that surrounded the study colony was insufficient considering the spatial layout of the study sites and the long-distance movements that swallows can take. Lastly, with high nest failure in 2020, due to weather and predation, nesting phenology was more spread out in the season and conducting manual and mobile telemetry became logistically challenging. In 2021 there was an intense effort to conduct mobile telemetry to compensate for the small telemetry stations array in the area; however, swallows in the Prairies appear to rapidly depart the natal site and travel long distances. Therefore, following the fledglings after leaving the immediate natal area, using triangulation to determine their location, as well as the identification of the habitat they were using was not always possible with the current Motus telemetry system. Future research

studying survival would benefit by using a larger scale network of telemetry stations to increase the capability of detection and to have more robust estimates of survival after birds reach independence.

4.4. FUTURE RESEARCH

The transition to more industrialized and modernized agriculture has meant the expansion of cropland, and landscape homogenization and simplification. In the last decades, many smaller farms have been substituted by larger industrial farming operations. As a result of these changes, old style farmsteads, which provide important habitats for farmland biodiversity, including foraging farmland bird species (Rosin et al., 2016), are becoming increasingly rare and, sometimes, have been replaced by new modern buildings. This reduces the availability of nesting sites and foraging areas for declining species such as Barn Swallows. In Europe, farmsteads and their buildings have been recognized as important hotspots of biodiversity in agricultural landscape (e.g., Grüebler et al., 2010; Rosin et al., 2016; Šálek et al., 2018). In North America further research is needed to study the potential importance and features of homesteads to conserve populations of Barn Swallows and other farmland birds.

Increasing evidence suggests that diet nutritional quality (i.e., omega-3 LCPUFA) may be more important than prey abundance for Tree Swallows (Twining et al., 2016b, 2018a) and other species of aerial insectivores (Génier et al., 2021, 2022). However, an important question remains whether some aerial insectivores need aquatic prey or if they have greater capacity to convert precursor molecules to obtain the omega-3 LCPUFA, necessary for many physiological processes. Given that some species may use this prey only opportunistically, it remains unclear if aquatic-emergent prey helps mitigate the impacts of agricultural intensification on nestling's health, even when they are not nutritionally dependent on them.

Further research is also needed to investigate if higher abundance of aquatic emergent prey

confers advantages on parental and offspring survival and ultimately, have positive consequences on parent's fitness. The study of the factors that can affect emergence of aquatic prey should also receive special attention when linking diet of aerial insectivores and changes in the landscape. Although challenging, it would be valuable to understand how different types of wetlands, and other specific physicochemical characteristics of wetlands may be impacting the abundance of nutrients transferred from aquatic habitat to the aerial insectivorous bird diets during the breeding season.

Wetlands in agricultural landscapes can not only act as a high quality nutritional source but also as vectors of exposure to toxicants and agrochemicals through emergence of aquatically derived prey (Kraus et al., 2021; Poisson et al., 2021). Recent evidence indicates negative effects of widely used pesticides on activity levels and body mass in songbirds (Eng et al., 2019). Further research is needed to investigate the toxicity of pesticides and other agrochemicals found in wetlands in agricultural landscapes, and at what extent the exposure through the diet could impair body condition, health, and fitness of breeding populations of farmland birds, including aerial insectivores.

There is still an enormous gap in our knowledge of the post-breeding behaviour and ecology of swallow fledglings, with an important lack of understanding about the relationship between post-fledging quality habitat and resource use. Future studies, with denser telemetry arrays, could investigate the spatial ecology and habitat selection of juvenile swallows. For example, given the increasing evidence of the important role of wetlands and riparian areas as important sources of prey (Elgin et al., 2020) and the positive responses of individuals and populations (Berzins et al., 2021, 2022), more research is needed to investigate if lower abundance of wetlands, at small and large spatial scales in the PPR, may have an effect in the post-fledging habitat use and longer term survival of swallows and other aerial insectivorous species. In addition, the study of the post-fledging survival in multiple species in areas where aerial insectivore populations are facing

different population trends is necessary to understand if such differences may be associated with survival during the post-fledging period, and the mechanisms that may be operating to increase mortality during this critical period.

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APPENDIX A

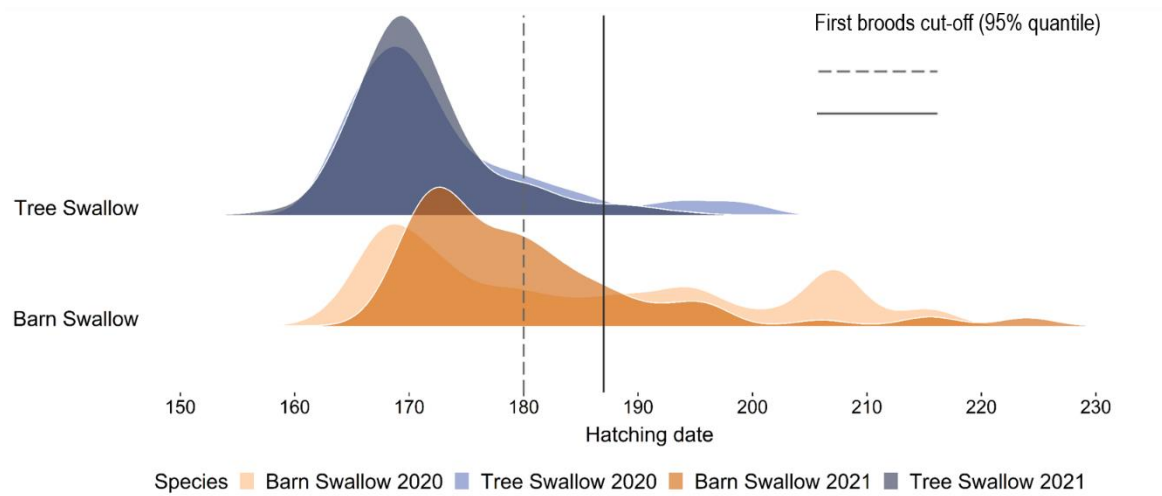


Figure A.1. Density plots of hatch dates for Tree Swallows and Barn Swallows followed in 2020 and 2021 to estimate cut-off dates for first broods. Hatching date is expressed in Julian date. Day 160 corresponds to June 8. Dash line on day 180 (June 28, 2020- June 29, 2021) represents the 95% quantile of Tree Swallows true first broods. Solid line on day 187 (July 5, 2020- July 7, 2021) represents the 95% quantile of Barn Swallow true first broods.

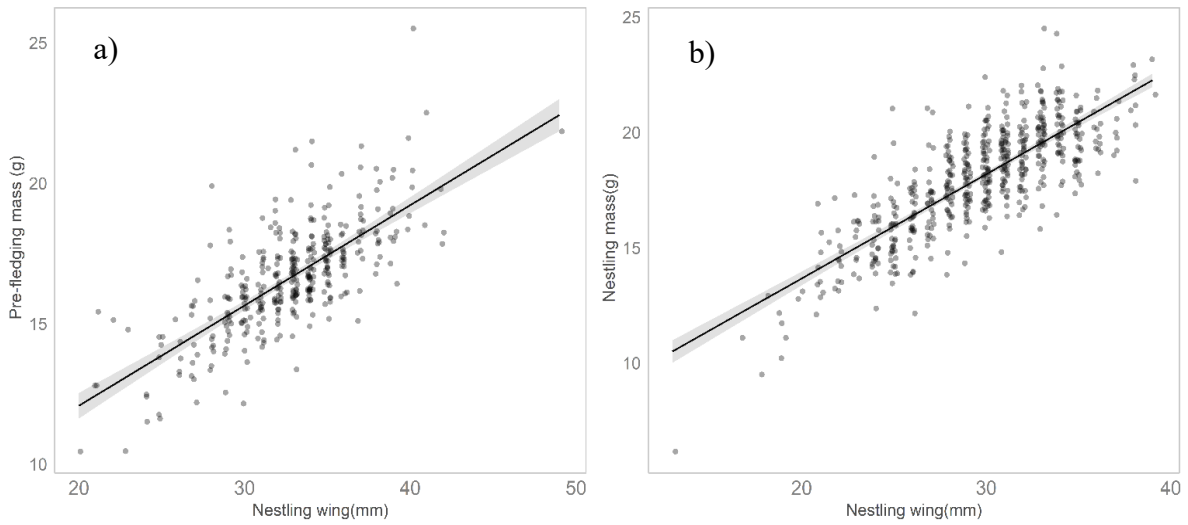


Figure A.2 Scatterplot of nestling mass (g) versus wing (mm) in Barn Swallows (a) and Tree Swallow (b) on Day 8 in 2020 and 2021. Measurements were taken on Day 8, for both species. Lines represent the quadratic relation between the two variables and the shaded represents the 95% confidence interval.

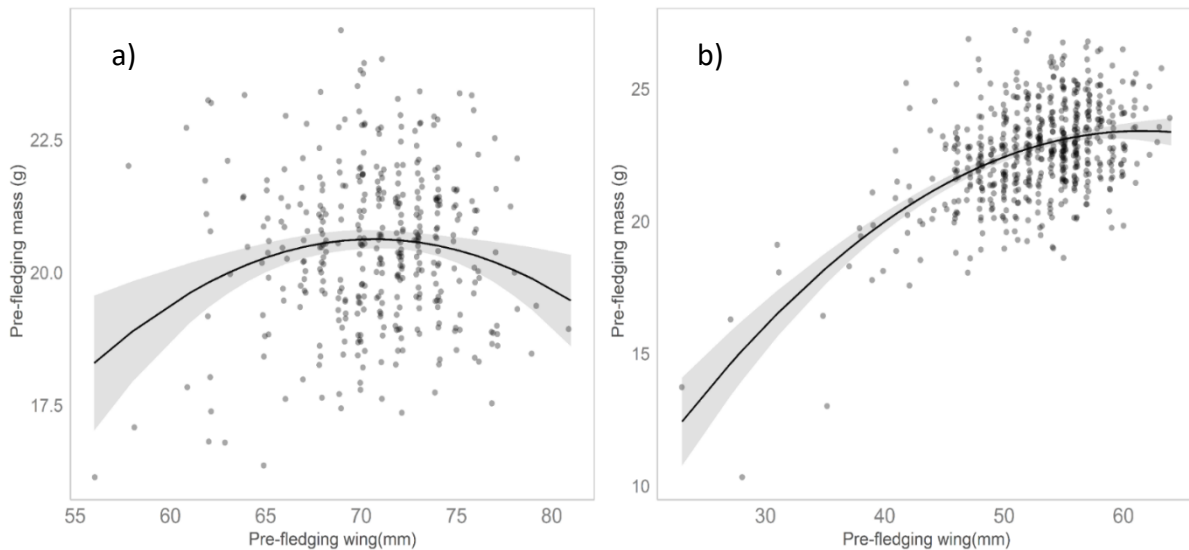


Figure A.3 Scatterplot of pre-fledging mass (g) and wing (mm) in Barn Swallows (a) and Tree Swallow (b) in 2020 and 2021. Measurements were taken on Day 15 and Day 12, respectively. Lines represent the quadratic relation between the two variables and the shaded represents the 95% confidence interval.

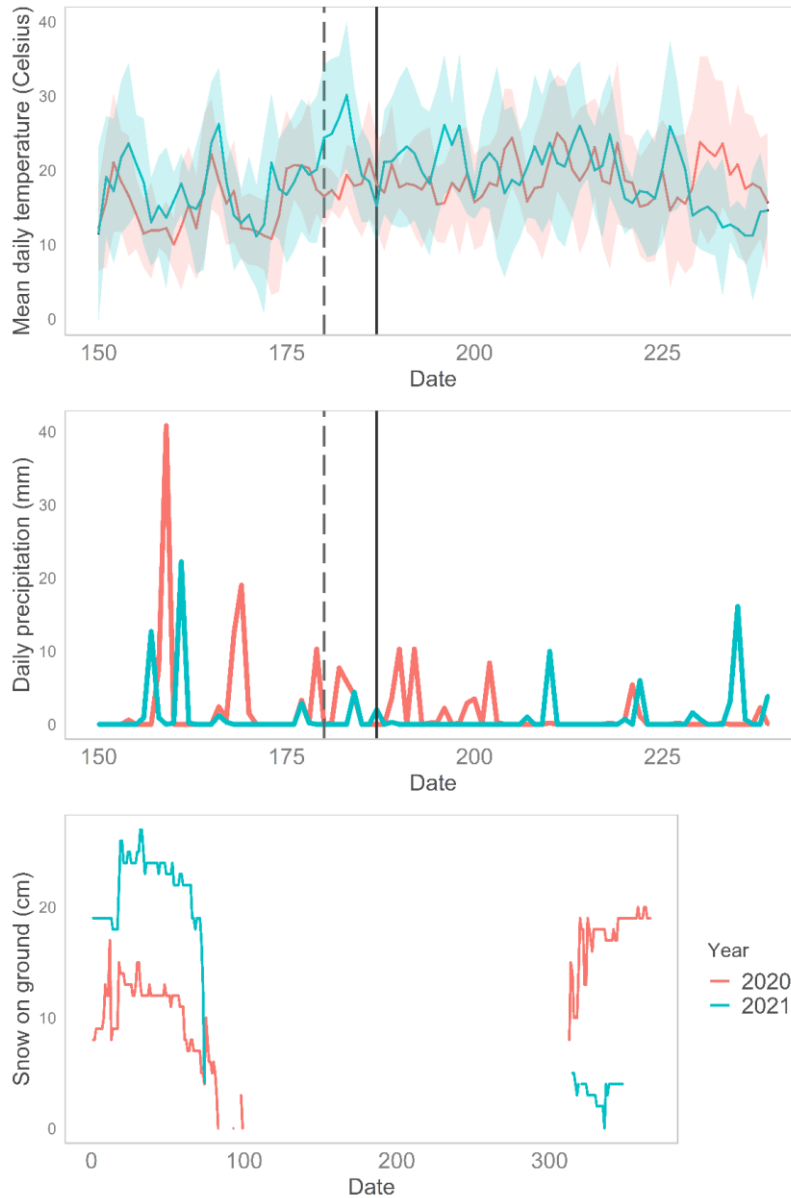


Figure A.4. Plots of daily mean temperature, total daily precipitation, and snow on ground in 2020 and 2021, from the Saskatoon RCS, nearest weather station to the study area. Day 1 (Date) is 1 January. Data extracted from Environment and Climate Change Canada). Dash lines on day 180 (June 28, 2020- June 29, 2021) represents the 95% quantile of Tree Swallows true first broods. Solid line on day 189 (July 7, 2020- July 8, 2021) represents the 95% quantile of Barn Swallow true first broods.

Table A.1 Summary of monthly average of daily temperature and total precipitation during the breeding season in 2020 and 2021 in Central Saskatchewan. Data obtained from the Saskatoon RCS, nearest weather station to the study area (Environment and Climate Change Canada).

<i>Year</i>	<i>Month</i>	<i>Min. Temperature (°C)</i>	<i>Max. temperature (°C)</i>	<i>Mean Temperature (°C)</i>	<i>Total precipitation (mm)</i>
2020	May	3.52	18.65	11.09	1.36
	June	9.49	21.11	15.3	3.56
	July	12.37	25.53	18.95	1.68
	August	9.48	27.07	18.27	0.54
2021	May	2.15	17.99	10.07	1.15
	June	9.92	26.1	18.02	1.39
	July	13.04	29.79	21.41	0.57
	August	11.02	24.55	17.78	1.24

Table A.2. $\delta^2\text{H}$ water values at three collection periods during the breeding season (mid-May, mid-June, and mid-July 2021). (-) indicates samples were not collected at that collection period.

<i>SITE</i>	<i>Type of wetland</i>	<i>First collection</i>	$\delta^2\text{H}$ values (‰)	<i>Second collection</i>	$\delta^2\text{H}$ values (‰)	<i>Third collection</i>	$\delta^2\text{H}$ values (‰)
SSP14E	natural	-	-	10-06-2021	-73	25-06-2021	-62
SSP14W	natural	18-05-2021	-70	10-06-2021	-64	25-06-2021	-59
SSP09	natural	18-05-2021	-73	09-06-2021	-70	25-06-2021	-64
SSP11	natural	18-05-2021	-68	10-06-2021	-64	25-06-2021	-57
SSP13	natural	21-05-2021	-129	-	-	25-06-2021	-57
SSP08	natural	18-05-2021	-80	09-06-2021	-61	25-06-2021	-73
SSP01	artificial	-	-	10-06-2021	-140	25-06-2021	-132
SSP10	artificial	18-05-2021	-103	10-06-2021	-83	25-06-2021	-68
SSP03	artificial	18-05-2021	-138	09-06-2021	-114	25-06-2021	-92
SSP07	artificial	18-05-2021	-150	09-06-2021	-138	25-06-2021	-126
SSP04	artificial	-	-	09-06-2021	-123	25-06-2021	-103
SSP02	artificial	-	-	09-06-2021	-131	25-06-2021	-128

Table A.3. Summary statistics for $\delta^2\text{H}$ values in insects separated by taxa, and site. Insect samples analyzed were collected from June 11 to July 16, 2020, and were homogenized and pooled to obtain the target mass necessary for $\delta^2\text{H}$ isotopes analysis. Six pooled samples were analyzed per site.

Site	Coleoptera $\delta^2\text{H}$ (<i>mean \pm SD</i>)	Nematocera $\delta^2\text{H}$ (<i>mean \pm SD</i>)
SSP01	-183.83 \pm 3.5	-167.65 \pm 4.99
SSP02	-212.98 \pm 22.21	-181.15 \pm 6.49
SSP03	-159.6 \pm 5.29	-180.03 \pm 4.05
SSP04	-218.36 \pm 41.85	-176.07 \pm 9.57
SSP05	-188.72 \pm 4.58	-189.16 \pm 16.91
SSP07	-183.15 \pm 16.31	-176.33 \pm 11.12
SSP08	-181.57 \pm 1.96	-216.42 \pm 5.44
SSP09	-202.17 \pm 22.28	-184.22 \pm 18.47
SSP10	-181.24 \pm 13.04	-197.62 \pm 8.92
SSP11	-177.79 \pm 7.60	-180.9 \pm 7.31
SSP12	-169.7 \pm 6.54	-184.57 \pm 5.30
SSP13	-205.3 \pm 4.90	-180.6 \pm 5.13

Table A.4. Summary statistics for nestling $\delta^2\text{H}_f$ values separated by species, year, and site and number of feathers analyzed (*n*).

<i>Site</i>	<i>Year</i>	Tree Swallows		Barn Swallows	
		δ^2H (<i>mean</i> \pm <i>SD</i> ‰)	<i>n</i>	δ^2H (<i>mean</i> \pm <i>SD</i> ‰)	<i>n</i>
SSP04	2020	-139.77 \pm 5.80	9	-130.49 \pm 4.08	8
	2021	-132.03 \pm 4.64	3	-129.39 \pm 3.68	15
SSP12	2020	-150.32 \pm 8.49	9	-140.2 \pm 4.46	5
SSP15	2021	-	-	-127.61 \pm 2.40	7
SSP02	2020	-142.57 \pm 4.42	3	-146.55 \pm 18.82	6
	2021	-134.14 \pm 3.10	21	-127.61 \pm 2.10	10
SSP07	2020	-155 \pm 17.71	6	-139.48 \pm 8.67	12
	2021	-134.76 \pm 5.77	19	-	-
SSP16	2021	-	-	-133.53 \pm 5.60	18
SSP17	2021	-135.75 \pm 4.36	11	-131.7 \pm 4.96	12
SSP03	2020	-139.36 \pm 5.15	9	-138.38 \pm 9.37	6
	2021	-132.29 \pm 3.61	29	-128.94 \pm 5.32	12
SSP10	2020	-153.33 \pm 7.71	12	-141.93 \pm 1.27	3
	2021	-134 \pm 2.77	23	-128.07 \pm 1.81	6
SSP01	2020	-151.23 \pm 16.59	9	-149.04 \pm 6.61	13
	2021	-140.4 \pm 2.38	3	-143.3 \pm 9.89	9
SSP13	2020	-156.03 \pm 7.95	18	-141.81 \pm 9.27	14
	2021	-141.89 \pm 4.85	23	-131.48 \pm 4.00	13
SSP08	2020	-151.03 \pm 11.56	15	-151.15 \pm 15.95	11
	2021	-150.83 \pm 9.43	3	-141.88 \pm 14.70	6
SSP11	2020	-148.11 \pm 7.70	15	-136.21 \pm 7.11	11
	2021	-137.92 \pm 5.34	10	-130.12 \pm 5.51	13
SSP09	2020	-151.04 \pm 5.55	9	-156.95 \pm 8.73	17
	2021	-143.19 \pm 3.28	26	-134.87 \pm 7.69	18
SSP14	2021	-136.67 \pm 2.33	15	-135.88 \pm 6.82	26

Table A.5. Linear mixed-effect model results to test for differences between Barn and Tree Swallow nestling $\delta^2\text{H}_f$ values collected in 2020 and 2021 (n=571).

$\delta^2\text{H}_f \sim \text{Species} + \text{hatching date} + \text{brood size} + \text{year} + (1 \text{site ID/nest})$				
Fixed effects	Estimates (‰)	SE	CI	t value
(Intercept)	-149.02	1.45	-152.00 – -145.30	-102.53
Barn Swallows	5.82	0.91	4.02 – 7.21	6.38
Hatching date	0.06	0.44	-0.93 – 0.82	-0.13
2021	11.38	1.90	7.45 – 15.31	5.98
Brood size	-0.43	0.43	-1.28 – 0.42	-0.99
Marginal R^2 / Conditional R^2	0.352 / 0.70			

APPENDIX B

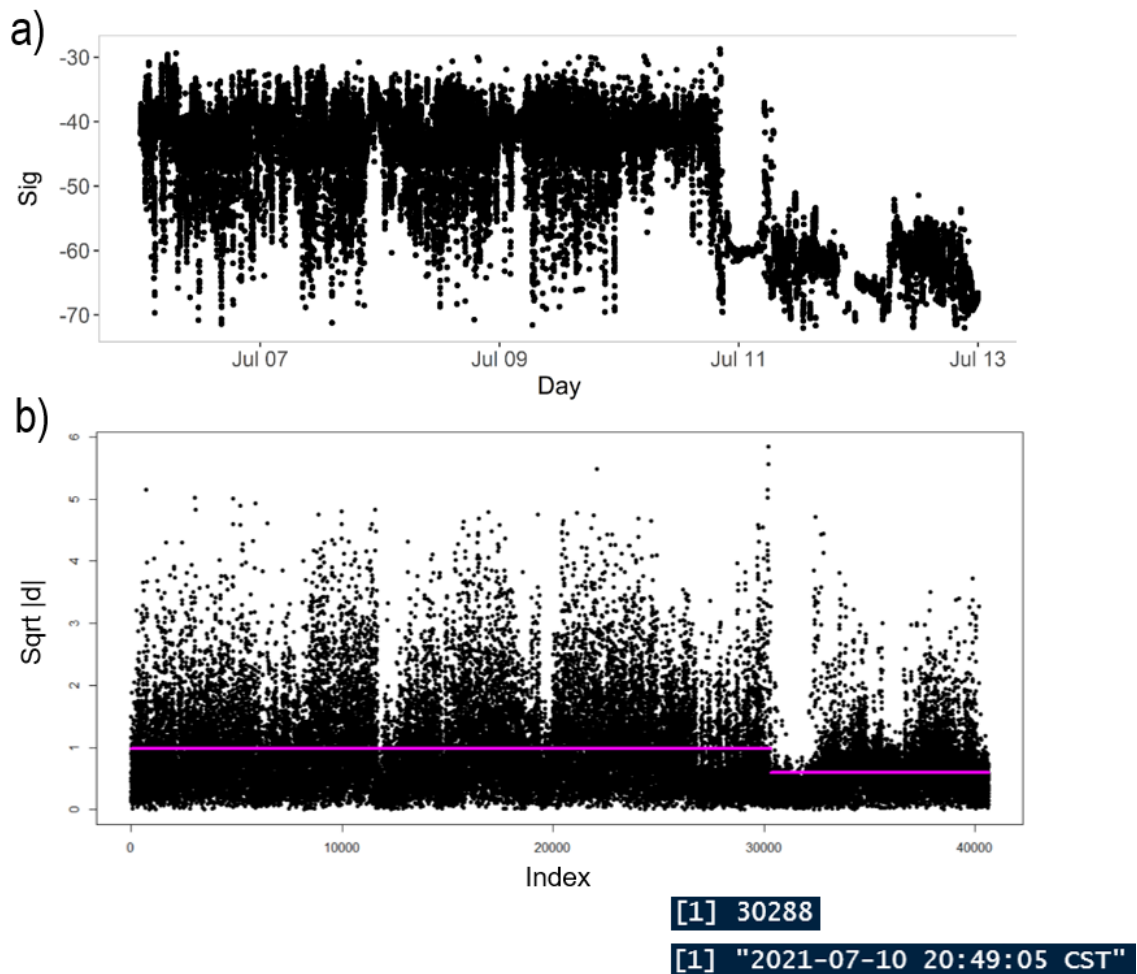


Figure B.1. Example of Motus detection by an omni station of a single tag deployed in a Barn Swallow nestling in Saskatchewan in 2021 (a). The plot shows signal strength by date. On July 10, there was a detectable change of signal strength and variability which corresponds to a fledging event. The bottom plot (b) shows the output of the change point analysis for the pre- and post-fledging period. The y-axis shows the square root of the difference between consecutive signal strength values or d ($\text{sig}_t - \text{sig}_{t-1}$). The purple horizontal lines show the mean values for consecutive observations from July 6 and July 13, 2021 (8-day period). The x-axis index value is used to extract the date and time when the change in the mean values occurred, in order to estimate the fledging date.

Table B.1. Model selection for probability of detection of Tree and Barn Swallows for the first two weeks after fledging (15 days) in 2020. Different structures of secondary sessions were tested: 6, 4, and 3 secondary sessions. The best supported secondary sessions based on ΔAICc was included in the rest of the models. The linear trend of age as well as the second-order and third-order polynomial trend of age (A) were tested. Best age structure at describing probability of detection was added to the best secondary session structure. The covariate Station accounted for the differences in probability of detection of birds whose natal site had a short range omnidirectional antenna station(500-1000m) or a larger range of detection station with 3 9-element yagi antenna(~15km). Apparent survival probability and temporary migration were held constant during this stage of the analysis. Equally supported models ($\Delta\text{AICc}<2$) are highlighted in bolt.

Tree Swallows 2020					
Detection models	AICc	ΔAICc	w_i	K	Deviance
$\Phi(\cdot) \gamma(\cdot) p(\mathbf{A} + \mathbf{A}^2 + \text{Station} + \text{time}_{6\text{ss}})$	2249.651	0	0.99999	11	2227.407
$\Phi(\cdot) \gamma(\cdot) p(\mathbf{A} + \mathbf{A}^2 + \text{time}_{6\text{ss}})$	2273.791	24.1401	0.00001	10	2253.588
$\Phi(\cdot) \gamma(\cdot) p(\mathbf{A} + \mathbf{A}^2)$	2420.528	170.8772	0	5	2410.473
$\Phi(\cdot) \gamma(\cdot) p(\mathbf{A} + \mathbf{A}^2 + \mathbf{A}^3)$	2422.54	172.8895	0	6	2410.463
$\Phi(\cdot) \gamma(\cdot) p(\mathbf{A})$	2433.463	183.8124	0	4	2425.427
$\Phi(\cdot) \gamma(\cdot) p(\text{time}_{6\text{ss}})$	2549.486	299.8349	0	8	2533.353
$\Phi(\cdot) \gamma(\cdot) p(\text{time}_{3\text{ss}})$	2636.67	387.0186	0	5	2626.614
$\Phi(\cdot) \gamma(\cdot) p(\text{time}_{2\text{ss}})$	2672.708	423.0575	0	4	2664.672
Barn Swallows 2020					
Detection models	AICc	ΔAICc	w_i	K	Deviance
$\Phi(\cdot) \gamma(\cdot) p(\mathbf{A} + \mathbf{A}^2 + \mathbf{A}^3 + \text{Station} + \text{time}_{6\text{ss}})$	2634.4844	0	1	12	2610.32
$\Phi(\cdot) \gamma(\cdot) p(\mathbf{A} + \mathbf{A}^2 + \mathbf{A}^3 + \text{time}_{6\text{ss}})$	2741.9742	107.4898	0	11	2719.835
$\Phi(\cdot) \gamma(\cdot) p(\mathbf{A} + \mathbf{A}^2 + \mathbf{A}^3)$	2830.7224	196.238	0	6	2818.678
$\Phi(\cdot) \gamma(\cdot) p(\mathbf{A} + \mathbf{A})$	2832.1992	197.7148	0	5	2822.168
$\Phi(\cdot) \gamma(\cdot) p(\mathbf{A})$	2832.2897	197.8053	0	4	2824.269
$\Phi(\cdot) \gamma(\cdot) p(\text{time}_{6\text{ss}})$	2866.5782	232.0938	0	8	2850.503
$\Phi(\cdot) \gamma(\cdot) p(\text{time}_{3\text{ss}})$	2909.3011	274.8167	0	5	2899.27
$\Phi(\cdot) \gamma(\cdot) p(\text{time}_{2\text{ss}})$	2933.1244	298.64	0	4	2925.103

Table B.2. Model selection for probability of detection of Tree and Barn Swallows for the first two weeks after fledging (15days) in 2021. Different structures of secondary sessions were tested: 6, 4, and 3 secondary sessions. The best supported secondary sessions based on ΔAICc was included in the rest of the models. The linear trend of age as well as the second order and third-order polynomial trend of age (A) were tested. Best age structure at describing probability of detection was added to the best secondary session structure. The covariate Station accounted for the differences in probability of detection of birds whose natal site had a short range omnidirectional antenna station(500-1000m) or a larger range of detection station with 3 9-element yagi antenna(~15km). Apparent survival probability and temporary migration were held constant during this stage of the analysis. Equally supported models ($\Delta\text{AICc}<2$) are highlighted in bolt.

Tree Swallows 2021					
Detection models	AICc	ΔAICc	w_i	K	Deviance
$\Phi(\cdot) \gamma(\cdot) p(\mathbf{A} + \mathbf{A}^2 + \mathbf{A}^3 + \text{Station} + \text{time})$	2614.612	0	0.97814	12	2590.367
$\Phi(\cdot) \gamma(\cdot) p(\mathbf{A} + \mathbf{A}^2 + \mathbf{A}^3 + \text{time})$	2622.214	7.6018	0.02186	11	2600.007
$\Phi(\cdot) \gamma(\cdot) p(\text{time}_{6\text{ss}})$	2856.252	241.6393	0	8	2840.139
$\Phi(\cdot) \gamma(\cdot) p(\mathbf{A} + \mathbf{A}^2 + \mathbf{A}^3)$	2866.689	252.0761	0	6	2854.623
$\Phi(\cdot) \gamma(\cdot) p(\mathbf{A})\}$	2869.384	254.7718	0	4	2861.35
$\Phi(\cdot) \gamma(\cdot) p(\mathbf{A} + \mathbf{A}^2)$	2869.957	255.3444	0	5	2859.91
$\Phi(\cdot) \gamma(\cdot) p(\text{time}_{3\text{ss}}) - 3$	2986.251	371.6383	0	5	2976.204
$\Phi(\cdot) \gamma(\cdot) p(\text{time}_{2\text{ss}}) - 2$	3030.403	415.7903	0	4	3022.372
Barn Swallows 2021					
Detection models	AICc	ΔAICc	w_i	K	Deviance
$\Phi(\cdot) \gamma(\cdot) p(\mathbf{A} + \mathbf{A}^2 + \mathbf{A}^3 + \text{Station} + \text{time}_{6\text{ss}})$	2842.462	0	0.99999	12	2818.291
$\Phi(\cdot) \gamma(\cdot) p(\mathbf{A} + \mathbf{A}^2 + \mathbf{A}^3 + \text{time}_{6\text{ss}})$	2864.739	22.2772	0.00001	11	2842.595
$\Phi(\cdot) \gamma(\cdot) p(\mathbf{A} + \mathbf{A}^2 + \mathbf{A}^3)$	3026.297	183.8349	0	6	3014.251
$\Phi(\cdot) \gamma(\cdot) p(\mathbf{A} + \mathbf{A}^2)$	3030.234	187.772	0	5	3020.201
$\Phi(\cdot) \gamma(\cdot) p(\mathbf{A})$	3032.905	190.4431	0	4	3024.883
$\Phi(\cdot) \gamma(\cdot) p(\text{time}_{6\text{ss}})$	3077.812	235.3501	0	8	3061.733
$\Phi(\cdot) \gamma(\cdot) p(\text{time}_{3\text{ss}})$	3169.955	327.4932	0	5	3159.923
$\Phi(\cdot) \gamma(\cdot) p(\text{time}_{2\text{ss}})$	3206.764	364.3017	0	4	3198.742

Table B.3. Model selection for probability of apparent daily survival of Tree and Barn Swallows for the first two weeks after fledging (15 days) in 2020. The linear trend of age as well as the second-order and third-order polynomial trend of age (A) were tested. Each age trend was tested independently and the best age structure at describing probability of daily survival was tested with the addition of four covariates: Duration of nesting period (Nest), nestling body condition index on Day 8 (BCI), brood size and wing chord length before fledging (wing). Temporary migration was held constant during this stage of the analysis and I used the best supported model for probability of detection that included station type, and secondary session for both species and the second order polynomial trend of age for Tree Swallows and the third order polynomial trend of age for Barn Swallows. Equally supported models ($\Delta AICc < 2$) are highlighted in bolt.

Tree Swallows 2020					
Apparent survival models	AICc	$\Delta AICc$	w_i	K	Deviance
$\Phi(A + A^2 + A^3 + \text{brood size})$	2184.218	0	0.31231	15	2153.76
$\Phi(A + A^2 + A^3 + \text{wing})$	2184.727	0.5089	0.24215	15	2154.269
$\Phi(A + A^2 + A^3)$	2185.106	0.8875	0.20039	14	2156.705
$\Phi(A + A^2 + A^3 + \text{BCI})$	2186.595	2.3766	0.09517	15	2156.136
$\Phi(A + A^2 + A^3 + \text{Nest})$	2186.951	2.7325	0.07966	15	2156.492
$\Phi(A + A^2)$	2187.599	3.3806	0.05761	13	2161.252
$\Phi(A)$	2191.124	6.906	0.00988	12	2166.827
$\Phi(.)$	2193.628	9.41	0.00283	11	2171.377
Barn Swallows 2020					
Apparent survival models	AICc	$\Delta AICc$	w_i	K	Deviance
$\Phi(A + A^2 + \text{Nest})$	2625.458	0	0.31917	15	2595.205
$\Phi(A + A^2)$	2626.12	0.6618	0.22925	14	2597.898
$\Phi(A + A^2 + \text{BCI})$	2626.944	1.4862	0.15181	15	2596.691
$\Phi(A + A^2 + \text{wing})$	2628.133	2.6756	0.08376	15	2597.88
$\Phi(A + A^2 + A^3)$	2628.134	2.6764	0.08372	15	2597.881
$\Phi(A + A^2 + \text{brood size})$	2628.149	2.6915	0.08309	15	2597.896
$\Phi(A)$	2630.583	5.1256	0.0246	13	2604.392
$\Phi(.)$	2630.585	5.1269	0.02459	12	2606.421

Table B.4. Model selection for probability of apparent daily survival of Tree and Barn Swallows for the first two weeks after fledging (15 days) in 2021. The linear trend of age as well as the second-order and third-order polynomial trend of age (A) were tested. Each age trend was tested independently and the best age structure at describing probability of daily survival was tested with the addition of four covariates: Duration of nesting period (Nest), nestling body condition index on Day 8 (BCI) brood size and wing chord length before fledging. Temporary migration was held constant during this stage of the analysis and I used the best supported model for probability of detection that included station type and secondary session and the third order polynomial trend of age for both species. Equally supported models ($\Delta AICc < 2$) are highlighted in bolt.

Tree Swallows 2021					
Apparent survival models	AICc	$\Delta AICc$	w_i	K	Deviance
$\Phi (A+ A^2 + A^3)$	2584.074	0	0.38493	15	2553.685
$\Phi (A+ A^2 + A^3 + Nest)$	2586.061	1.9866	0.14256	16	2553.619
$\Phi (A+ A^2 + A^3 + BCI)$	2586.118	2.0436	0.13855	16	2553.676
$\Phi (A+ A^2 + A^3 + wing)$	2586.123	2.0485	0.13821	16	2553.681
$\Phi (A+ A^2 + A^3 + brood size)$	2586.126	2.0518	0.13799	16	2553.684
$\Phi (A+ A^2)$	2589.044	4.9693	0.03209	14	2560.703
$\Phi (.)$	2590.107	6.0323	0.01886	12	2565.854
$\Phi (A)$	2592.141	8.0665	0.00682	13	2565.846
Barn Swallows 2021					
Apparent survival models	AICc	$\Delta AICc$	w_i	K	Deviance
$\Phi(A+ A^2 + Nest)$	2800.762	0	0.50848	15	2770.4977
$\Phi (A+ A^2 + A^3)$	2802.642	1.8806	0.19857	15	2772.3783
$\Phi (A+ A^2)$	2804.609	3.8476	0.07426	14	2776.3784
$\Phi (A+ A^2 + BCI)$	2804.807	4.0454	0.06727	15	2774.5431
$\Phi(A)$	2805.096	4.3346	0.05821	13	2778.8963
$\Phi (A+ A^2 + wing)$	2805.908	5.1466	0.03879	15	2775.6443
$\Phi (A+ A^2 + brood size)$	2806.042	5.2799	0.03629	15	2775.7776

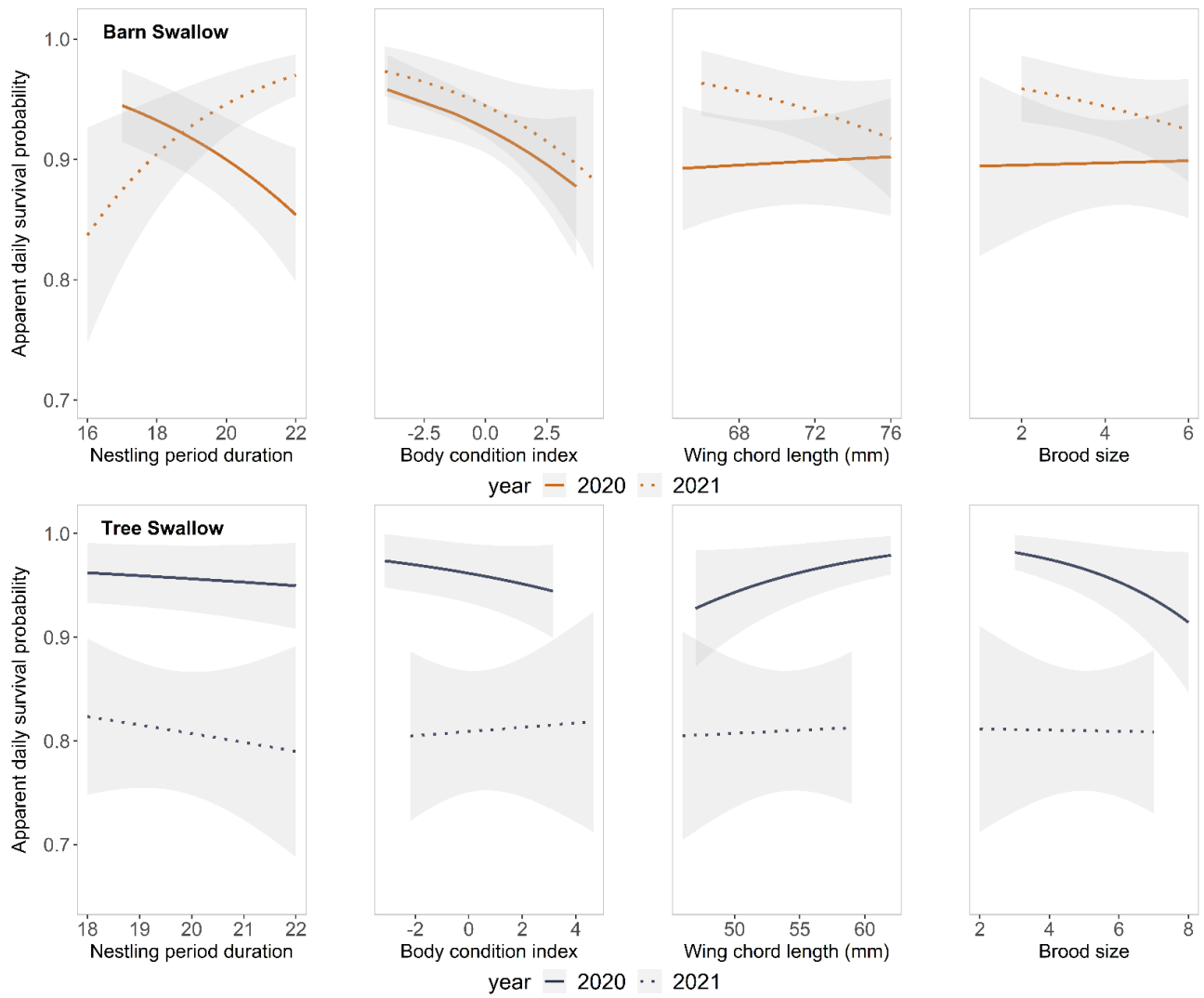


Figure B.2. Relationship between probability of apparent daily post-fledging survival (with 95% CI) and the individual predictors of nestling period duration, nestling body condition, wing length and brood size in Barn and Tree Swallows in 2020 (solid line) and 2021 (dashed line).

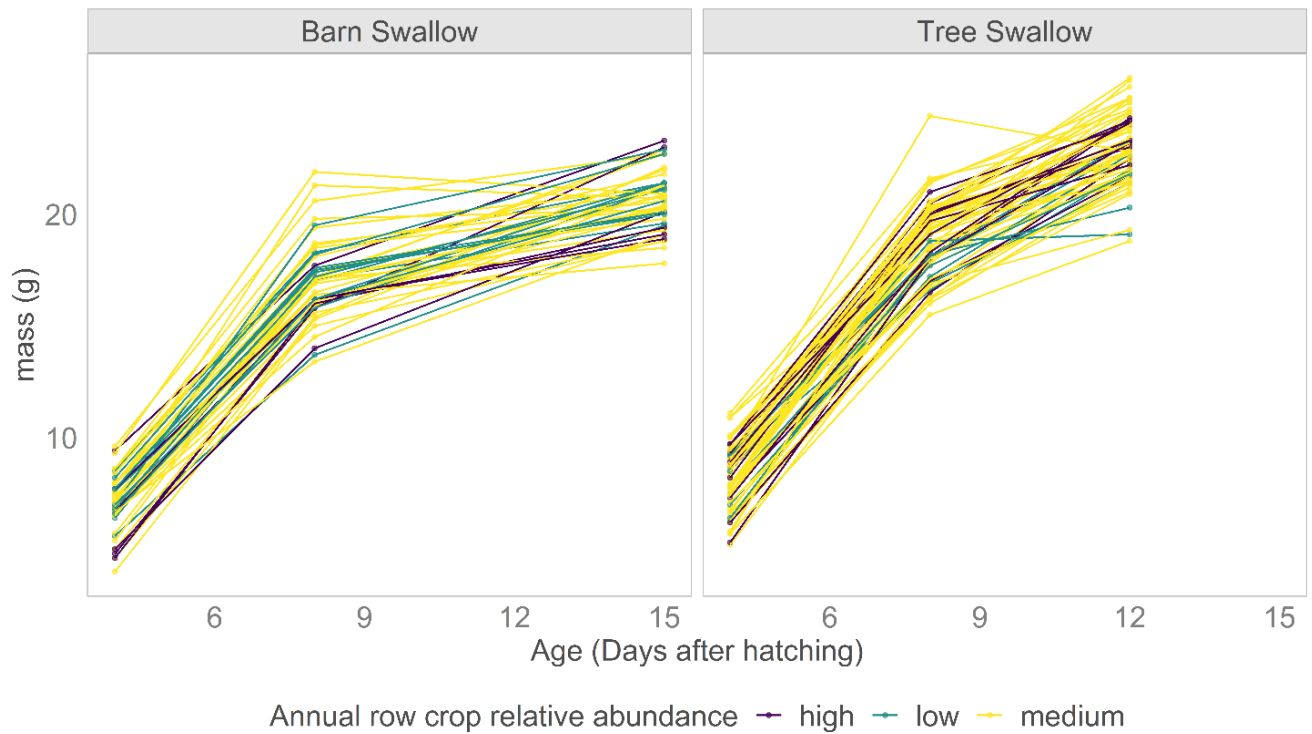


Figure B.3 Growth curve lines for Barn and Tree Swallows in 2020 and 2021. Colors indicate two categories of the natal site annual row crop abundance in a 2000m radius from the nest. Low indicates site where less than 25% of the area around the nest was covered by row crop, medium indicates 25 to 75% area covered by row crop and high indicates sites where row crop covers 75% or more of the area around the nests.

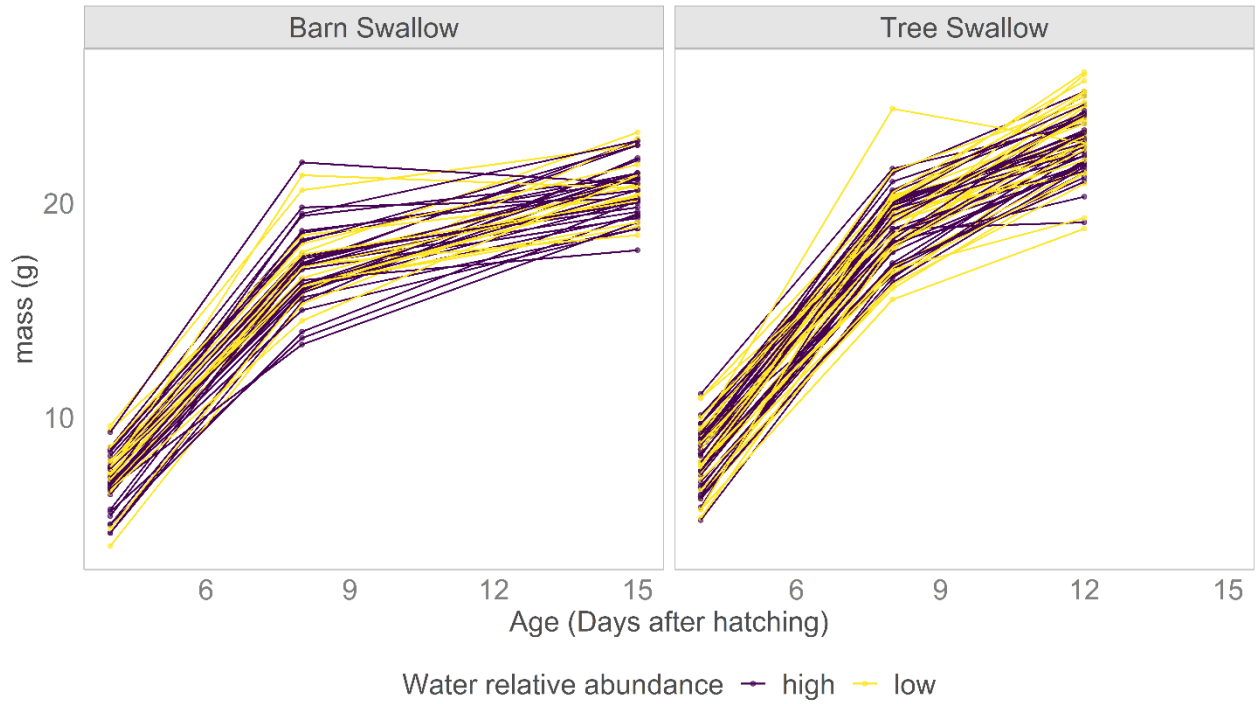


Figure B.4 Growth curve lines for Barn and Tree Swallows in 2020 and 2021. Colors indicate three categories open water coverage in a 2000m radius from the nest. Low indicates site where less than 3% of the area around the nest was covered by open water and high indicates sites where the open water of wetlands covered more than 3% of the area around the nests.

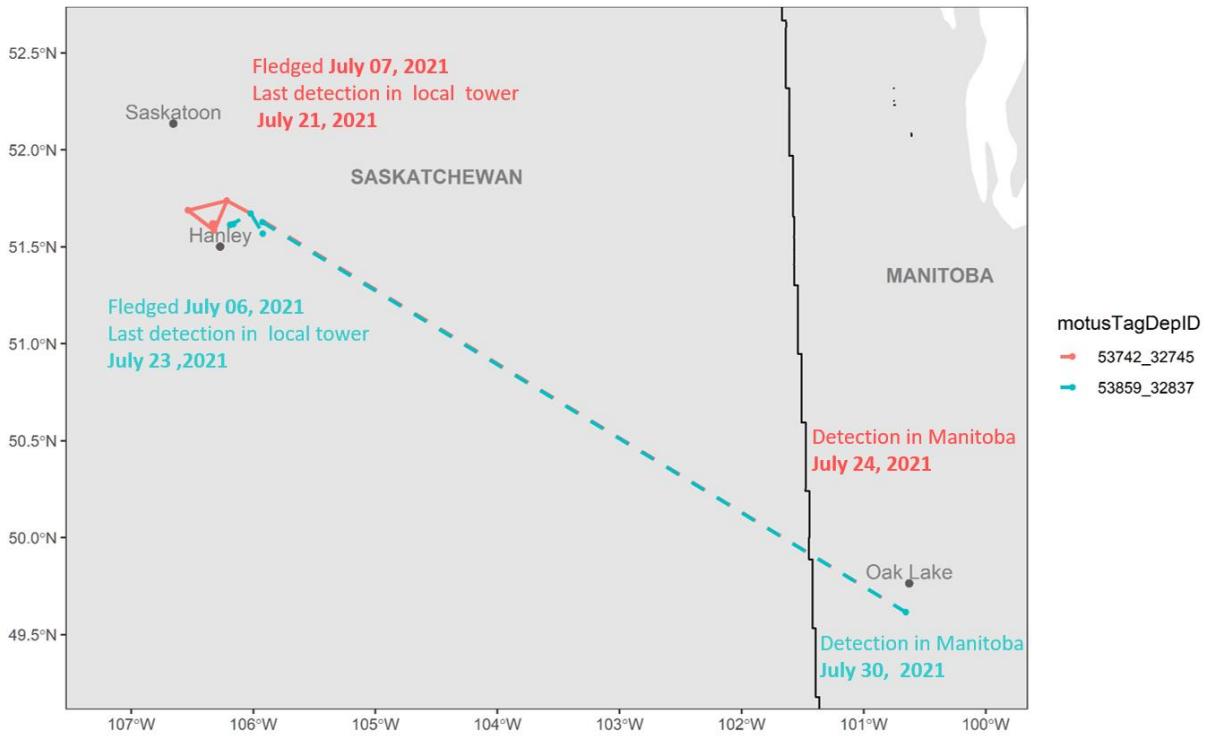


Figure B.5. Map of detection of two Tree Swallows tagged in Central Saskatchewan on June 23 (blue) and June 30 (red) in 2021. Last detection of these Tree Swallows occurred on July 30 and July 24, 2021 in Oak Lake, Manitoba. One individual fledged on July 07 2021 and was detected in Manitoba 17 days later in Manitoba (July 24th), after being detected for the last time in the local network on July 21st. The other individual fledged on July 06 2021, and was detected on July 30th in Manitoba, after being detected in the local network 7 days earlier.

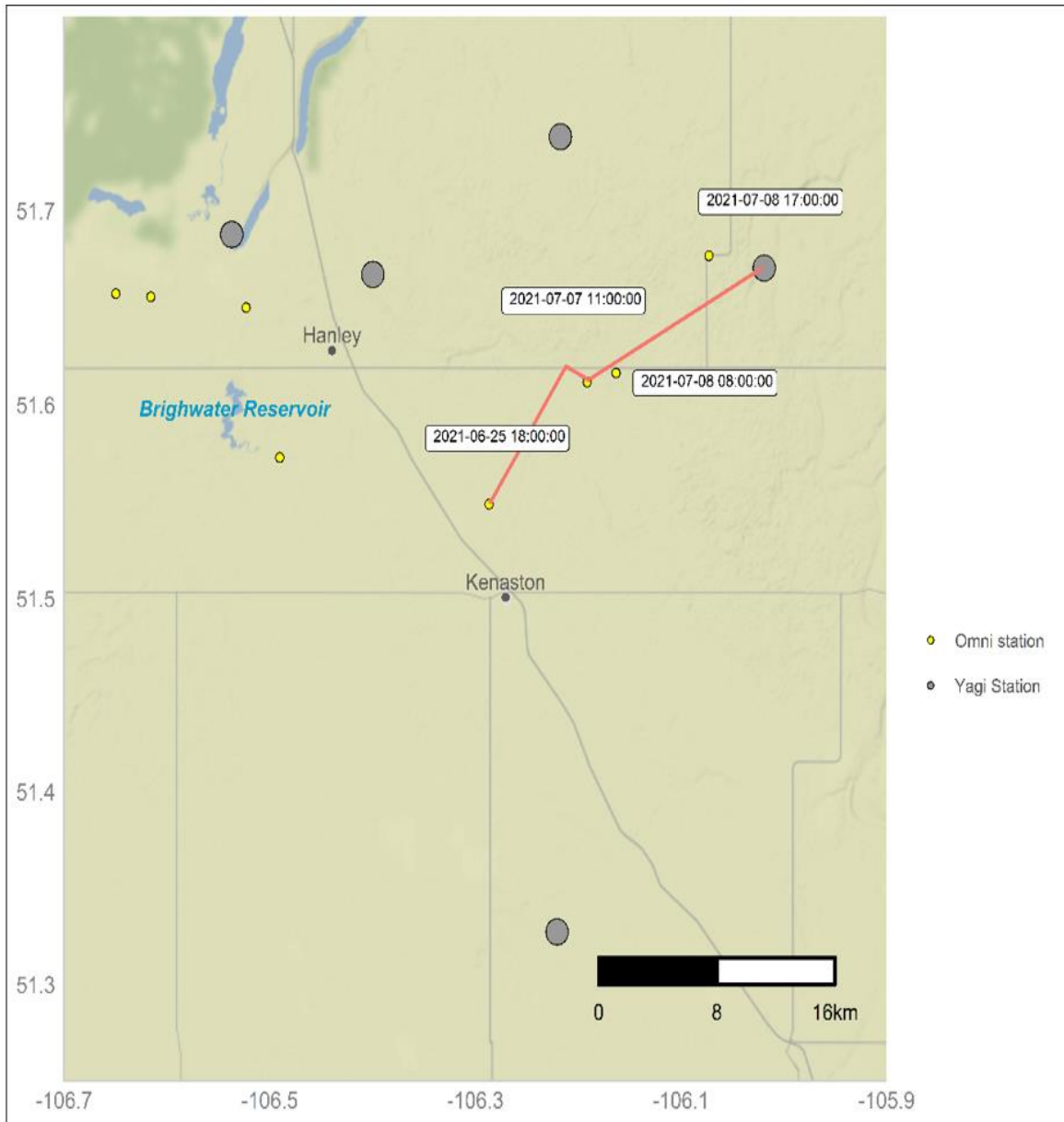


Figure B.6. Example of map of detections of Tree Swallow tagged in Central Saskatchewan on June 25, 2021 and fledged on July 03, 2021. The juvenile was not detected for three consecutive days after leaving the nest and the natal colony. Last detection occurred on July 8th, four days after leaving the nest by a yagi station located 20 km away from the natal colony.

Table B.5. Estimates of daily post-fledging survival for Tree and Barn Swallows, tracked in 2020 and 2021. The table includes days post-fledging (Day), standard error (SE) and lower (LCI) and upper (UCI) 95% confidence intervals.

Species	Day	2020				2021				
		Estimates	SE	LCI	UCI	Day	Estimates	SE	LCI	UCI
Tree Swallows	1	0.958	0.030	0.838	0.990	1	0.810	0.058	0.671	0.899
	2	0.971	0.014	0.929	0.989	2	0.931	0.021	0.875	0.963
	3	0.972	0.012	0.935	0.988	3	0.965	0.015	0.919	0.985
	4	0.966	0.015	0.920	0.986	4	0.975	0.012	0.935	0.991
	5	0.951	0.020	0.895	0.978	5	0.976	0.012	0.939	0.991
	6	0.925	0.024	0.861	0.961	6	0.972	0.012	0.935	0.988
	7	0.885	0.030	0.812	0.932	7	0.962	0.014	0.922	0.982
	8	0.838	0.039	0.746	0.901	8	0.944	0.019	0.894	0.971
	9	0.802	0.050	0.687	0.882	9	0.919	0.026	0.851	0.957
	10	0.802	0.054	0.677	0.887	10	0.890	0.035	0.802	0.942
	11	0.848	0.053	0.712	0.926	11	0.870	0.039	0.771	0.930
	12	0.920	0.051	0.748	0.978	12	0.871	0.043	0.760	0.935
	13	0.975	0.031	0.774	0.998	13	0.901	0.054	0.735	0.968
	14	0.996	0.009	0.797	1.000	14	0.946	0.054	0.685	0.993
	Day	Estimates	SE	LCI	UCI	Day	Estimates	SE	LCI	UCI
Barn Swallows	1	0.897	0.035	0.805	0.949	1	0.946	0.026	0.867	0.979
	2	0.922	0.021	0.870	0.954	2	0.953	0.017	0.905	0.977
	3	0.937	0.015	0.901	0.960	3	0.957	0.013	0.923	0.976
	4	0.946	0.013	0.914	0.966	4	0.959	0.011	0.929	0.976
	5	0.951	0.013	0.918	0.971	5	0.959	0.012	0.928	0.977
	6	0.952	0.014	0.918	0.973	6	0.957	0.013	0.923	0.976
	7	0.951	0.014	0.913	0.972	7	0.953	0.015	0.915	0.975
	8	0.946	0.016	0.906	0.970	8	0.947	0.016	0.905	0.971
	9	0.937	0.017	0.894	0.963	9	0.937	0.018	0.892	0.964
	10	0.922	0.019	0.876	0.952	10	0.923	0.020	0.874	0.954
	11	0.899	0.023	0.845	0.936	11	0.902	0.024	0.845	0.940
	12	0.861	0.032	0.786	0.913	12	0.872	0.033	0.791	0.924
	13	0.803	0.053	0.677	0.888	13	0.827	0.055	0.692	0.910
	14	0.714	0.093	0.506	0.859	14	0.762	0.095	0.535	0.899