

**Breeding productivity, phenology and habitat use of
two co-occurring aerial insectivores**

by
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Abstract

Aerial insectivores have been declining across North America for several decades, but the main causes of, and reasons for geographical variation in, these declines remains unclear. I directly compared variation in breeding phenology and productivity in co-occurring populations of Barn Swallows (*Hirundo rustica*) and Tree Swallows (*Tachycineta bicolor*), and the post-fledging survival and habitat use of Barn Swallows, in the lower mainland, BC, Canada. Barn Swallows had smaller clutches, and later average lay dates, but both species responded similarly to warmer spring temperatures, and interspecies differences were largely independent of habitat. Barn Swallows also had low post-fledgling survival rates, which could negatively impact population dynamics of the species in this region. Overall, our results indicate there are minor interspecies differences on the breeding grounds and therefore variation in species population trajectories in the lower mainland likely occur during the post-fledging stage, migration or on the wintering grounds.

Keywords: Barn Swallow, Tree Swallow, annual variation, breeding productivity, post-fledging period, survival

*This work is dedicated to my mom, who taught me how to be strong and resilient
and told me I can do anything I put my mind to.*

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Chapter 1. Introduction

Farmland and grassland birds have been declining disproportionately to other species for the last several decades across both Europe and North America (Conover et al. 2014, Donald et al. 2006). Furthermore, studies have shown that agricultural intensification is correlated both with declining farmland birds and fluctuating insect abundances (Donald et al. 2001, Donald et al. 2006, Paquette et al. 2013). Crop type (Evans et al. 2007), livestock presence (Moller 2001, Gruebler et al. 2010) and daily weather (Paquette et al. 2013, Gruebler et al. 2008) have also been shown to alter aerial insect abundance, which in turn impacts avian predators that forage over farmland, such as aerial insectivores. Ultimately, the transfiguration of farmland through increased crop production and the decrease of natural habitat has caused changes to the landscape, which can have implications for species fitness and survival (Boutin et al. 1999).

Aerial insectivore populations have also been in decline, however, this guild has declined more steeply than any other group of birds, including grassland and farmland birds (North American Bird Conservation Initiative Canada 2012). These sharp declines are suggested to be driven by several different mechanisms, such as climate and weather effects (García-Pérez et al. 2014), agricultural intensification (Benton et al. 2002, Paquette et al. 2013) and associated shifts in prey abundance (Nocera et al. 2012). Differences in population status between taxa (i.e. swallows, swifts and nightjars declining, while flycatchers generally stable; Smith et al. 2015), as well as geographic variation in declines across the guild (more species declining in the northern and eastern areas of North America; Nebel et al. 2010), highlight variation of population status within the guild and therefore the difficulty of pinpointing a single cause for these declines. Further evidence suggests that in co-occurring aerial insectivores, there is only weak a weak correlation in population trajectories, which suggests there are highly variable, and complex, spatio-temporal patterns of population change, perhaps related to region-specific environmental conditions such as changing weather or land use (Michel et al. 2015). Currently there is a lack of detailed empirical data for co-occurring aerial insectivore populations to address what region-specific factors might underpin population changes, particularly in the Pacific Northwest.

Study species

Barn Swallows (*Hirundo rustica*) and Tree Swallows (*Tachinyceta bicolor*) belong to the aerial insectivore guild, which forage solely on aerial insects caught on the wing. Tree Swallows forage primarily on Dipterans (Paquette et al. 2014), as well as Odonota, Ephemeroptera, Trichoptera (Winkler et al. 2011), while Barn Swallows are more opportunistic, although they commonly consume Diptera and other flies (Brown and Brown 1999). Both are medium-sized swallows, adults weighing on average 17-22 g, however plumage and a long forked tail on Barn Swallows make it easy to visually distinguish the two species (Brown and Brown 1999, Winkler et al. 2011). Barn Swallow females and males have steely blue upperparts and rufous coloured underparts (although males have darker underparts and longer tail streamers), while Tree Swallow males and females have iridescent blue upperparts, and white underparts, but younger females have typically dusky brown upperparts (Brown and Brown 1999, Winkler et al. 2011). Swallows are part of the Hirundinidae family, known for their hawking flight styles, but there are several life history parameters that differentiate the two species. Barn Swallows build open-cup mud nests, often on man-made structures such as buildings or under bridges and commonly nest in relatively large colonies, providing a large number of nests to monitor. Tree Swallows are secondary-cavity nesters, and commonly use man-made nest boxes, making them an ideal study species. Both are considered migrant species, however Barn Swallows winter as far as southern South America and are considered long-distance migrants, although western breeding populations of Barn Swallows (from Washington state and Saskatchewan) have been found wintering further north, from Oregon to Colombia (Hobson et al 2015). Tree Swallows typically over-winter in Mexico and Central America and are classified as short-distance migrants (Winkler et al. 2011). Barn Swallows arrive on their breeding grounds in the lower mainland of British Columbia in late March to early April, while Tree Swallows arrive earlier from mid-February to the end of March (Campbell et al. 1997). Another major life-history difference between the two species is that Barn Swallows are multi-brooded, producing on average two broods each season (Turner 2006), while Tree Swallows typically only lay a single brood in a season (Winkler et al. 2011).

Study system and focus of thesis

In this thesis we examined reproductive success, phenology, post-fledging habitat use and survival in two co-occurring aerial insectivores, Barn Swallow and Tree Swallows. The study system consisted of eleven different sites located in the lower mainland of BC, Canada (49°10'8.15"N, 123° 5'58.60"W) and is an ideal area to study these two species as they co-occur naturally where Barn Swallows breed on man-made structures and Tree Swallows breed in man-made nest boxes. Therefore, at the beginning of this study in 2013, nest boxes were set up for Tree Swallows at eleven sites throughout the lower mainland where Barn Swallows were already naturally breeding. Of the eleven sites, three were classified as non-agriculture habitats (a park, marina and works yard), four sites deemed livestock habitat (with both horses and cows) and the remaining four were cropped agriculture habitats (multiple crops including peas, beans potatoes, corn, barley, several squash varieties and strawberries).

The second chapter focuses on reproductive success, annual variation and factors influencing these two variables, particularly weather and landscape type, comparing Tree Swallows and Barn Swallows. Our two main objectives were, 1) to determine if there is species-specific and annual variation in breeding phenology (lay date, number of broods), clutch size and breeding productivity (brood size at fledging and fledging success) that might help explain differences in population trajectories of Barn and Tree Swallows (Michel et al. 2015), and 2) to determine if weather and habitat (crop, livestock or non-agriculture) were potentially important factors in explaining within- and between-species variation in reproduction. Chapter three examines post-fledging habitat use, survival rates and influencing factors in Barn Swallows. Our main objectives for this chapter were, 1) to determine if natal habitat has an effect on post-fledgling behaviour and chick quality (variation in fledge date, mass, tarsus, wing, brood size, maximum days since fledged and maximum distance travelled from the nest), 2) to quantify habitat used by post-fledglings relative to availability and 3) determine post-fledging survival rates over two years. In the last chapter we summarize the findings of this study, and discuss limitations, conservation recommendations and future studies.

Chapter 2. Reproductive success, phenology and weather in two co-occurring aerial insectivores

Introduction

Farmland birds have been declining across Europe and North America for several decades, with many individual species showing significant negative population trends, whereas birds found in other habitats (e.g. marine or coastal habitats) have shown fewer population changes (Donald et al. 2001, Donald et al. 2006, Conover et al. 2014). Aerial insectivores (swallows, swifts, nightjars, some flycatcher species), in particular, have been steeply declining across North America since the 1980's and in Canada this guild has declined more than any other group of birds since 1970, even more than grassland birds and shorebirds (Nebel et al. 2010, North American Bird Conservation Initiative Canada 2012, Smith et al. 2015). Although the causes of these population declines are not fully resolved, agricultural intensification (Benton et al. 2002; Paquette et al. 2013), climate and weather effects (García-Pérez et al. 2014), associated shifts in prey abundance (Nocera et al. 2012), and pesticide use, e.g. neonicotinoids (Hallmann et al. 2014), have all been suggested as mechanisms behind these population declines. In general, a greater diversity of agricultural landscapes promotes bird biodiversity and species richness (Conover et al. 2014), however many farms have shifted to a less diverse, more intensively managed, agricultural landscape leading to a decrease in avian food supplies, including seeds and invertebrates (Fuller 2000). Areas of lower management intensity also support more specialist species of farmland birds and higher bird abundance, indicative of a need for less intensive management of agroecosystems (Doxa et al. 2010). Overall, insect abundance is greater in areas with native vegetation and insect richness is greater in less intensively managed agricultural fields (Attwood et al. 2008). Differences among agricultural habitats and changes in crop type are therefore also linked to changes in the abundance of insects with higher numbers of insects found over pasture compared to cereal fields, which could affect aerial insectivore foraging (Evans et al. 2007).

Climate change, and shorter-term weather effects might also be negatively impacting aerial insectivores. Lay date has increased in association with increasing spring temperature in 19 long-distance migrants, including Barn Swallows (*Hirundo*

rustica; Ockendon et al. 2013) and over a thirty-year period Tree Swallow (*Tachycineta bicolor*) hatch and lay dates have advanced by several days (6 and 4 days, respectively; Irons et al. 2017). In addition to temperature, changes in wind speed and precipitation have also been implicated in changing breeding phenology (Irons et al. 2017). Due to their reliance on flying insects, foraging in aerial insectivores can be strongly affected by abiotic factors, which can drive changes in insect abundance: higher temperature increases insect abundance but higher precipitation decreases it (Paquette et al. 2013, Gruebler et al. 2008). Insect abundances for foraging aerial insectivores can therefore vary day to day (McCarty and Winkler 1999), especially in the spring months (Bryant 1975). Bryant (1975) showed that temperature, rainfall, wind intensity and duration and hours of sun radiation explained 50% of variation in insect abundance.

There is evidence that at least some populations are declining across all species in the guild of aerial insectivores (North American Bird Conservation Initiative Canada 2012). However, there are some differences between taxa: species that use a hawkler foraging strategy (swifts, swallows and nightjars) are experiencing greater, and more widespread, population declines than those species that use sallier foraging strategies (flycatchers; Smith et al. 2015). In addition, some studies suggest there is geographic variation in population declines, where aerial insectivores as a guild are declining more in the northern and eastern portions of North America compared to western breeding areas (Nebel et al. 2010). A recent analysis by Michel et al. (2015) suggested that there might not be a single, global cause for all aerial insectivore population declines. In co-occurring aerial insectivore species there is only weak correlation in population trajectories, e.g. Tree Swallows and Barn Swallows in the Pacific Northwest region show dissimilar spatio-temporal population trajectories (Michel et al. 2015). Tree Swallows have experienced a smaller decline in annual abundance across Canada (-1.8 annual trend index) and in the Northern Pacific Rainforest (NPR) region of British Columbia (-4.33 annual trend index) compared to Barn Swallows (-3.28 annual trend index in Canada, -5.19 annual trend index in NPR region of BC; Environment and Climate Change Canada 2017). Thus, Tree Swallows show stronger trends in breeding population decline in the north east, but appear relatively stable across the rest of North America, while Barn Swallows show an overall greater decline across North America (Michel et al. 2015). In addition, Barn Swallows are currently listed as Threatened in Canada under COSEWIC (COSEWIC 2011), whereas Tree Swallows have not received

any at-risk designation. This suggests there might be highly variable, and complex, spatio-temporal patterns of population change, perhaps related to region-specific interactions of breeding phenology, productivity and environmental conditions such as changing weather or land use. However, there is currently a lack of empirical evidence to address what region-specific factors might underpin population changes for aerial insectivores in the Pacific Northwest.

In this study, we compared and contrasted breeding phenology and breeding productivity in two co-occurring aerial insectivores, Barn Swallows and Tree Swallows, in relation to habitat and weather over 4 years in the lower mainland, British Columbia. We did this by establishing nest-box breeding populations of Tree Swallows at each of 11 sites in three different habitat types (crop, livestock, and non-agricultural) where there were already naturally-established breeding colonies of Barn Swallows. We predicted that if Barn Swallows are declining at a greater rate than Tree Swallows in the Pacific Northwest region then, a) Barn Swallows will have lower reproductive potential (shorter breeding season) and lower breeding productivity (smaller clutch size, lower fledging success, and smaller brood size at fledging), b) Barn Swallows will be more susceptible to changes in habitat which influence breeding productivity compared with Tree Swallows, for example, in Europe presence of livestock increases population density and breeding productivity of Barn Swallows (Ambrosini et al., 2012; Gruebler et al., 2010), but in BC there has been a province-wide trend of declines in cattle farming (-38% in livestock farms and number of cattle since 2001 (Statistics Canada 2012; Metro Vancouver 2014) and, c) Barn Swallows will not respond or will respond negatively compared to Tree Swallows to annual variation in temperature, rainfall or wind, and in terms of the effects these climate variables have on breeding phenology or productivity. Our two main objectives were therefore, 1) to determine if there is species-specific and annual variation in breeding phenology (lay date, number of broods), clutch size and breeding productivity (fledging success and brood size at fledging) that might help explain differences in population trajectory of Barn and Tree Swallows (Michel et al. 2015), and 2) to determine if weather and habitat (crop, livestock or non-agriculture) were potentially important factors in explaining within- and between-species variation in reproduction.

Methods

Study area

Field work was conducted in the lower mainland of British Columbia, Canada (49°10'8.15"N, 123° 5'58.60"W) from 2013 to 2016. In 2013 Barn Swallow nest sites (Fig. 2.1) were chosen, with a minimum distance between sites of 500 meters. Tree Swallow boxes were put up 5 meters apart around each site (n = 10 for all sites initially, except Sea Island n = 8). A total of 11 nest sites were used each year, categorized into three landscape types; agriculture with crop (hereafter, crop), agriculture with livestock, including both cows and horses (hereafter, livestock) and non-agriculture. Non-agricultural sites (n=3) included a park, a marina and a municipal works yard. The number of nests per site and year were variable, with a total number of 1046 active nests (nests with at least one egg) for Barn Swallows and 219 for Tree Swallows for all years combined.

Nest monitoring

Barn Swallow nests were checked twice a week from late April to mid-August and Tree Swallow nests were checked twice a week from late April to mid- to late July in all 4 years. Barn Swallow nests were monitored using an iPhone camera on an extendable pole synced together via Bluetooth to an iPad, so a live video of each nest could be seen. Each time a nest was checked we recorded lay date (date the first egg was laid), clutch size, hatch date, brood size, survival to day 10, fledging success (1 = at least one nestling successfully fledged, 0 = no nestlings fledged), evidence of predation, and mite prevalence on nestlings. To age nestlings, we used an aging guide from Morales Fernaz et al. (2012) for Barn Swallow nestlings, and a nestling growth guide (<http://www.treeswallowprojects.com/cgrowth.html>) for Tree Swallows setting hatch date for both species as 0 days old. We defined nests as successful in both species if nestlings were in the nest on day 18 (minimum fledging age in both species) or if nests were empty after day 18 and there was evidence of successful fledging (such as feces in or below the nest). As Barn Swallows use open-cup nests, if eggs or chicks disappeared from the nest before day 18, predation was assumed, but an unknown predation fate

was used for Tree Swallows. A nest did not fledge successfully if all nestlings were found dead in a nest. Nest success was unknown if there was no sign of predation or successful fledge after minimum fledge age (day 18) and if nestlings were not confirmed to reach day 18 (due to end of field season or observations of that nest). We estimated reproductive success in two ways, by examining the fledging success of each nest (at least one chick left the nest alive; 1 = successful nest, 0 = failed nest) and brood size (number of nestlings) within a nest (best estimate closest to fledge date) for successfully fledged nests.

Breeding phenology and annual variation in productivity

While breeding data were collected as consistently as possible throughout the four field seasons, there was some uncertainty around lay dates, hatch dates, and breeding outcome (success/failure, brood size), as well as whether clutches or broods represented 'true' first or second nesting attempts or replacement clutches/broods. For our main analysis (see below) we needed to compare true 'first' clutches or broods between species, therefore, we came up with a set of rules for back-calculating estimated lay dates (first egg dates) where these were unknown but where hatch dates were known, and for assigning clutches or broods as first, replacement or second.

For Barn Swallows, which are multi-brooded, we first calculated the mean interval between lay date and hatch date, for different clutch sizes, for nests where both these dates were known precisely (± 1 day). Based on these data we estimated lay date as (hatch date - 18 days) for clutch sizes ≤ 4 eggs, and as (hatch date - 19 days) for clutch sizes of ≥ 5 eggs, for nests where only hatch dates were precisely known. We then calculated the 5-95% quantile range of lay dates for 'true' first and second clutches based on a sub-sample of individual nests where a second clutch followed successful fledging of chicks from a first clutch in the same nest (Table 2.1). Any "unknown" nest with a lay date less than the 95% quantile Julian date for first clutches (e.g. 157 for 2013, Table 2.1) was assigned as a first clutch/brood. Similarly, any unknown nest with a lay date greater than the 5% quantile Julian date for second clutches (e.g. 180 for 2013, Table 2.1) was assigned as a second clutch/brood. Any unknown nest with a lay date falling between these dates (i.e. 158-179) was assigned as a replacement clutch/brood.

Tree Swallows are generally thought to be single-brooded especially at higher latitudes, although they will lay replacement clutches after nest failure (Winkler et al. 2011). Our data confirm this (see Results) and we only had a small sample size of known replacement nests (a new nest in the same box after failure, $n = 10$) or known second broods (a second nest in the same box after successful fledging of first brood chicks, $n = 9$). Therefore, we used a cut-off for 'true' first broods of Julian date = 142 (May 22) based on the range of lay dates in Ontario (Winkler et al. 2011). This matched well with the tail of the first peak of lay dates for Tree Swallows in each year in our study (see Results and Fig. 2.2). Unknown nests were then assigned as second broods if their lay dates were greater than the 5% quantile lay date for the small sample of known second broods (Julian date = 180 for 2014 and 173 for 2016; no data for other years). Any unknown nest with a lay date falling between these dates (i.e. 143-180 or 143-173) was assigned as a replacement clutch/brood.

Weather data

We obtained historical weather data from Environment and Climate Change Canada (<https://vancouver.weatherstats.ca>) for all four years (2013-2016) from a Vancouver weather station (YVR Airport, 49°11'42.000" N, 123°10'55.000" W, elevation 4.30 m) since our sites were spread around the Metro Vancouver area. We analyzed data on average daily temperature (°C), average daily precipitation (mm) and average daily wind speed (km/hr). We calculated averages for a) the pre-laying period, either 2 or 4 weeks (to account for nest-building period and arrival on breeding grounds) before the first egg date for each species in each year (see Table 2.2), and b) for the month of June (Julian dates = 152-181) which coincided with the main chick-rearing period for first broods in both species.

We also conducted an analysis of potentially smaller-scale effects of weather by identifying several putative high-nest failure events. We identified high-nest failure events by looking for anomalies in the normal unimodal or bi-modal distribution of laying dates for Tree Swallows and Barn Swallows, respectively (see asterisks in Fig. 2.2). We assumed these represented new peaks of laying of replacement clutches due to periods of poor weather causing abandonment of eggs or nestlings. We then used data on

known re-laying intervals (e.g. 185 in 2013; Table 2.1) to back calculate a range of dates where nests would have failed (leading to the peak of replacement nests). We calculated average temperature and average wind speed for these periods and compared them with the overall averages for the complete chick-rearing period (June) in all years.

Statistical analysis

Modeling and statistical analysis was conducted using R (version 1.0.136, RStudio Team, 2016). Frequency distributions of count data were analyzed using chi-square, and those for binomial data (0/1), specifically fledging success were analyzed using chi-square and logistic regression.

Although we set up nest boxes for Tree Swallows at each of the three non-agricultural sites, most boxes were used by Violet-Green Swallows (*Tachycineta thalassina*), limiting Tree Swallow data to only 1 of 4 years. Therefore, we restricted analysis of lay date, clutch size, brood size at fledging and fledging success to crop and livestock habitats only, and ran separate analyses for non-agricultural sites where we had sufficient data for specific comparisons (Table 2.2, 2.3). We also restricted analysis to first broods in order to equally compare the two species. We used linear mixed effects models (nlme) and initially ran full models with species, year and habitat as main effects, all 2-way and 3-ways interactions, with nest ID nested within site as a random effect. We then deleted non-significant terms and report significant effects for final reduced models. We estimated overall main effects using anova (fit = marginal) and calculated lsmeans and conducted pair-wise multiple comparisons with Tukey-adjusted P values. For clutch size and brood size at fledging we restricted analysis to nests where these variables were known with certainty. We also included lay date as a covariate in clutch size models, as clutch size is known to decrease over the season. We calculated breeding productivity based on successful fledging of 1+ chick (1 = successful nest, 0 = failed nest) and analyzed these data using chi-square tests, and if significant we followed up with a logistic regression using fledging success as a main effect, family = binomial. For brood size at fledging (of only successful nests) we only compared years 2014-16, because in 2013 there were only 3 Tree Swallow nests with known brood size, of which

all were in agriculture. Again, we ran this analysis separately for (crop and livestock), and non-agricultural habitats.

For weather data we first tested for annual variation in each weather variable (temperature, rainfall, wind speed) for the pre-laying periods (2 and 4 weeks before the first recorded egg) and the chick-rearing period (June) using ANOVA. We then compared the averages for weather variables with first and average lay dates and clutch size for each species and year combination and June weather with brood size for each species. We tested average weather and breeding variables two ways: a) over four years ($n = 4$) using Pearson's correlation test, and b) over all sites for each year with species pooled ($n = 44$ for each species) using linear mixed effects models, with breeding variables (see above) as fixed effects compared to average weather variables (see above) with a species interaction, and site as a random factor. For small-scale weather effects we plotted the average temperature and average wind speed for each nest failure event ($n = 6$) to visually compare variance (standard deviation) in relation to the overall average temperature and wind speed.

Results

Species variation in breeding phenology

Barn Swallow lay dates displayed a strong bimodal pattern in all 4 years, with first peaks around May 20 (Julian date 140; range 137-142) and second peaks around July 7 (Julian date 188; range 181-191). In contrast, Tree Swallows showed a unimodal pattern of lay dates in each year with a peak around May 14 (Julian date 134; range 130-138; Fig. 2.2). Barn Swallows therefore had a longer breeding season when comparing duration between minimum and maximum lay dates. Barn Swallows initiated first broods over a period of 23-28 days, whereas Tree Swallows initiated first broods over only 12-20 days (Table 2.2). Barn Swallows initiated second clutches up to Julian date 215 (August 3; latest lay date from all active nests), while Tree Swallows only initiated clutches until Julian date 183 (July 2; latest lay date from all active nests). The total range of dates, based on 5-95% quantiles, over which nests were initiated was

therefore much longer in Barn Swallows (mean 63 days, range 60-67 days) compared with Tree Swallows (mean 39 days, range 31-53 days).

Overall, there was a highly significant difference in the frequency distribution of nesting attempts classified as first, replacement and second clutches/broods between species ($\chi^2_2 = 77.0$, $p < 0.001$; Table 2.4). Thirty-four percent ($n = 351/1046$) of Barn Swallows nests had a second brood across all four years, with the highest number in 2016, where forty percent of the total number of nests had a second brood ($n = 92/230$; Table 2.4). Second broods for Tree Swallows nests were rare ($n = 13/219$; 6%) and were only recorded in 2014 -16 (Table 2.4). The estimated frequency of replacement broods across the four years was very similar in the two species and only accounted for twenty-one percent ($n = 222/1046$) of Barn Swallow nests and twenty percent ($n = 45/219$) of Tree Swallow nests.

Variation in lay date

Lay date for first broods varied between species ($F_{1,301} = 169.55$, $p < 0.001$; Fig 2.3), and across years ($F_{3,171} = 33.01$, $p < 0.001$; Fig 2.3) in crop/livestock habitat, but there was no effect of habitat ($F_{1,100} = 0.0$, $p = 0.97$) and no two-way or three-way interactions were significant in the full model ($p > 0.18$ in all cases). Across the years, Tree Swallows laid on average 7.8 days earlier than Barn Swallows (average Julian lay date = 133.9 ± 0.66 vs. 141.7 ± 0.3 , or May 13 and May 21, respectively) and average lay date was 6-9 days earlier in Tree Swallows compared with Barn Swallows in each of the four years ($p < 0.001$ in all cases; Table 2.2). Overall, average lay date was 6.2 days earlier in 2016 (Julian date 134.6 ± 0.5) compared with 2013 (140.8 ± 0.9 ; $t_{171} = 6.65$, $p < 0.001$) with lay date in 2014 and 2015 being intermediate, and this same pattern occurred in both species (Table 2.2). There was no difference in lay date between species in 2014 in non-agriculture habitat ($F_{1,14} = 3.44$, $p = 0.085$).

In contrast to variation in average lay date, the first egg dates (minimum lay date) only differed by 1-2 days between species in each year (Table 2.2). However, across all first broods Tree Swallows laid more synchronously after initiation of egg-laying compared to Barn Swallows (i.e. they had a more rapid cumulative laying; Fig. 2.4).

Among years, the coefficient of variation for lay date was 4.5-7.3% in Barn Swallows compared with 2.3-3.5% for Tree Swallows.

Variation in clutch size

In the full model for clutch size of first broods there was a two-way interaction between species and year ($F_{3, 148} = 5.0$, $p = 0.003$) and a three-way interaction between habitat, species and year ($F_{3, 148} = 3.59$, $p = 0.015$). Therefore, we analyzed variation in clutch size in relation to species and year for each habitat separately, and year and habitat for each species separately.

Clutch size in crop habitat varied significantly between species ($F_{1,130} = 27.4$, $p < 0.001$) and with lay date ($F_{1,53} = 8.83$, $p = 0.005$; Fig 2.5), but there was no difference between years ($F_{3,53} = 1.70$, $p = 0.18$) and no interaction between species and year ($F_{3,53} = 1.70$, $p = 0.18$). Overall, Tree Swallows had a larger mean clutch size (5.2 ± 0.1) compared to Barn Swallows (4.9 ± 0.1) across all years ($t_{53} = -2.47$, $p = 0.017$; Table 2.3).

Clutch size in livestock habitat was different between species ($F_{1,181} = 21.23$, $p < 0.001$), and by lay date ($F_{1,94} = 6.76$, $p = 0.011$) and there was a species by year interaction ($F_{3,94} = 7.22$, $p < 0.001$), but no year variation ($F_{3,94} = 2.04$, $p = 0.11$). Overall, Tree Swallows in livestock habitat had a significantly larger clutch size (5.2 ± 0.1) compared to Barn Swallows (4.5 ± 0.1) in 2016 ($t_{94} = -4.23$, $p = 0.001$; Table 2.3), but not in other years ($p > 0.25$ in all cases). There was no difference in clutch size between species in non-agriculture habitat in 2014 ($F_{1,13} = 0.006$, $p = 0.94$).

Barn Swallow clutch size was significantly different between crop and livestock habitats ($F_{1,93} = 4.62$, $p = 0.034$) and with lay date ($F_{1,76} = 11.90$, $p < 0.001$), but there was no year effect ($F_{3, 76} = 1.14$, $p = 0.34$) and no interaction between habitat and year ($F_{3,76} = 0.70$, $p = 0.56$). Overall, average clutch size was larger in crop habitat (4.8 ± 0.7) compared to livestock habitat (4.6 ± 0.7) for Barn Swallows.

Tree Swallow clutch size was significantly different across years ($F_{3,71} = 4.30$, $p = 0.008$), with lay date ($F_{1,71} = 4.14$, $p = 0.046$) and there was an interaction between year

and habitat ($F_{3,71} = 4.0$, $p = 0.011$), but no habitat variation ($F_{1,68} = 2.62$, $p = 0.11$). Analyzing data by year, Tree Swallows had larger clutches in crop (5.8 ± 0.2) than livestock (5.0 ± 0.2) in 2014 ($F_{1,36} = 10.69$, $p = 0.002$), but there was no difference in clutch size between crop and livestock in other years ($p > 0.15$ in all cases). However, when we ran a pairwise comparison of year and habitat, none of the habitat contrasts were significant in any year ($p > 0.14$ in all cases at the Tukey-corrected p value).

Variation in breeding productivity

Fledging success was significantly different across years ($X^2_3 = 14$, $p = 0.003$), but not between species ($X^2_1 = 2.9$, $p = 0.088$) or crop/livestock habitat ($X^2_1 = 0.37$, $p = 0.54$). Fledging success was lower in 2014 ($z_{569} = -2.44$, $p = 0.015$), 2015 ($z_{569} = -3.39$, $p < 0.001$) and 2016 ($z_{569} = -3.23$, $p = 0.001$) compared to 2013, with 22-28% of nests failing to fledge from 2014-16 vs. 9.9% of nests failing to fledge in 2013. There was no difference in fledging success between species in non-agriculture habitat in 2014 ($z_{17} = -0.004$, $p = 1.0$).

There was a significant species*year interaction for brood size at fledging in the full model ($F_{2,29} = 5.53$, $p = 0.009$) and an effect of year ($F_{2,29} = 5.42$, $p = 0.01$), but no main effect of species or habitat ($p > 0.36$ in both cases) and no other 2-way or 3-way interactions were significant ($p > 0.42$ in all cases). We ran a pairwise comparison of year and species, but none of the species contrasts were significant in any year ($p > 0.12$ in all cases at the Tukey-corrected p value). Therefore, we analyzed data by year (2014-16) without Tukey corrected p -values, and found Barn Swallows had higher brood size at fledge in 2014 (4.5 ± 0.6 vs. 3.8 ± 1.3 ; $F_{1,48} = 8.09$, $p = 0.007$), there was no difference in 2015 ($F_{1,62} = 2.02$, $p = 0.16$), and in 2016 Tree Swallows had a larger brood than Barn Swallows (4.1 ± 1.2 vs. 3.5 ± 1.1 ; $F_{1,66} = 4.52$, $p = 0.037$). However, in a model with species, year and a species by year interaction, none of these pairwise contrasts of brood size at fledge by year were significant with the Tukey-corrected p value ($p > 0.19$). There was no difference in brood size in 2014 in non-agriculture habitat ($F_{1,8} = 0.25$, $p = 0.63$).

Broad-scale weather effects on phenology and breeding productivity

Average temperature varied significantly across years based on Barn Swallows first egg dates in the 2-week pre-laying period ($F_{3,56} = 3.18$, $p = 0.031$) and 4-week pre-laying period ($F_{3,112} = 5.33$, $p = 0.002$), but there was no difference in average wind speed or average rain for either period ($p > 0.066$ in all cases). The lowest temperature was recorded in 2015 during the 2-week (10.7 ± 1.7 °C) and 4-week period (9.99 ± 1.7 °C) and highest temperature was in 2016 during the 2-week (13.1 ± 2.0 °C) and 4-week period (12.0 ± 2.0 °C), with average temperature in 2013 and 2014 being intermediate over both periods (2-week: 11.8 ± 2.7 °C, 12.0 ± 1.9 °C; 4-week: 10.3 ± 2.7 °C, 11.0 ± 1.8 °C). Average temperature also varied significantly during the Tree Swallow 4-week pre-laying period ($F_{3,112} = 5.84$, $p < 0.001$), but average rain ($F_{3,112} = 1.87$, $p = 0.14$) and average wind speed ($F_{3,112} = 0.29$, $p = 0.83$) did not vary, and there was no difference in average temperature ($F_{3,56} = 1.66$, $p = 0.19$), average rain ($F_{3,56} = 2.66$, $p = 0.057$) or average wind speed ($F_{3,56} = 0.26$, $p = 0.85$) during the 2-week pre-laying period. During the 4 week pre-laying period for Tree Swallows the lowest temperature was recorded in 2015 (10.0 ± 1.7 °C) and the highest in 2016 (12.0 ± 2.0 °C), while 2013 (10.3 ± 2.7 °C) and 2014 (11.0 ± 1.8 °C) were relatively similar.

Average temperature ($F_{3,116} = 6.74$, $p < 0.001$; Fig 2.5a) and average wind speed ($F_{3,116} = 2.73$, $p = 0.047$; Fig 2.6b) varied significantly across years in the chick-rearing period (June), but there was no difference in average rain ($F_{3,116} = 1.45$, $p = 0.23$). Average temperature during the chick-rearing period was highest in 2015 (17.8 ± 2.2 °C), lowest in 2014 (15.7 ± 1.4 °C) and intermediate in 2013 (16.3 ± 2.0 °C) and 2016 (16.1 ± 2.1 °C). The windiest year was in 2015 (15.3 ± 4.4 km/h), while 2013 had the lowest wind speed (12.6 ± 3.6) and 2014 (13.6 ± 3.5) and 2016 (13.9 ± 3.0) were intermediate years (Fig 2.6).

Average wind speed during the chick-rearing period (June) across 4 years ($n = 4$) was positively correlated with brood size at fledging for Tree Swallows ($t_2 = 5.22$, $p = 0.035$, $\text{cor} = 0.97$; Fig 2.7a), but not Barn Swallow brood size at fledging ($t_2 = -0.26$, $p = 0.82$, $\text{cor} = -0.18$; Fig 2.7b), and there was no correlation in the average June temperature for either Tree Swallow brood size at fledging ($t_2 = 1.10$, $p = 0.38$), or Barn Swallow brood size at fledging ($t_2 = -0.35$, $p = 0.76$). There were no correlations between

average temperature and average lay date across four years ($n = 4$) in the Barn Swallow 2-week pre-laying period ($t_2 = -0.58$, $p = 0.62$), Barn Swallow 4-week period ($t_2 = -1.16$, $p = 0.37$), Tree Swallow 2-week period ($t_2 = -0.80$, $p = 0.51$) and Tree Swallow 4-week period ($t_2 = -0.90$, $p = 0.47$). For first egg date and clutch size over four years there was no correlation across any pre-breeding period for either species ($p > 0.23$ in all cases).

Comparing across sites and years ($n = 44$ for each species), average lay date varied significantly with average temperature in the 2-week pre-laying period ($F_{1,60} = 4.67$, $p = 0.035$), but there was no species effect ($F_{1,60} = 0.29$, $p = 0.59$), and no species by year interaction ($F_{1,60} = 0.004$, $p = 0.95$). Similarly, during the 4-week period, average lay date varied significantly with average temperature ($F_{1,60} = 14.11$, $p < 0.001$; Fig 2.8) and species ($F_{1,60} = 4.08$, $p = 0.048$), but there was no species by year interaction ($F_{1,60} = 2.02$, $p = 0.16$). First egg date varied significantly with average temperature ($F_{1,60} = 5.71$, $p = 0.02$; Fig 2.8) in the 4-week period, but there was no effect of species ($F_{1,60} = 0.29$, $p = 0.59$), no two-way interaction ($F_{1,60} = 0.11$, $p = 0.74$), and no variation in the 2-week period ($p > 0.32$ in all cases). Average clutch size did not vary with temperature, between species and there were no two-way interaction during the 2-week ($p > 0.12$ in all cases) or 4-week period ($p > 0.071$ in all cases). Average brood size at fledging did not vary by June temperature ($F_{1,53} = 0.20$, $p = 0.66$), or species ($F_{1,53} = 1.24$, $p = 0.27$) and there was no average temperature and species interaction ($F_{1,53} = 1.23$, $p = 0.27$). Brood size at fledging also did not vary with average wind speed ($F_{1,53} = 0.002$, $p = 0.97$), between species ($F_{1,53} = 2.23$, $p = 0.14$) and there was no interaction between average wind speed and species ($F_{1,53} = 2.20$, $p = 0.14$).

Small-scale weather effects and nest failure

We looked at a total of 4 nest failure events (2013, 2014 and 2 in 2016) for Barn Swallows, and 2 nest failure events (2014, 2016) for Tree Swallows (indicated by asterisks in Fig. 2.2). Average temperature and wind speed across all events were similar to overall average temperature and average wind speed (Fig. 2.9), suggesting a period of harsh weather cannot account for nest failure periods.

Discussion

We compared annual variation in breeding phenology, reproductive success and the effect of weather and habitat in two co-occurring aerial insectivores, Barn Swallows and Tree Swallows, which could help explain differences in population trajectory (Michel et al. 2015). There was significant variation in overall breeding phenology between species as well as annual variation in lay date. Barn Swallows had a strongly bi-modal breeding pattern in all four years with second broods accounting for 29-40% of all nesting attempts. In contrast, Tree Swallows were largely single-brooded with 0-12% of all nesting attempts classified as second broods across the 4 years. Average lay date varied among years, in both species, with 2016 being the earliest year and 2015 the latest year. However, absolute differences between years were relatively small: 6.9 and 6.6 days between earliest and latest years in Barn Swallows and Tree Swallows, respectively. Average lay dates for first broods were earlier in Tree Swallows than Barn Swallows all 4 years, by 6-9 days. However, the difference between species in first egg dates of the earliest nests were much less (1-2 days) and there was evidence for more rapid cumulative onset of egg-laying across all first broods in Tree Swallows.

In addition to these differences in breeding phenology, there was variation in clutch size between species, year and habitat. Tree Swallows had a larger average clutch size than Barn Swallows in crop habitat across years, but only in one year (2016) in livestock habitat. For Barn Swallows, average clutch size was larger in crop than livestock habitat, while for Tree Swallows clutches were larger in crop than livestock in only 1 of 4 years, although these results were minimally significant. There were little interspecies differences in breeding productivity (fledging success, brood size at fledge), but there was a small species and year interaction in brood size and annual variation in fledging success. Fledging success varied across years, with 2013 having higher fledging success than other years, but there were no species or habitat differences. Average brood size at fledging was greater in Barn Swallows compared to Tree Swallows in 2014, larger in Tree Swallows in 2016, but not different between species in 2013, with these results being minimally significant. Finally, there was significant annual variation in average temperature and average wind speed among the four years during June and variation in average temperature across the 2 and- 4 week pre-laying period. However, the warmest, windiest June and coldest pre-breeding year (all in 2015) did not

correspond with annual differences in breeding phenology or productivity in either species. When comparing across species and years, warmer Spring temperatures were associated both with earlier average lay dates and first egg dates, suggesting both species had the capacity to adapt to variation in early season temperatures. Overall, we found evidence for relatively few interspecies differences between Barn Swallows and Tree Swallows, and local weather impacted both species similarly, and therefore these minor interspecies differences could be driven by variation in foraging habitat. In addition, it is more likely that larger population variation suggested by Michel et al. (2015) between the two species is driven by variation in survival during the post-fledging period, migration or on the wintering grounds.

Over our four year study period (2013-16) Barn Swallows showed a strong bimodal pattern of lay date and 34% of nesting attempts were classified as second broods. While less is known about Barn Swallows in western Canada, compared to Europe, over a third of Barn Swallow nesting attempts were considered second broods, which is similar to other studies of marked individuals across North America (Turner 2006) and in British Columbia (Campbell et al. 1997), although we did not mark individuals in our study. In contrast, Tree Swallow nests rarely had nests with two broods (6%) and nesting attempts classified as second broods occurred only in 3 of the 4 years. Other studies have also found Tree Swallows to be predominantly single-brooded at higher latitudes within North America, such as New York (Winkler et al. 2011).

Tree Swallows bred on average one week earlier than Barn Swallows each year. Barn Swallows are long-distance migrants, and winter in southern Mexico and throughout South America (Brown and Brown 1999), although western breeding populations of Barn Swallows (from Washington state and Saskatchewan) have been found wintering further north, from Oregon to Colombia (Hobson et al. 2015). Tree Swallows, which are short-distant migrants, winter from southern United States to Central America (Winkler et al. 2011). A longer migratory distance could account for Barn Swallows arriving later on the breeding grounds and subsequently their later average lay dates. However, our first lay date records indicated that across years, both species initiate breeding 1-2 days apart, and Tree Swallows have a much shorter breeding period (only considering first broods) than Barn Swallows, which explains their earlier average lay dates and further refutes our first prediction. Regardless, this is a puzzling result, as Barn Swallows are a multi-brooded species and we would predict that

the majority of pairs (rather than a few) would start laying earlier to fit in two broods and to compensate for the greater distances they travel to their wintering grounds. However, due to their longer migration, there could be greater variation in breeding condition upon arrival and therefore first egg dates are more spread out. In addition, as Barn Swallows are long-distance migrants they are more likely to be exposed to higher mortality and therefore double-brood to compensate, whereas Tree Swallows likely experience lower mortality rates due to shorter migration and therefore trade-off costs of reproduction for survival. The only other study to compare reproductive biology of these two species found lay dates between the two species to be similar, although their sample sizes were relatively small and only over one year (Ramstack et al. 1998). This study was conducted at a lower latitude (New York) than ours, and it is possible that similar lay dates are due to shorter distances from the Barn Swallow wintering grounds to breeding grounds in this area. In addition, the study was conducted over twenty years ago, and it is therefore also possible that while both species may have advanced their lay dates, Tree Swallows have adapted to breed more synchronously at the beginning of the breeding season compared to Barn Swallows.

Lay date showed significant variation across our four-year study period (2013-16). From 2013-16 the average lay date advanced a total of 6.9 days in Barn Swallows and 6.6 days in Tree Swallows, while the first egg date increased by 5 days in Barn Swallows and 6 days in Tree Swallows, although the latter were not significant trends given we only had 4 years of data. Earlier breeding associated with climate change has been documented in both species. In Eastern Germany Barn Swallows have advanced their average breeding date by 2.5 days from 1997-2010 (Grimm et al. 2015) and Tree Swallows have advanced their average lay date by 4-6 days over a 16 year period in Alaska (Irons et al. 2017) and a total of 9 days from 1959-1991 across North America (Dunn and Winkler 1999). There is general consensus that these earlier breeding dates are caused by variation in local weather conditions, specifically warmer temperatures due to climate change (Dunn and Winkler 1999, Bowers et al. 2016) and other broad-scale weather variation, such as the North Atlantic Oscillation (Grimm et al. 2015). We found similar results when looking across species and sites where warmer local temperatures led to earlier average lay dates and first egg dates, and this trend appeared relatively consistent across both species. Barn Swallows and Tree Swallows appear to have advanced their lay dates at a similar rate over the four years, suggesting

both species are responding similarly to warmer temperatures. However, fewer pairs of Barn Swallows lay as early as Tree Swallow pairs relative to date, suggesting the majority of Barn Swallow pairs are not able to adjust as quickly to warmer spring temperatures due to longer migration and associated costs. Furthermore, Barn Swallows are less synchronous in their breeding than Tree Swallows, even though they begin laying around the same time.

In addition to variation in average lay date, average clutch size was also different between species. Tree Swallows had significantly larger clutches than Barn Swallows in crop habitat, and as well in livestock habitat in 1 year (2016), although average clutch size was overall larger in Tree Swallows and the lack of significant results in livestock could be an effect of Tree Swallows not being as well established at those sites in 2013 resulting in smaller sample sizes. This corresponds with other studies, albeit comparing birds at different sites, e.g. Tree Swallows in Ontario have an average clutch size of 5.9 (Hussell and Quinney 1985) and 5.2 in Southern Quebec (Ghilain and Belisle 2008), while Barn Swallows have an average clutch size of 4.6 across several American cities (Brown and Brown 1999). Ramstack et al. (1998) also found that Tree Swallows have larger clutches (6 eggs on average) than Barn Swallows (5 eggs on average) in one year. Although our trend is not significant across all habitats, Tree Swallows having larger clutches on average corroborates our prediction that if Barn Swallows are declining, they will have lower reproductive potential, i.e. smaller clutches, than Tree Swallows. However, Barn Swallows are also double brooded and we found no variation in brood size between species, which suggests seasonal reproductive potential is likely higher in Barn Swallows than Tree Swallows. It is also possible that Barn Swallows have smaller clutch sizes in general or due to evolutionary life history factors, but as there has been little comparative research of these two species co-occurring in the same region under the same environmental conditions, this is difficult to confirm.

It is possible that Tree Swallows have larger clutches because they consume higher quality or larger prey, perhaps related to the two species foraging in different habitats. Tree Swallows during the breeding season primarily utilize wetlands and over-water for foraging (Winkler et al. 2011), while Barn Swallows prefer open fields, pastures and the presence of livestock (Brown and Brown 1999, Gruebler et al. 2010, Evans et al. 2007). While both species breed in livestock and crop habitats, Tree Swallows may selectively forage over water and wetlands, which are in close proximity to the majority

of our field sites. If Barn Swallows are primarily foraging in agriculture (both crop and livestock), their prey sources could be more susceptible to pesticides used over crop fields, which have been shown to alter the insect community (Nocera et al. 2012), and specifically insecticides, like neonicotinoids, can deplete the abundance of aerial insects (Hallmann et al. 2014). Dissimilar foraging habitat could ultimately lead to the two species consuming different sizes and quality of prey, which could lead to smaller clutches in Barn Swallows if their prey is smaller or of lower quality (Twining et al. 2016). Furthermore, Barn Swallows forage generally at lower heights than Tree Swallows (generally no higher than 10m and primarily <1m above ground; Brown and Brown 1999), and could also be foraging on different prey in the air column even if both species use the same foraging habitat, and as suggested above, this could ultimately be related to smaller clutches. Reliance on agricultural sources of prey may leave Barn Swallows at a disadvantage if agricultural intensification reduces those prey differentially compared to aquatic aerial insects favoured by Tree Swallows.

We found relatively little evidence for strong effects of habitat on reproduction in either species. There was no effect of habitat in any models for lay date, fledging success, or brood size at fledging. For clutch size, Tree Swallows had larger clutches compared with Barn Swallows in all 4 years in crop habitat but only 1 of 4 years in livestock habitat, suggesting a positive effect of livestock habitat in terms of relative clutch size for Barn Swallows. However, when we looked within species we found that for Barn Swallows crop habitat (4.8 ± 0.7) had larger clutches than livestock habitats (4.6 ± 0.7), and Tree Swallows also had larger clutches in crop habitat, but only in 1 of 4 years, and these results were minor. These results vary from some European studies of Barn Swallows, where Moller (2001) found that Barn Swallow clutch size in Denmark was smaller in the absence of cattle. Previous studies have suggested that breeding habitat can be important for both species, with some habitats shown to be of higher quality than others for reproductive output, particularly livestock and hayfields, contrary to our results. Generally, livestock has been shown to increase the type and size of aerial insect prey available for breeding aerial insectivores (Orlowski and Karg 2013) and aerial insects have been found in higher abundances over pasture fields than other crop types, such as cereals (Evans et al. 2007). In terms of reproductive success, the presence of livestock (including pigs, chickens and cows) and manure heaps has been shown to increase the survival and annual output of nestlings in double-brooded pairs of

Barn Swallows (Grüebler et al. 2010). In addition, nestling body mass has been found to increase during the breeding season, when nestlings were in rooms with livestock, although nestling quality and brood size were not affected (Ambrosini et al. 2006). A higher proportion of both hayfields and pastures has been shown to increase the number of Tree Swallow fledglings and probability of successful fledging (Ghilain and Belisle 2008). In addition, hayfields alone (not included with pasture or livestock) surrounding a breeding site have been shown to positively affect Barn Swallow nestling mass and feather development (Sicurella et al. 2014) and Barn Swallow adults will selectively forage over hayfields within close proximity to breeding areas (< 400m; Ambrosini et al. 2002). However, in BC the number of livestock (cows, pig, horses) and area of pasture fields has declined (Statistics Canada 2012, Metro Vancouver 2014), and therefore reduced the size of 'high-quality' foraging habitat for breeding adults, which could account for clutches being larger in crop compared to livestock habitat in both species. As the majority of our study sites were near marshes or other bodies of water it is also possible that Barn Swallows and Tree Swallows in this region are supplementing their agriculture prey with aquatic insects.

Over our four year study period (2013-16), average temperature and average wind were highest in June of 2015, while the lowest average temperatures of the 2 and 4 week pre-breeding period, also occurred in 2015. This annual variation in wind and temperature, however, did not appear to impact either Tree Swallow or Barn Swallow clutch size or breeding productivity (brood size at fledge and fledge success), as there was no significant annual variation in breeding variables in 2015. Similarly, local weather did not effect Tree Swallow clutch size or the number of fledglings produced in a study in Kamloops, BC, however clutch size, number of nestlings and number of fledglings were all negatively associated with global climate effects, specifically the Southern Oscillation Index (McArthur et al. 2017). Similarly, European Barn Swallow clutch sizes were positively related to the North Atlantic Oscillation Index, however fledge success was not effected (Moller 2002). This suggests that global weather patterns not local weather, may have a greater impact on breeding biology in our region, which we did not test for in our study. Furthermore, the only evidence we found that species responded differently to local weather was that Tree Swallow brood sizes were larger with higher wind speeds in June, although these were small sample sizes. In addition, other studies found the opposite, where higher wind speeds negatively impact foraging swallows (Irons et al.

2017), perhaps confirming that our result is more likely an effect of small sample size, as we would expect to see smaller brood sizes with more windy conditions. Overall, however, we found that Tree Swallows and Barn Swallows respond similarly to local weather conditions in terms of breeding phenology.

Our results suggest that Barn Swallows in comparison to Tree Swallows have smaller clutches, later average lay dates, and are less synchronous in their timing of breeding. However, Barn Swallows are also double brooded, have similar first egg dates (only 1-2 day difference) and respond similarly to increasing spring temperatures in the Pacific Northwest region. Variation in foraging habitat during the breeding season could explain these minor interspecies differences (particularly clutch size), as Barn Swallows could be consuming lower quality or less aerial insect prey due to preference of different foraging habitat, specifically open fields and pasture, compared to Tree Swallows that prefer wetlands and water. Michel et al. (2015) showed there is variation in population trajectories in this region between Barn Swallows and Tree Swallows, but these minor interspecies differences may not account for larger population differences. Instead, different survival rates during the post-fledging period or even during migration and on the wintering grounds may be driving variation in populations of these two species. Our research is one of the few studies that has empirically compared co-occurring aerial insectivores, and we recommend further research is necessary to have a better understanding of interspecies differences, given the differing population trends. Specifically, comparisons between Barn Swallows and Tree Swallows during the post-fledging stage and exploration into each species annual survival are needed to further elucidate interspecies variation in population trajectories.

Table 2.1. Range of estimated Julian lay dates (5-95% quantiles) for Barn Swallow first broods, replacement broods (likely replacement or late first brood nests) and second broods from 2013-16 and Tree Swallow estimated first, replacement and second broods in 2014 (n=3 nests) and 2016 (n=6 nests). Due to insufficient data in 2013 and 2015 average minimum brood date in 2014 and 2016 (eg. 180, 173) were used to estimate second broods for these years.

Species	Year	First Brood	Replacement Brood	Second Brood
Barn Swallow	2013	131-157	158-179	180-201
	2014	134-154	155-180	181-204
	2015	131-152	153-175	176-199
	2016	126-150	151-175	176-202
Tree Swallow	2014	130-134	135-179	180-181
	2016	123-131	132-172	173-182

Table 2.2. Julian lay date (clutch initiation date) variation from 2013-16 for first broods of Barn Swallows and Tree Swallows, across habitat types, including average lay date across habitat types and years and the total minimum lay date across years. Julian lay dates included with standard deviation and sample size in parentheses.

Species	Year	Crop	Livestock	Non-Ag	Average Lay Date	Earliest Lay Date	Latest Lay Date
Barn Swallow	2013	144.2 ± 6.4 (39)	145.1 ± 6.2 (57)	152.9 ± 6.0 (10)	145.5 ± 6.7 (106)	129	157
	2014	142.0 ± 6.8 (48)	141.7 ± 6.2 (72)	146.1 ± 4.9 (14)	142.3 ± 6.4 (134)	131	154
	2015	140.8 ± 5.7 (48)	140.3 ± 5.9 (77)	144.9 ± 7.2 (12)	140.9 ± 6.0 (137)	127	152
	2016	138.9 ± 5.8 (35)	138.5 ± 6.7 (55)	138.2 ± 1.9 (6)	138.6 ± 6.1 (96)	124	150
	Average	141.5 ± 6.4 (170)	141.4 ± 6.6 (261)	146.3 ± 7.1 (42)	141.9 ± 6.7 (473)	127.8	153.3
Tree Swallow	2013	138.6 ± 1.7 (7)	132.7 ± 3.4 (4)	NA	136.5 ± 3.7 (11)	128	141
	2014	136.0 ± 1.9 (15)	135.7 ± 3.4 (27)	141.0 ± 2.0 (4)	136.3 ± 3.2 (46)	130	142
	2015	133.3 ± 3.4 (18)	133.4 ± 3.8 (31)	NA	133.3 ± 3.6 (49)	125	142
	2016	129.7 ± 5.2 (23)	130.2 ± 4.1 (32)	NA	129.9 ± 4.6 (55)	122	142
	Average	133.2 ± 4.9 (63)	132.9 ± 4.4 (94)	141.0 ± 2.0 (4)	133.2 ± 4.7 (161)	126.3	141.8

Table 2.3. Average clutch size (CS) and average brood size at fledging (BS) for Barn Swallow first broods and Tree Swallow first broods (lay date cut off at Julian date 142) over four years, with standard deviation and sample sizes in parentheses.

Species	Year	CS Crop	CS Livestock	CS Non-Ag	Average CS	BS Crop	BS Livestock	BS Non-Ag	Average BS
Barn Swallow	2013	4.8 ± 0.7 (35)	4.5 ± 0.8 (53)	4.4 ± 1.1 (10)	4.6 ± 0.8 (98)	3.9 ± 1.0 (10)	4.0 ± 0.8 (18)	4.4 ± 1.3 (7)	4.1 ± 1.0 (35)
	2014	4.8 ± 0.5 (46)	4.7 ± 0.6 (68)	4.7 ± 0.8 (13)	4.8 ± 0.6 (127)	4.6 ± 0.6 (19)	4.5 ± 0.6 (22)	4.7 ± 0.8 (10)	4.6 ± 0.6 (51)
	2015	4.7 ± 0.7 (44)	4.7 ± 0.7 (69)	4.4 ± 1.3 (11)	4.7 ± 0.7 (124)	3.8 ± 1.0 (13)	4.1 ± 0.9 (33)	4.2 ± 0.8 (5)	4.0 ± 0.9 (51)
	2016	4.8 ± 0.8 (32)	4.5 ± 0.8 (45)	4.5 ± 0.5 (6)	4.6 ± 0.8 (83)	3.4 ± 1.3 (18)	3.5 ± 1.0 (27)	3.0 ± 1.4 (2)	3.5 ± 1.1 (47)
	Average	4.8 ± 0.7 (157)	4.6 ± 0.7 (235)	4.5 ± 1.0 (40)	4.7 ± 0.7 (432)	4.0 ± 1.1 (60)	4.0 ± 0.9 (100)	4.4 ± 1.1 (24)	4.0 ± 1.0 (184)
Tree Swallow	2013	5.2 ± 0.8 (6)	4.0 ± 2.0 (4)	NA	4.7 ± 1.4 (10)	3.3 ± 0.6 (3)	NA	NA	3.3 ± 0.6 (3)
	2014	5.6 ± 0.6 (14)	4.9 ± 0.8 (25)	4.8 ± 0.5 (4)	5.1 ± 0.8 (43)	3.7 ± 1.4 (6)	3.0 ± 1.4 (10)	NA	3.8 ± 1.3 (16)
	2015	4.9 ± 1.4 (15)	5.2 ± 0.60 (29)	NA	5.1 ± 0.9 (44)	4.3 ± 1.5 (10)	4.4 ± 0.9 (15)	NA	4.4 ± 1.2 (25)
	2016	5.6 ± 0.9 (23)	5.4 ± 0.7 (32)	NA	5.5 ± 0.8 (55)	4.4 ± 0.9 (10)	3.9 ± 1.3 (20)	NA	4.1 ± 1.2 (30)
	Average	5.4 ± 1.0 (58)	5.1 ± 0.8 (90)	4.8 ± 0.5 (4)	5.2 ± 0.9 (152)	4.1 ± 1.2 (29)	4.1 ± 1.2 (45)	NA	4.1 ± 1.2 (74)

Table 2.4. Percent of first, replacement and second broods for Barn Swallows and Tree Swallows by year and the average across years.

Species	Brood Number	2013	2014	2015	2016	Average
Barn Swallow	First	43%	43%	53%	42%	45%
	Replacement	28%	23%	16%	18%	21%
	Second	29%	34%	31%	40%	34%
Tree Swallows	First	52%	70%	87%	72%	74%
	Replacement	48%	26%	11%	16%	20%
	Second	0%	4%	2%	12%	6%

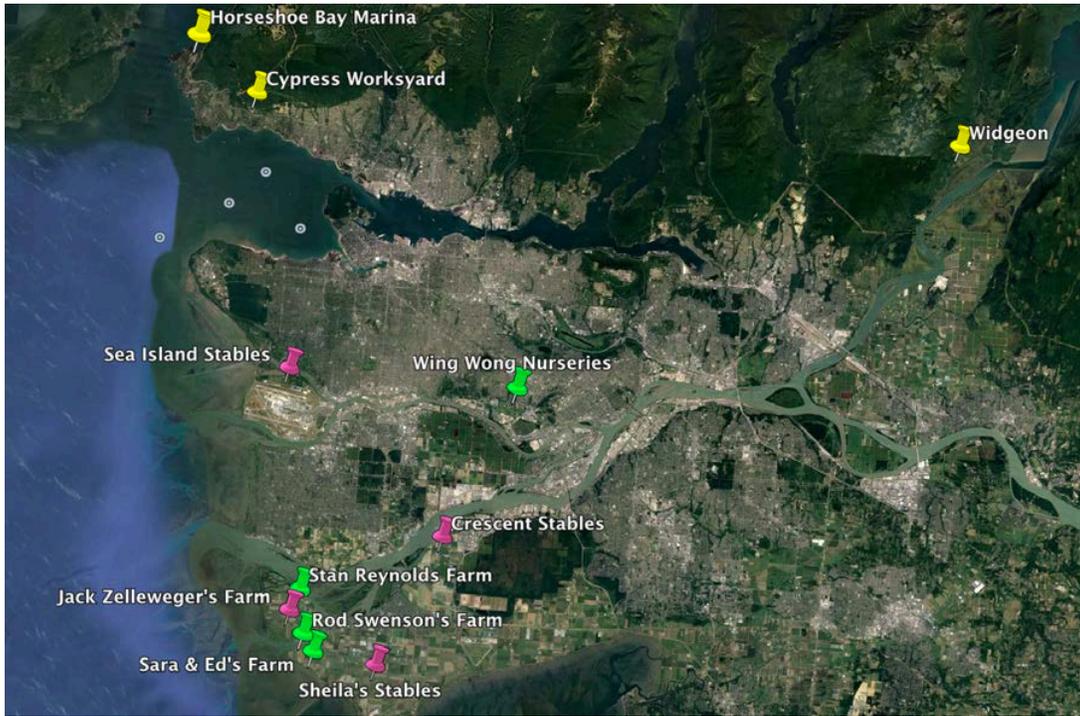


Figure 2.1. Satellite map of Barn Swallow and Tree Swallow nesting sites in the lower mainland of British Columbia ($n = 11$). Pink markers indicate livestock nesting sites ($n = 4$), green markers indicate crop nesting sites ($n = 4$) and yellow markers indicated non-agriculture sites ($n = 3$).

Map data © 2017 DigitalGlobe Data NOAA

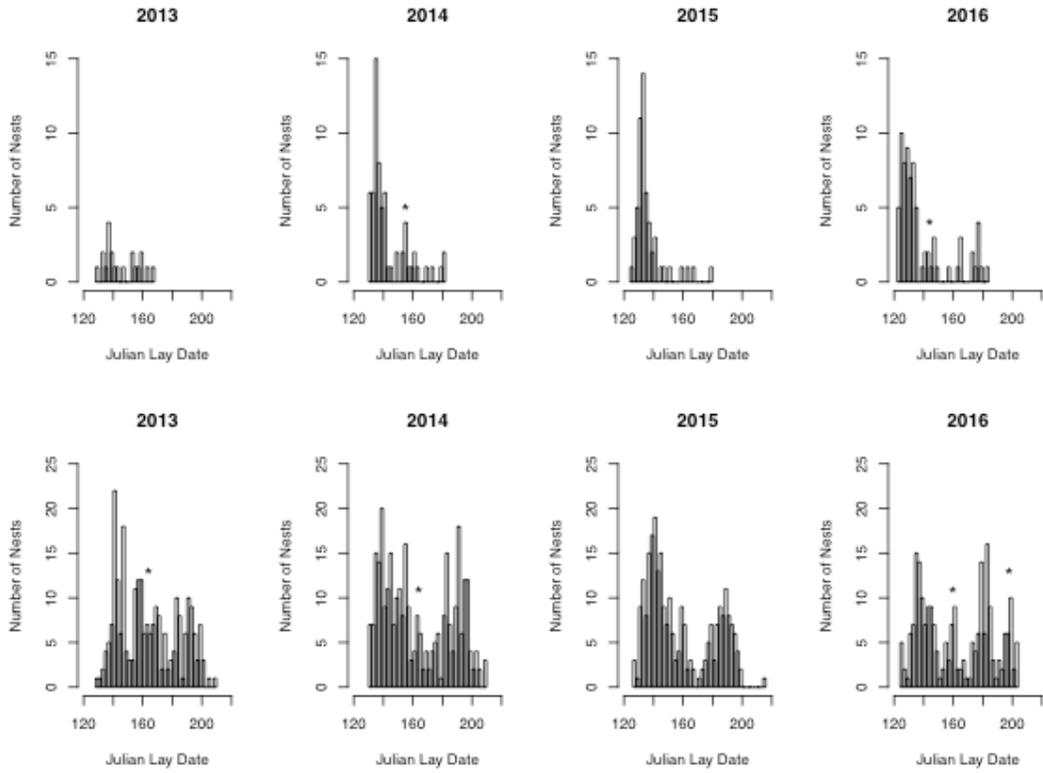


Figure 2.2. Number of nests by lay date from 2013-16 for Tree Swallows (top row) and Barn Swallows (bottom row). Includes all active nests for both species, including replacement and second broods. Asterisks indicate putative nest failure events used to examine small- scale weather effects.

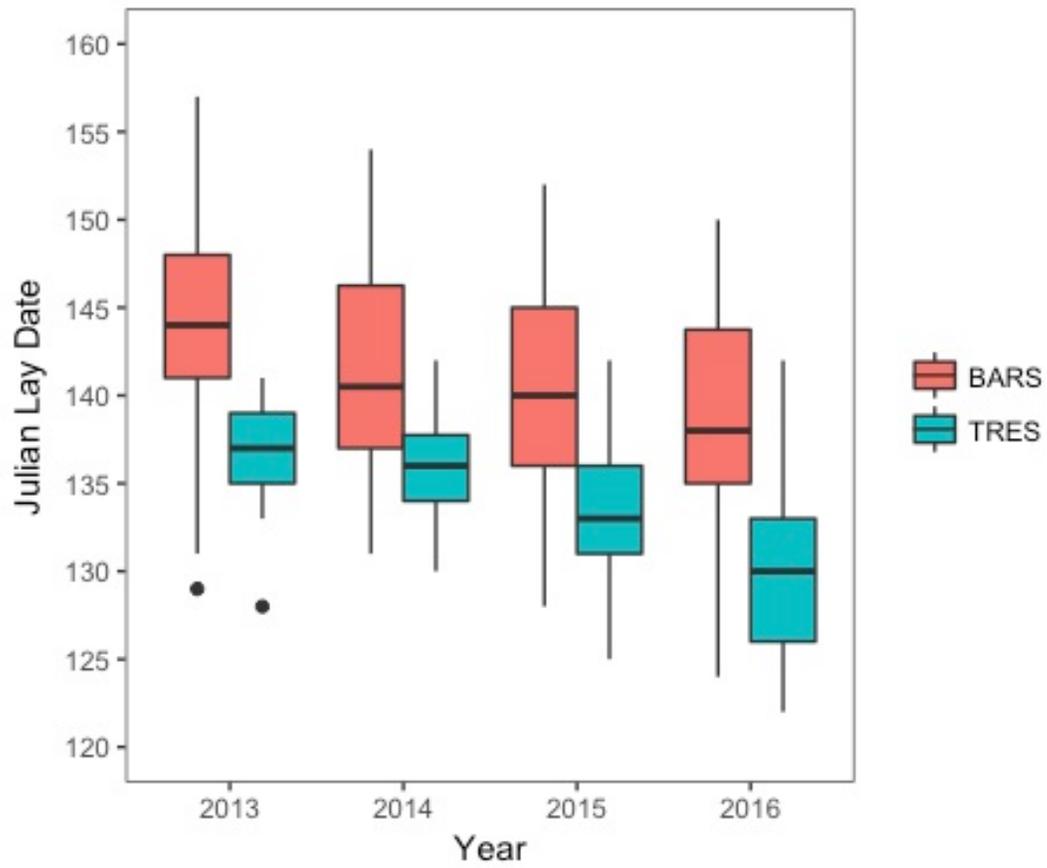


Figure 2.3. Average Julian lay date (clutch initiation dates) for first broods of Barn Swallows (red) and Tree Swallows (blue) from 2013-16.

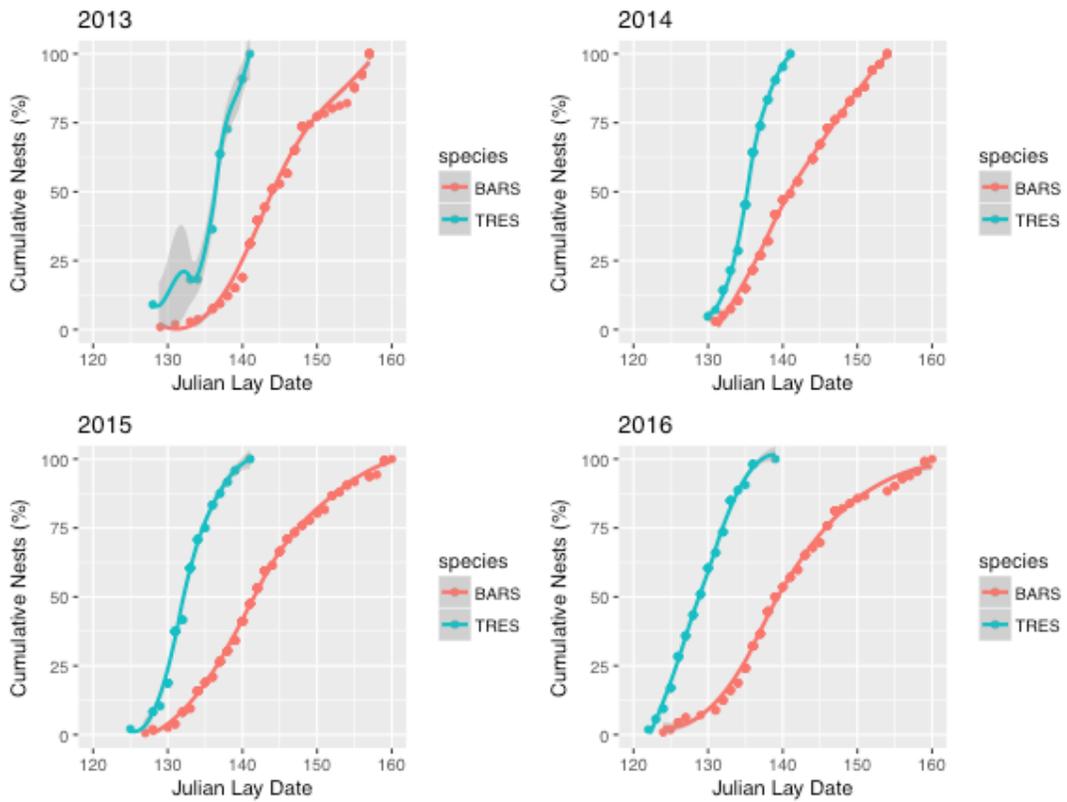


Figure 2.4. The cumulative number of nests (percent of total nests in each year) for all first broods of Barn Swallows (red points) and Tree Swallows (blue points) for all four years of study (2013-16) by the relative lay date.

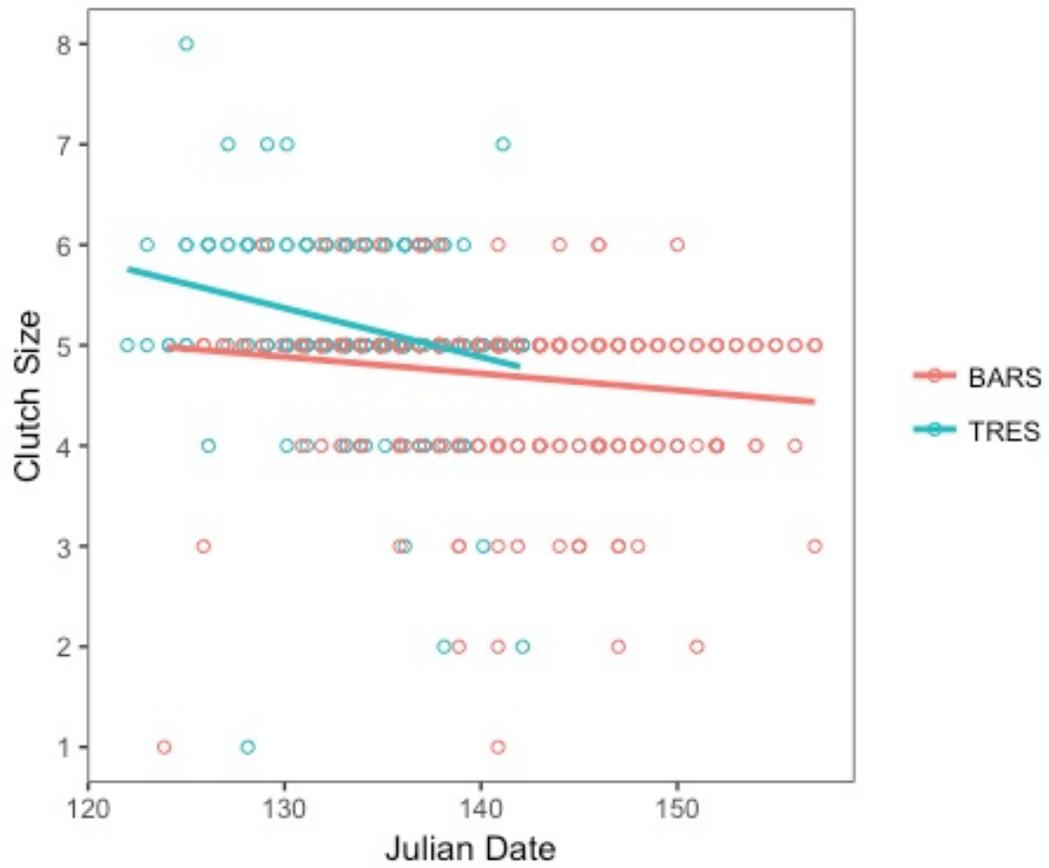


Figure 2.5. Average clutch size across years and habitats by Julian date for Barn Swallow (red) and Tree Swallow (blue) first broods.

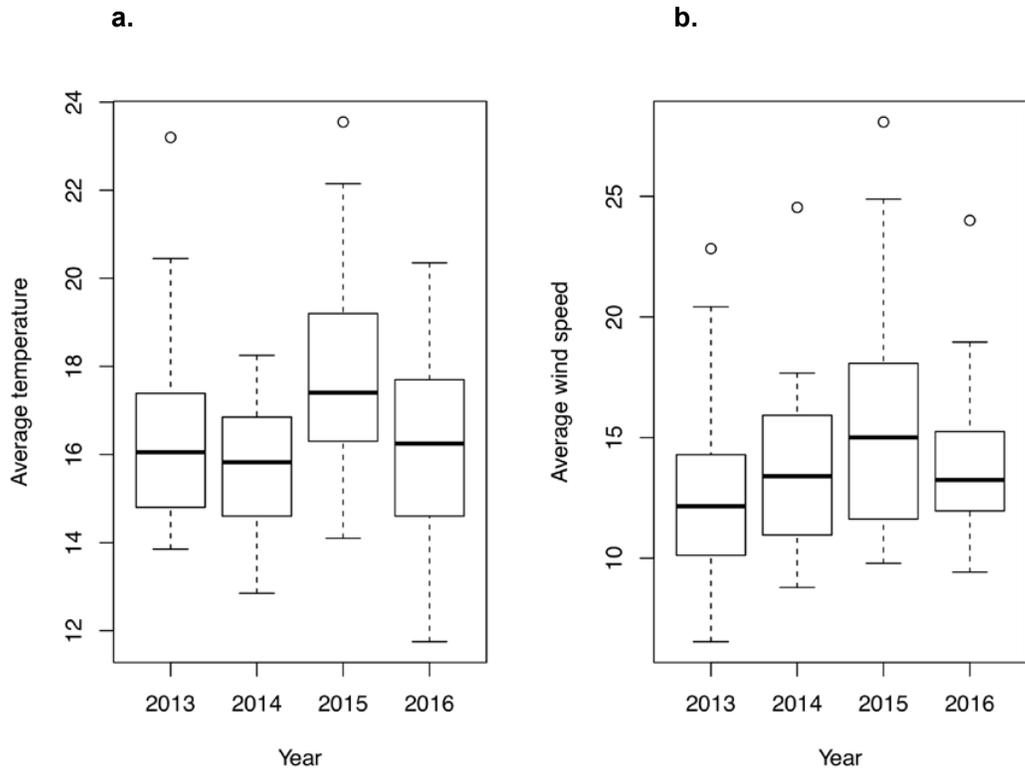


Figure 2.6. a) Average temperature (°C) and b) average wind speed (km/h) across years (2013-16) for the chick-rearing period (month of June; Julian dates 152-181).

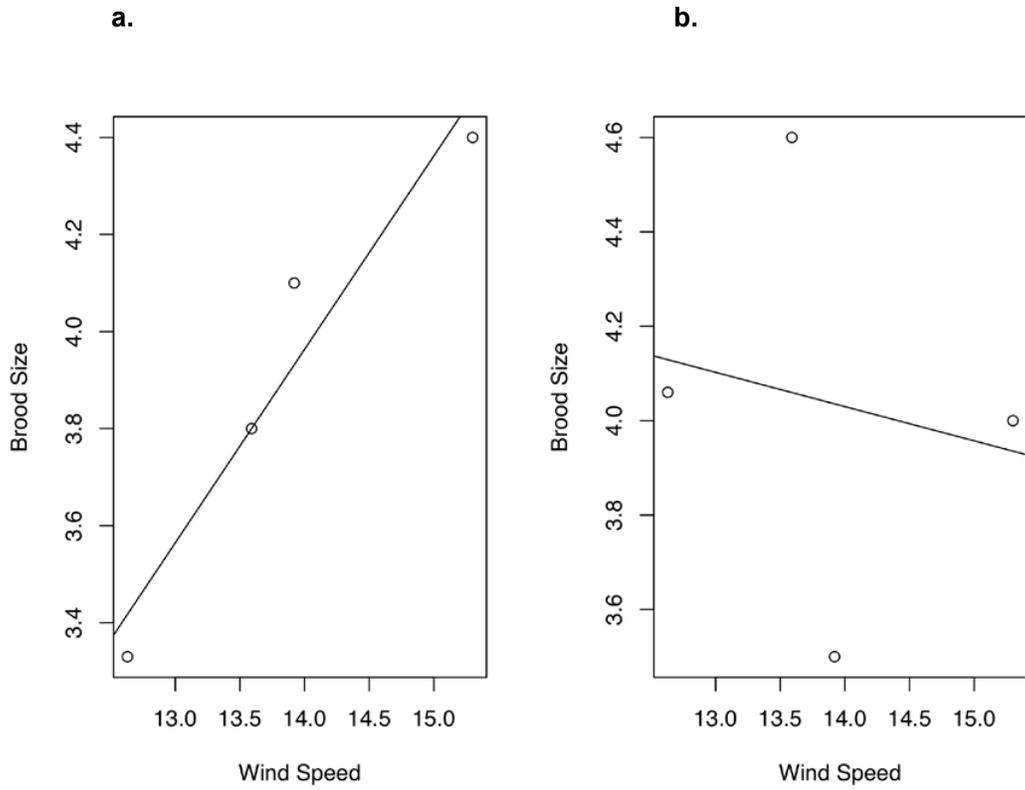


Figure 2.7. Average brood size for a) Tree Swallow first broods and b) Barn Swallow first broods, across sites by average wind speed (km/h). Each point represents average brood size in each year (2013-16), for a) Tree Swallows and b) Barn Swallows.

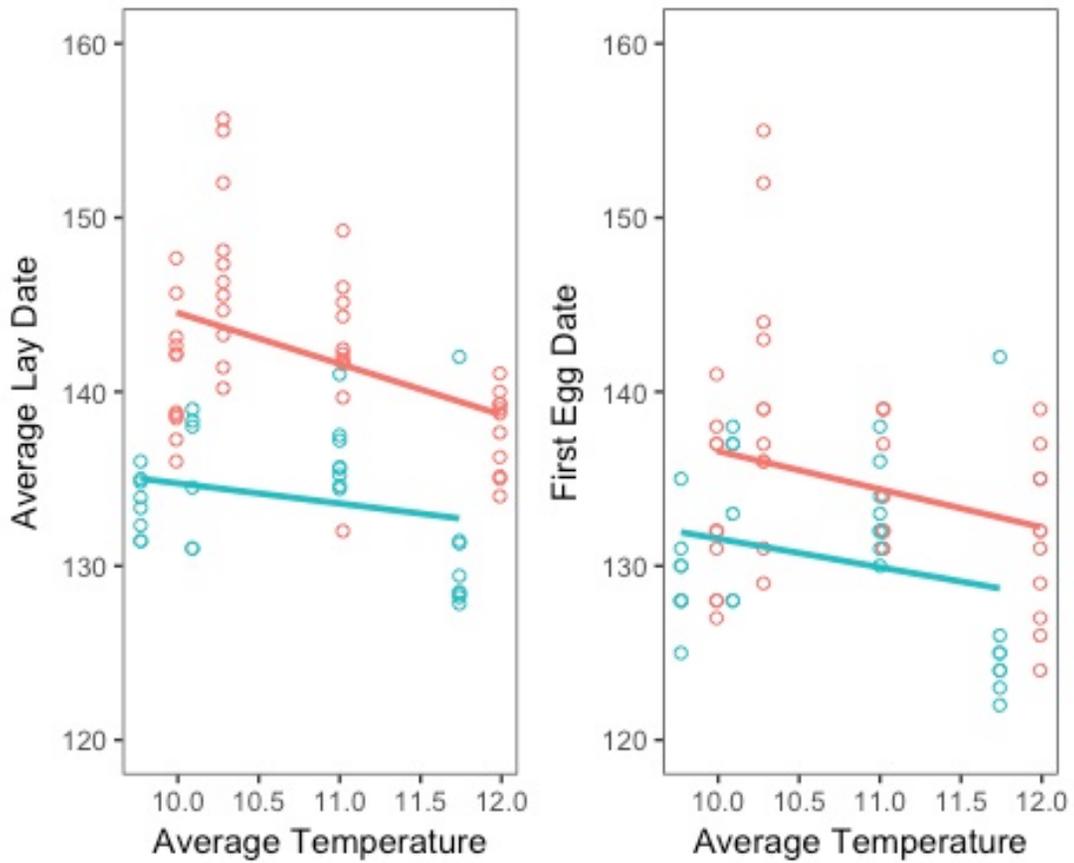


Figure 2.8. Average lay date and first egg date by average temperature ($^{\circ}\text{C}$) across sites (with years pooled) during the 4-week pre-laying period for Barn Swallows (red) and Tree Swallows (blue).

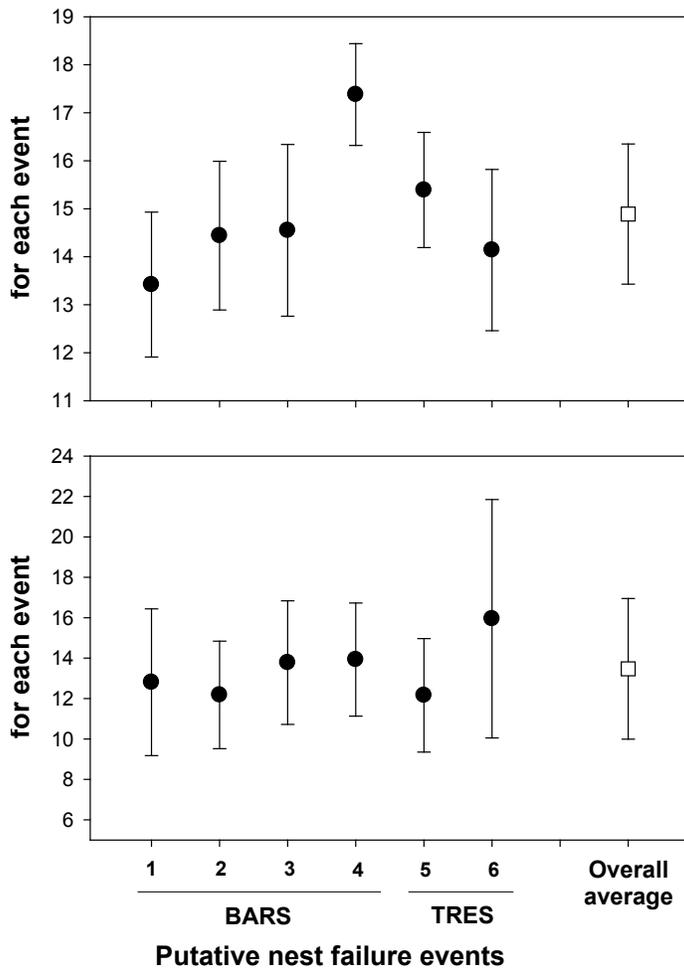


Figure 2.9. The average daily temperature (°C) with standard deviation (top graph; black points) for each nest failure event (1-4 represents Barn Swallow weather events from 2013, 2014 and two in 2016, 5-6 represents 2014 and 2016 weather events for Tree Swallows) and average wind speed (km/h) for each nest failure event (bottom graph; black points). The white squares represent the overall average temperature, and overall average wind speed across the 6 event periods.

Chapter 3. Post-fledging habitat use and survival of Barn Swallows (*Hirundo rustica*)

Introduction

Over the last several decades farmland birds have been declining across Europe (Donald et al. 2001, Donald et al. 2006) and North America (Conover et al. 2014). In particular, the guild which feeds on flying insects over farmland, aerial insectivores, have experienced steep declines since the 1980's in some parts of North America (Nebel et al. 2010, Smith et al. 2015). Many potential causes of these declines have been proposed such as, climate and weather effects (García-Pérez et al. 2014), agricultural intensification (Paquette et al. 2013), newer neonicotinoid pesticides (Hallmann et al. 2014), and shifts in prey abundance due to older pesticides (Nocera et al. 2012). Numerous studies suggest that changes to agriculture practice are likely an important factor. Agriculture land use and farming practices have shifted dramatically in the last several decades towards greater intensification (Conover et al. 2014) with an increase in crop field sizes, causing a decrease in the amount of non-crop habitat available, such as hedgerows and native vegetation strips (Boutin et al. 1999). Natural prairie and pasture have slowly been converted to row crops, allowing for increased crop production (Boutin et al. 1999), but the less diverse agricultural landscape leads to a decrease in food supply, such as seeds and invertebrates for bird populations (Fuller 2000). Changes in crop type are linked to the abundance of insects on agricultural fields with higher numbers of insects found over pasture compared to cereal fields, suggesting a greater benefit of natural pasture for species such as aerial insectivores that feed on insects (Evans et al. 2007). Increasing intensity in agricultural practices can also lead to increased interspecific competition among bird species, such as House Sparrows (*Passer domesticus*) that adapt more efficiently to an intensified landscape, while indirectly outcompeting Tree Swallows (*Tachinyeta bicolor*) for food and nesting sites (Robillard et al. 2013). Ultimately, these agricultural changes will affect how species use their habitat. Therefore, it is important to know how each species utilizes its habitat throughout its life cycle, e.g. for adults versus juveniles.

Juveniles can display differences in habitat use compared with adults, particularly during the post-fledgling stage (the period after nestlings have left the nest for the first

time, prior to migration or dispersal). For example, fledglings of some migratory species, such as Blackpoll Warbler (*Setophaga striata*), display exploratory behaviour and different habitat use than adults of the same species prior to fall migration (Brown and Taylor 2016). Fledgling Eastern Bluebirds (*Sialia sialis*) have been shown to utilize a greater amount of forest than breeding adults (Jackson et al. 2011), and fledgling Ovenbirds (*Seiurus aurocapilla*) selected for greater vegetation cover compared to adults (King et al. 2006). Prior to dispersal, some resident fledglings select different habitat than their natal sites, for instance, White-throated Robin fledglings selected for forest habitat over their natal agriculture habitat (Cohen and Lindell 2004). Migratory fledglings may also select habitat that differs from their natal habitat based on vegetation type preferences, as seen in Black-capped Vireos (*Vireo atricapilla*) (Dittmar et al. 2014). The high level of within- and between-species variation of adult and post-fledgling habitat use highlights the importance of focusing on all life stages, particularly the less understood post-fledging stage.

Juvenile survival, particularly in the immediate post-fledging period, is a major contributor to population growth rate and may be related to age-dependent habitat use (Robinson et al. 2004, Schaub et al. 2012, Sim et al. 2011). Adult survival is correlated to juvenile survival (which encompasses the post-fledging period) in some species (Sæther and Bakke 2000) further suggesting that the post-fledging period is critical in songbird life history (Templeton et al. 2011). Thus, due to greater mortality during this time period low post-fledging survival may contribute to aerial insectivore declines by negatively impacting population growth (Grüebler et al. 2014). Until recently the post-fledging stage was one of the least understood periods in avian life cycles, as it is one of the most difficult stages to observe. However, recent advancements in radio-tracking technology in the last several decades have increased the ability to track juveniles in the post-fledging period, increasing understanding of this life stage in relation to survival rates and habitat selection (King et al. 2006).

Evans et al. (2007) suggested that pasture (fields where livestock graze) had higher numbers of foraging Barn Swallows compared to crop fields, and Grüebler et al. (2010) showed that the presence of livestock increases productivity and nestling survival for double-brooded Barn Swallows, both suggesting pasture is a high quality habitat. We therefore predicted Barn Swallows born in higher quality pasture/livestock habitat to a) stay closest to the nest (have the shortest maximum distances), b) fledge at higher

quality (higher mass, longer tarsi and wing chord at fledging; Dunn et al. 2017, Arizaga et al. 2015), c) have earlier fledge dates (Naef-Daenzer et al. 2001), d) use high-quality habitat disproportionately relative to its availability, and e) have the highest survival rates compared to other habitat types in the post-fledging period. Post-fledging survival of Barn Swallows has been studied in Europe (Grüebler et al. 2014, Grüebler and Naef-Daenzer 2008), but to our knowledge there has been no similar research for their North American counterparts.

We studied the survival and habitat use of post-fledgling Barn Swallows over two years (2015-16) in the lower mainland of British Columbia, Canada. Our specific objectives were to 1) determine if natal habitat has an effect on post-fledgling behaviour and quality (variation in fledge date, mass, tarsus, wing, brood size, maximum days since fledged and maximum distance travelled from the nest), 2) to quantify habitat used by post-fledglings relative to availability and 3) determine post-fledging survival rates over two years.

Methods

Study area

Field work was conducted in the lower mainland of British Columbia, Canada (49°10' 8.15"N, 123° 5' 58.60"W) in 2015 and 2016 at 11 sites representing three habitat types: agriculture with crop (hereafter: crop, n = 4), agriculture with livestock, including both cows and horses (hereafter: livestock, n = 4) and non-agriculture (hereafter: non-agriculture; a park, a marina and a municipal works yard, n = 3).

Nest monitoring

Barn Swallow nests were checked twice a week from May 4 to August 6 in 2015 and May 2 to August 10 in 2016. We recorded the date on which the first egg of a clutch was laid (hereafter: lay date), clutch size, hatch date, brood size (best estimate closest to fledging), and if a nest fledged successfully (1 = at least one nestling successfully

fledged, 0 = no nestlings fledged). We determined the hatch date (day 0) of nestlings using a nestling ageing guide by Morales Fernaz et al. (2012). We assumed the average fledge date was day 21 (hatch day 0) based on data from Campbell et al. (1997; mean 20.5 days, range 19-24), as well as known average fledging age for our study sites, which was also 21 days (range 18-23) over 2 years (n = 14). Nests were considered to have fledged young if the nest was empty, and nestlings were day 18 or older (minimum fledging age, noted above), with no signs of predation (ie. broken nest, blood, dead nestlings). We assumed that nests fledged on the day following the last day they were observed in the nest (ie. i.e. a tagged bird was in the nest June 24, tracked out of nest June 26, assumed fledged on June 25). Nest siblings were also assumed to have fledged on the same day (Turner 2006).

Radio-telemetry

We used radio-telemetry to determine survival and habitat use of juvenile Barn Swallows. Nestlings were fitted with radio-transmitters typically 15-days post-hatching (range 14-17) and were calmed by covering the nest with a piece of felt to prevent premature fledging (Grüebler and Naef-Daenzer 2008). We used leg-loop harnesses to attach radio transmitters (0.35 -0.42 g; Rappole and Tipton 1991) with harness size of 42 mm loop span, based on an allometric function from Naef-Daenzer (2007) for European Barn Swallows and adjusted accordingly once radio tags were fitted to nestlings. We used a non-permanent harness comprised of Stretch Magic material tied together with a small portion of rubber elastic so the tag would fall off after several months (Kesler 2011). In 2015, 35 LOTEK (Picopip Ag379) VHF radio transmitters, with a battery life of ~29 days and range of ~1 km were put on nestlings at 10 of the 11 nest sites (no transmitter attachment at one site due to high nest predation). Each tag had an individual frequency and ID number. In 2016 48 LOTEK digitally coded nano-tag radio transmitters (NTQB-2) with a ~33 day battery life, ~5.0 sec burst interval rate and range of ~1 km were put on nestlings from 8 of the 11 sites. Radio tags plus harnesses weighed less than 0.6 g, which is less than 5% of average nestling Barn Swallows body weight (Fair et al. 2010). Each year, 1-2 nestlings were randomly taken from a nest for radio attachment, depending on the number of active nests per site. We attached a standard Canadian Wildlife Service aluminum band and measured tarsus (to the nearest

0.05 mm with digital calipers), wing chord (to the nearest 0.5 mm, with wing ruler), tail length (to the nearest 0.5 mm with wing ruler; 2016 only), fat score and mass (to the nearest 0.5 g with a Pesola scale) of each nestling equipped with a radio tag. In 2015 a total of 12 nestlings from livestock nest sites, 12 from crop nest sites and 11 from non-agriculture nest sites were tagged. Two nestlings were found dead less than a week after radio tags had been applied, so the tags were collected and re-deployed on nestlings from another nest at the same site. In 2016, due to hand-held tracking logistics (non-agricultural sites were geographically distant from other sites), tags were only put on nestlings from crop and livestock sites (25 tags on nestlings from livestock and 23 tags on nestlings from crop).

In 2015 and 2016 fledglings were tracked for approximately a month after fledging, using LOTEK Biotracker (2015) and LOTEK SRX800 M/MD (2016) hand held receivers and 3-element folding YAGI antennae. In both years, initial tracking began at the nest site, to determine fledge date. In 2015 we used a combination of e-bird sightings and personal observations to narrow down search locations to increase the likelihood of locating tagged birds once they moved away from natal sites. We attempted to locate each individual fledgling a minimum of 1-2 times per week. In 2016 we conducted more standardized surveys once a week for each site (n=8) with tagged birds. A central point at each nest site was considered the first station point, then three to four stations per site (dependent on site topography), were spaced out around the first station point. These stations were 500 m away from the nest site in the first week, 1 km in the second survey week, 2 km in the third, then 3 km in the fourth week of surveying. At each station a 2 minute scanning survey was conducted with the antennae directed in each cardinal direction for 15 seconds (so each direction was scanned twice during a survey) at 80 gain (out of 99). Gain magnifies the power and directionality of the radio signal, so higher gain allows for a greater detection range, whereas the signal strength is an indicator of the proximity of the radio signal (tagged bird) and the higher the signal strength, the closer the signal is to the receiver. After each survey if a tagged bird was detected, it was pursued on foot to try and better identify the individual from which the signal was coming. Additionally, informal scanning surveys were also conducted once a week per site guided by automated radio tower data (see below) and 2015 habitat and location data.

Before radio tracking commenced in 2016 we validated the radio tag signal distance by having one person stand stationary with a radio receiver and the other walking away with an activated radio tag on a water bottle (to simulate a bird, as tags emit weaker signals alone than when on a live organism). With the gain set to 80 the radio tag could be detected up to 1 km away, with a relatively low signal strength of 20-30 ('high' signal strength greater than 60-70). In the field, we were then able to pinpoint a fledgling's location using signal strength. During a radio tracking session when a signal was first detected for an individual fledgling the observer took several steps to determine the location of the tagged bird. Direction of the signal was first determined, then the approximate distance of the fledgling was determined using a combination of signal strength and moving/walking towards the signal. Once the observer was confident in a direction and distance they attempted to visually confirm if there were any swallows in the area, Barn Swallows in the area, fledgling Barn Swallows in the area and lastly if a tagged fledgling was able to be identified, based on high signal strength and a visual sighting of the radio tag antennae. Therefore, for each location of a fledgling, there were varying levels of confidence and only location points with a confidence ranking between 1-3 (low-high) were used for analysis (Table 1). Different from location points, 'detections' were points where a fledgling and its location could not be identified (confidence ranking > 3), and therefore were not included in analyses. In addition, if a tagged bird was located in its nest or a radio tag was collected, the point fell under a confidence ranking of 1.

Once a fledgling was confidently located, a GPS waypoint was taken and an estimate of the distance and direction of the fledgling from that waypoint was recorded. Additional information recorded for each location point included time, date, ID number, habitat type (e.g. crop field), prominent vegetation (e.g. sedges), activity of bird (e.g. perched or flying), number of birds and species sighted (e.g. 5 Barn Swallows), radio tagged fledgling visual (Y/N) and hatch year/fledgling (but untagged) Barn Swallow visual sighting (Y/N).

In 2016 an automated radio tower system (Taylor et al. 2017), consisting of 4 towers, was erected (towers between 6-7 metres high) in Ladner and Richmond, BC. Two of the towers were placed near nesting sites at Crescent Stables (49° 7'28.77"N, 123° 2'50.10"W) and Sea Island (49°12'28.15"N, 123°10'39.81"W), one near Boundary Bay (49° 3'36.15"N, 123° 1'28.74"W) and one on a barn on Westham Island (49°

5'56.03"N, 123° 9'56.39"W) to maximize local detections. Each tower consisted of 4 directional Yagi antennae (5 or 9 elements) connected to a LOTEK SRX 800 automated receiver or a SensorGnome receiver (sensorgnome.org). The three semi-permanent towers had a range of approximately 1-2 km, with the permanently mounted tower on Westham Island having a greater range between 5-10 km. Towers were put up before nestlings were equipped with radio-tags from June 9-17 and were used to locate tagged birds after leaving their natal site and to increase hand-held tracking efficiency, as well as confirming fates (dead or alive) of individuals.

Post-fledging habitat use

In order to assess whether fledgling Barn Swallows were preferentially selecting certain habitat types, we quantified available (potential for fledglings to encounter) habitat around each nest site using ArcGIS (ESRI, Redlands, California, USA). We used a 5 km buffer around each site based on preliminary analysis of location distances (see Results). A digital map was created for each site based on several different landcover datasets; a crop cover dataset (Land Cover Classification: Public Project Report (Public), 2017), the Sensitive Ecosystems Inventory dataset (Sensitive Ecosystem Inventory for Metro Vancouver & Abbotsford 2010-2012, 2009), the Metro Vancouver Land Cover Classification dataset (Land Cover Classification: Public Project Report, 2010) and a free-drawn polygon to represent the Tsawwassen Mills mall and surrounding construction (49° 2'20.57"N, 123° 5'9.28"W). The layering of several datasets into one map allowed us to look at differences in crops and pasture fields, as well as incorporating important marsh and urban habitat around each site, as no individual dataset covered all of these different habitat classes. We standardized the datasets by combining habitat classes between and within each dataset that had similar attributes (e.g. barren and bare soil classes were combined). We grouped the 16 initial habitat types (Fig 3.4) into 9 broad habitat classes: marsh (wetlands, riparian, estuary, intertidal), crops (vegetable crop, grain crop, fruit crop, winter cover crop), pasture (includes pasture fields, harvested crops and fallow fields), barren (includes uncultivated fields which encompasses bare and harvested fields), water, grass (includes herbaceous cover, mostly lawns and shrubs), trees (coniferous and deciduous), unknown, and urban (the built environment). Location points for each individual fledgling from both 2015 and

2016 were overlaid onto each habitat map, to identify habitat used (encountered and selected) by each tagged bird in comparison to habitat availability (e.g. Fig 3.4). If a bird's location could not be confidently assigned to one habitat, the classification was split between multiple habitat classes (e.g. 50% crop, 50% marsh). If there was a discrepancy between the habitat information collected in the field when the bird was located and the mapped habitat category, field data was used as it was difficult to account for crop rotation differences between years and a general increase of urban sprawl.

Statistical analysis

Modeling and statistical analysis was done in R (version 1.0.136, RStudio Team, 2016). Initially we tested for heterogeneity among potential covariates, fledge date, mass, tarsus, wing chord, brood size and maximum distance (the furthest distance each fledgling travelled from the nest) by natal habitat and year using one-way ANOVA and Welch's two-sample t-tests. Based on these preliminary analyses, we ran an initial set of linear mixed-effects models to determine whether there were differences between natal habitat (crop, livestock, non-agriculture) and maximum distance from the nest between years. We used maximum distance as the main effect, nest location and nest ID as nested random effects to control for pseudoreplication and year, natal habitat, tarsus, fledge date, and wing chord were used as covariates where appropriate. We ran a second set of linear mixed-effects models, which had an interaction between year and natal habitat (without non-agricultural born nestlings) and compared both sets of models using ANOVA to find the best fitting model.

We tested the relationship between overall distance from the nest and number of days since birds fledged and compared each year (2015, 2016) separately using a Pearson's correlation test. In addition, linear regressions were used to examine post-fledging behaviour, specifically examining the effect of nestling mass on maximum distance fledglings travelled and its relationship with fledge date.

For the habitat use analysis, the area for each habitat class was calculated in ArcGIS (ESRI, Redlands, California, USA) and then the percentage of each habitat

available per site was calculated. We used a chi-square analysis to compare available (expected) habitat to used (observed) habitat across sites (n=8) and a secondary chi-square test comparing agriculture, pasture and marsh habitat to all others (n=8), based on preliminary results. Available habitat was calculated per habitat, by dividing the area of each habitat per site by the total area of each site multiplied by the number of location points per site, so each habitat class was weighted by the number of locations per site. Used habitat was calculated as the number of observed bird locations in each habitat, divided by the total number of bird locations for each site.

Prior to fitting data for survival models we examined the relationship between different variables of interest, including mass, tarsus, fledge date, natal habitat and year. We used Cox proportional hazards models to evaluate factors affecting survival of fledglings to day 21 using radio-tracking data. We selected day 21 based on European Barn Swallows fledgling data from Naef-Daenzer and Gruebler (2014) where fledglings generally don't emigrate from their natal site prior to day 21 and our own data that showed the majority of fledglings moved farther from the natal site after day 21. We recorded the last seen date for each tagged bird, defined as the date of the last confirmed sighting where a fledgling was alive (i.e. if only tag found, last confirmed sighting of fledgling alive was used). Initially, we considered the event of interest to be mortality, however, we only confirmed deaths for 6 of 81 fledglings (13.5%), where a bird was considered dead if either remains of the bird or feathers were found with a radio tag, location of the tag didn't change for 3 days or more, or a tag was found damaged with feathers. Furthermore, there was a year bias (five events occurred in 2015, one event in 2016) so we had insufficient data for a robust analysis of year or habitat using these data. Therefore, we classified fledglings where the signal was lost before day 21, the harness and tag were found intact, or where fledglings were only tracked in the nest and never located out of the nest as mortality events (n = 45 over both years). The majority of the unknown fates were of fledglings that disappeared and never reappeared over varying times throughout the tracking period. The European Barn Swallow post-fledging data suggests that fledglings don't emigrate before three weeks (Naef-Daenzer and Gruebler 2014), so we assumed these fledglings had died. In addition, fledglings that disappeared in 2016 were never detected by the automated radio towers after their last hand-tracking detection.

We examined two sets of survival models using the `coxph` command in R. The first set of models used mass, fledge date, natal habitat and year as potential factors influencing survival. The second set of models used the same variables, but replaced mass with tarsus as a measure of body size, compared to condition. We started with the most complex models and used a stepwise procedure to eliminate variables from the models. A final set of models included one variable each (tarsus, mass, fledge date, natal habitat and year; Table 3.2) and were compared using ANOVA to determine the best fit model. Kaplan Meier curves were used to plot the difference in survival between natal habitat and the overall survival probability.

Results

We confirmed that all radio-tags emitted a signal for each nestling and that all nestlings fledged successfully, except for one individual, where all nestlings from the nest were gone one day after the nestling was radio-tagged, and we assumed it was depredated and was therefore excluded from analysis. Over both years we deployed 83 radio tags and confirmed 82 out of 83 birds fledged successfully. We attempted to track thirty-five fledglings in 2015 (eleven from non-agricultural sites, twelve from crop sites and twelve from livestock sites) and forty-seven fledglings in 2016 (twenty-two from crop and twenty-five from livestock sites). Of the eighty-three birds tagged, seventy-two (87%) were successfully tracked out of the nest for 2-37 days, and a total of 289 post-fledging locations were recorded over both years. Ten (12%) of the fledglings were not detected after leaving the nest (1 in 2015, 9 in 2016) and were assumed to have died.

Post-fledging behaviour and quality in relation to year and natal habitat

Mass was negatively correlated with age ($t_{80} = -2.42$, $p = 0.018$, $r = -0.26$), presumably due to pre-fledge mass loss, wing chord was positively correlated with age ($t_{81} = 7.25$, $p < 0.01$, $r = 0.63$), and tarsus length was independent of chick age ($t_{81} = 0.50$, $p = 0.62$, $r = 0.056$). We therefore used adjusted age-specific wing chord and mass values as covariates for all analyses. Both mass and wing chord were fitted to a linear

model and the best fit line (linear for both mass and wing), slope and intercept of each calculated and adjusted to the median age (day 15). We found no relationship between age-adjusted mass and tarsus ($F_{1,79} < 0.01$, $p = 0.99$) and therefore used both as metrics of nestling condition and body size in subsequent analyses. Only nestlings not measured at the median age have adjusted wing and mass values ($n = 19$). Fledge date and hatch date were highly correlated ($r_{80} = 0.975$, $P < 0.001$) so fledge date was used as a covariate to control for timing of breeding.

Natal habitat had a significant effect on fledge date ($F_2 = 6.41$, $p = 0.0026$), where fledglings born in non-agriculture habitats fledged at a later date (182.4 ± 4.3) than fledglings born in both crop (177.8 ± 3.7) and livestock (177.9 ± 4.0) habitats. Fledglings born in non-agriculture habitats also had smaller tarsi (11.3 ± 1.0) than fledglings born in either agricultural type (crop: 11.9 ± 0.6 ; livestock: 11.6 ± 0.7 ; $F_2 = 3.74$, $p = 0.028$). Natal habitat had no significant effect on the maximum distance fledglings were tracked from the nest ($F_2 = 2.11$, $p = 0.13$), but non-agricultural born fledglings stayed within 5 km of their nests, compared to agriculture fledglings which travelled just under 20 km (Fig 3.1). Natal habitat had no effect on mass ($F_2 = 0.079$, $p = 0.92$), brood size ($F_2 = 1.26$, $p = 0.29$) or wing chord ($F_2 = 1.87$, $p = 0.16$).

The maximum distance fledglings were detected from their natal site varied significantly with year, and was greater in 2016 (19.3 ± 6.2) compared to 2015 (9.4 ± 2.0 ; $t_{50} = -4.11$, $p < 0.001$). There was also variation across years in wing chord ($t_{81} = 2.84$, $p = 0.006$), which was longer in 2015 (72.0 ± 4.5) compared to 2016 (68.6 ± 5.8). There was no difference in average fledge date of radio-tracked nestlings between years ($t_{80} = 1.14$, $p = 0.26$) or in nestling body mass, tarsus length or brood size between years ($p > 0.19$ in all cases).

For linear mixed-effects models that included fledglings from all natal habitats, but no interaction term, year was the only significant term in the models ($p < 0.022$ in all cases). When fledglings from non-agriculture habitats were removed with maximum distance as the dependent variable and a year and natal habitat interaction was added, there were no significant terms in any of the models ($p > 0.078$ in all cases). As there was no significant interaction of natal habitat by year in the linear mixed-effects models, we assumed a greater maximum distance in 2016 compared to 2015 was an artifact of

our different sampling approaches between the years, and therefore included the fledglings from non-agriculture habitats from 2015 in the remainder of the analyses.

The overall distance fledglings travelled was positively correlated with the number of days since they fledged for both years ($t_{373} = 9.40$, $p < 0.001$, $r = 0.44$; Fig. 3.2). However, several individuals showed movements that were random and appeared to be exploratory (Fig. 3.3b,c,d), while others gradually increased their distance from the nest as they aged (Fig 3.3a). Mass had no effect on fledge date ($F_{1,79} = 2.05$, $p = 0.157$), maximum distance fledglings travelled from the nest ($F_{1,73} = 0.46$, $p = 0.50$) or the maximum days since fledge that birds were located ($F_{1,73} < 0.01$, $p = 0.97$).

Post-fledging habitat use

We found a significant overall difference in habitat use based on observed locations relative to habitat availability ($\chi^2_8 = 145.88$, $p < 0.001$). Specifically, birds used cropped habitat more than expected based on availability ($\chi^2_1 = 38.47$, $p < 0.001$; Table 3.3), and were recorded over less marsh habitat than predicted ($\chi^2_1 = 11.82$, $p < 0.001$; Table 3.3). Although fledglings were recorded in pasture more than expected (3.33 location points compared to expected 2.19), it was not a significant trend ($\chi^2_1 = 0.0038$, $p = 0.95$).

Post-fledging survival

Two fledglings were removed from survival analysis due to missing values for mass and fledge date (final $n = 81$). Over both years we found only one fledgling depredated, likely by an accipiter, with only feathers, a leg with a band and the intact radio tag found, 5.2 kilometres from its nest, killed between 9-17 days post-fledge.

Survival probability to day 21 post-fledging over both years was 0.44 and varied slightly between fledglings born in different natal habitats, with non-agriculture fledglings experiencing the highest survival probability (Fig. 3.5a) while fledglings tagged in 2015

had a slightly lower survival probability than those tagged in 2016 (Fig. 3.5b), although neither of these were significant trends.

Models that included mass, fledge date, natal habitat and year as either single or multiple factors did not explain survival ($p > 0.4$), nor did the second set of models using tarsus over mass as a measure of fledgling quality ($p > 0.1$). Therefore, final models included only one variable and were each tested against a null model (Table 3.2). The best fit model only included tarsus ($LR_2 = 2.61$, $p = 0.11$), but it was not significant. As we were unable to find an effect on survival with the first two sets of models, we further tested for an effect of natal habitat on survival by controlling for each variable (mass, tarsus, fledge, year), but the conclusion did not change ($p > 0.2$).

Discussion

We investigated factors affecting survival and habitat use in the critical post-fledging period of North American Barn Swallows. Contrary to our predictions, we found little effect of natal habitat on post-fledging survival, fledgling quality or behaviour (variation in fledge date, mass, tarsus, wing chord, brood size and maximum distance travelled from the nest). We found that fledglings used crop habitat, preferentially compared to other habitat available across sites, including pasture. Over two years the probability of post-fledgling survival was relatively low (0.44) in comparison to other altricial and northern temperate species, however, potential explanatory variables, specifically fledge date, tarsus, mass, year and natal habitat were all independent of survival. Overall, our results suggest that natal habitat had no effect on post-fledging success, but fledgling Barn Swallows in the region are experiencing low survival rates, which could have negative implications for conservation efforts.

Across different natal habitats there was no significant difference in maximum distance fledglings travelled in the post-fledging period or in mass, brood size, or wing chord prior to fledging. However, we found a later fledge date and shorter tarsi in fledglings from non-agriculture habitats. Data for fledglings from non-agriculture sites were only available in one year, so it is possible shorter tarsi are an artifact of only sampling in one year, and not an indicator of generally smaller body sizes. While there

was no significant difference in maximum distance travelled, non-agriculture fledglings only travelled maximum distances of 5 km away from the nest site, compared to both crop and livestock fledglings, which travelled up to 19 km from their nest sites. This could be in part due to sampling efforts in 2015 compared to 2016 (non-agriculture fledglings only tracked in 2015) or the difficulty of tracking around the non-agriculture sites due to terrain. We found no other indication that fledglings born in non-agriculture habitats were low-quality as there was no difference between mass, wing chord or brood size across natal sites. In addition, a later fledge date is likely explained by non-agriculture sites having a later lay date, and an overall slightly later breeding season (approximately a week later) observed over a four year period (Boynton, unpublished data).

We found no evidence that natal habitat, found to be of higher quality elsewhere (i.e. pasture with livestock), had any effect on post-fledging success, indicating this type of habitat is less important for Barn Swallows in the lower mainland during the post-fledging stage at our study sites. In Europe aerial insect abundances are higher over pasture (Evans et al. 2007) and in the presence of livestock (Gruebler et al. 2010) and adult Barn Swallows forage predominantly where there is a higher abundance of aerial insects (Evans et al. 2003). However, similar patterns have not been shown for post-fledgling Barn Swallows and our data suggests post-fledglings don't follow this same pattern. We would expect that if livestock habitat is vital to post-fledgling Barn Swallows, those hatched in livestock habitat would stay close to the natal site for the duration of the post-fledging period before migrating, i.e. they would have shorter maximum post-fledging distances. Conversely, fledglings born in non-livestock habitats should have higher maximum distances if they moved preferentially to forage in livestock habitats. However, fledglings born in livestock habitat exceeded distances from the nest of 15 kilometres, whereas fledglings born in non-agriculture stayed closer to their nest and natal site (< 5 kilometres), although these trends were not significant.

Our data are consistent with other studies of passerines during the post-fledging period, which show that as fledglings get older they steadily increase the distance from their nests, e.g. White-throated Robins (*Turdus assimilis*; Cohen & Lindell 2004), Dickcissels (*Spiza americana*; Berkeley et al. 2007), Eastern Bluebirds (*Sialia sialis*; Jackson et al. 2011) and Grasshopper Sparrows (*Ammodramus savannarum*; Streby & Andersen 2013). Eastern Bluebirds moved an average of 250 m away from their nests

after 36-40 days post-fledge (Jackson et al. 2011) and Ovenbirds reached distances greater than 1 km in 24 days (Streby and Andersen 2013), while several of our tagged fledglings reached a distances of 19 km at 16 days post-fledge. Movement away from natal sites is also indicative of exploratory behaviour in the post-fledge stage. White & Faaborg (2008) defined exploratory movement as movement greater than 300m from an area and a subsequent return to that area, compared to dispersal where individuals make similar initial movement, but do not return to the natal area (Vitz & Rodewald 2010). Several of our tagged Barn Swallows demonstrated exploratory behaviour moving several kilometers away from the natal area (Fig. 3.3c), or staying under 1 km (Fig. 3.3d), but then all subsequently returning to the natal site. Other individuals showed gradual movement away from the natal site, but remained relatively close regardless (Fig. 3.3a). Similar exploratory movements have been seen in post-fledgling Wood Thrush (*Hylocichla mustelina*; Vega Rivera et al. 1998) and Black-poll Warblers (*Setophaga striata*; Brown and Taylor 2015), and is potentially a common post-fledge behaviour for migrants. Exploratory movement has also been described as fledglings visiting unfamiliar terrain (Baker 1993), which is comparable with exploratory behaviour of our fledglings that were located over 'novel' habitats not used for breeding, such as marsh and water.

In terms of habitat use, post-fledgling Barn Swallows used crop habitat more than it was available. While the proportion of crop habitat that is available is quite high (15.1%), marsh covers an even greater area (31%), but we found Barn Swallows avoided this type of habitat, indicating selective behaviour for crop habitats. Barn Swallow fledglings also showed no preference for foraging in pasture habitat, contrary to our predictions. Barn Swallow fledglings could be selecting for crop habitats during the post-fledging period because there is a higher proportion of aerial insects in the boundary edges of bordering hedgerows on crop fields, in comparison to pasture fields (Evans et al. 2003). Crop rotation is common in this region between years, which could provide a larger diversity of prey for fledglings leading to crop habitat preference, and as adult Barn Swallows are shown to be less selective in prey type, it is possible fledglings have similar diet selectivity (Brown and Brown 1999). Crop habitat is also preferred by White-throated Robins (*Turdus assimilis*) over pasture during the post-fledge period (Cohen and Lindell 2004) and perhaps provides more benefits than just prey for post-fledglings, such as protection from predators during roosting, as some of our location

points were likely roosting points. In addition, adult North American Barn Swallows use similar habitat and are often found foraging in open areas, specifically fields and meadows during the breeding season (Brown and Brown 1999). Similar habitat use between adults and post-fledglings has been shown in European turtle doves (*Streptopelia turtur*; Dunn et al. 2017) and a similar pattern between UK post-fledging and adult Barn Swallows has been suggested (Evans et al. 2007).

The estimated survival of Barn Swallow fledglings in our study was higher (0.44) than that reported for post-fledgling European Barn Swallows (0.32) over a three week period (Grüebler et al. 2014). However, based on a range of survival probabilities for northern temperate zone species (including migrants and residents) from Lloyd and Martin (2015), who found a range of 0.3-0.8 survival rates for passerines between 18-24 days post-fledge, our survival estimate is relatively low. Furthermore, Naef-Daenzer and Grüebler (2016) classify a range of survival rates between 0.37-0.68 as low in a review on post-fledging survival of altricial birds. Based on our results, low survival of post-fledging Barn Swallows in the region could have implications for overall population stability. Michel et al. (2015) suggest there is a negative population trajectory for Barn Swallows in our study area and it is therefore possible this trend is being driven by low survival of juveniles. However, we found no explanatory variable for survival rates in post-fledging Barn Swallows even though we predicted a higher mass and an earlier fledge date would have a positive effect on survival. Nevertheless, post-fledging survival has been found to be independent of fledging mass in several species, including Dickcissels *Spiza americana* (Berkeley et al. 2007), and Yellow-eyed Juncos (*Junco phaenotus*) (Sullivan 1989) as well as non-passerines such as Puffins (*Ratercula arctica*) (Harris & Rothery 1985) so the relationship between mass and survival is not a taxawide pattern (Magrath 1991, Schwagmeyer and Mock 2008).

In Guillemot (*Uria aalge*; Hedgren 1981) and Rose-breasted Grosbeak chicks (*Pheucticus ludovicianus*; Moore et al. 2010) post-fledging survival was independent of fledge date, but conversely in Great and Coal Tits (*Parus major*, *Periparus ater*; Naef-Daenzer et al. 2001) fledge date affected survival. This again suggests variability between species and taxa in factors affecting post-fledging survival. Although we tested several variables shown to have an effect on survival in other species, we did not test for the effect of post-fledge habitat (due to small sample sizes), and it is therefore possible post-fledge habitat could be driving low survival rates in our study area (Berkeley et al.

2007, Fisher and Davis 2011). Weather could also negatively impact survival of post-fledglings as Barn Swallow prey (aerial insects) abundance is negatively affected by high precipitation, high wind and low temperatures (Grüebler et al. 2008) and inclement weather could result in higher levels of starvation and mortality. The majority of our assumed dead individuals disappeared from their natal sites, with no tag signal picked up thereafter, which points more directly to depredation as predators often destroy transmitters (Naef-Daenzer et al. 2001), so mortality due to weather is less likely a factor in our study. Since Barn Swallow juveniles were found to selectively use crop fields, a decline or transformation of these fields through agricultural intensification could negatively affect survival. This could have several implications for conservation of this species, currently listed as Threatened (COSEWIC 2011). If low juvenile survival in the post-fledge stage is driving declines in this species, protection of post-fledge habitat could be critical. While our research fills in some major knowledge gaps about the Barn Swallow post-fledging period, our sample sizes are relatively small and there is still further research needed to explore this critical period in life history in a species where recent declines are still not well understood.

Table 3.1. Confidence ranking of locations of fledgling Barn Swallows as determined by radio-telemetry.

Confidence Ranking	Confidence of Bird Location	Signal Strength	Distance to Bird	Gain
1	90-100 %	80+	<500m	<90
2	60-90 %	50+	500-900 m	<90
3	<50%	20-50	900-1km	>80

Table 3.2. Final model output from 1-variable Cox proportional hazard models of fledgling Barn Swallow survival to post-fledge day 21.

Variable	Effect Size (Likelihood Ratio)	95% CI	X ²	P
tarsus	2.61	0.43-1.10	2.61	0.11
year	0.4	0.46-1.49	0.40	0.53
nathab	1.15	0.60-2.07	1.15	0.56
fledge	0.01	0.94-1.07	0.0056	0.94
amass	0	0.87-1.16	0	1.0

Table 3.3. Used habitat (observed) compared to available habitat (expected) of fledgling Barn Swallows from radio telemetry location points (RT), for fledglings in crop and livestock natal sites from 2015-16.

Habitat Class	Area Available (ha)	% of Total Area Available	Expected RT Points	Observed RT Points
Crop	9457.21	15.1%	47.67	115.83
Pasture	431.44	0.69%	2.19	3.33
Tree	1992.97	3.2%	6.64	4.83
Unknown	1964.61	3.1%	9.83	5.5
Grass	9235.32	14.7%	36.02	43.25
Urban	9100.64	14.5%	26.23	25
Water	9372.45	14.9%	48.36	12.75
Marsh	19433.84	31.0%	104.34	65.67
Barren	1772.05	2.8%	7.73	12.83

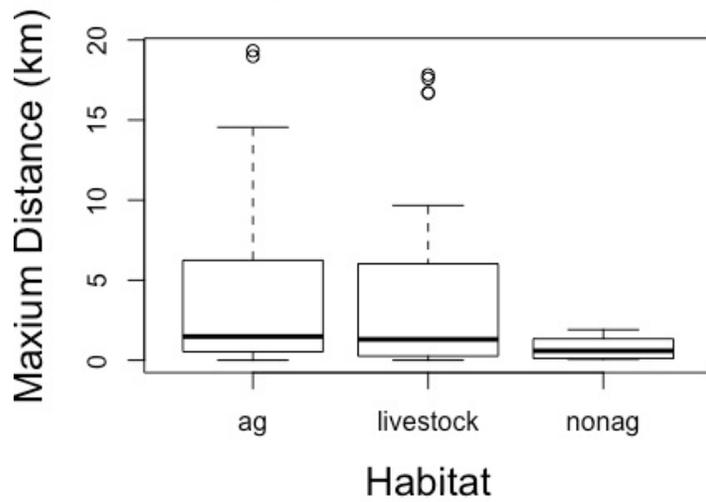


Figure 3.1 Maximum distance Barn Swallow fledglings travelled away from their nest by day 21 post-fledge in 2015 and 2016 by natal habitat (ag = crop habitat, livestock = livestock habitat including cows and horses, nonag = non-agriculture habitat including a park, marina and works yard).

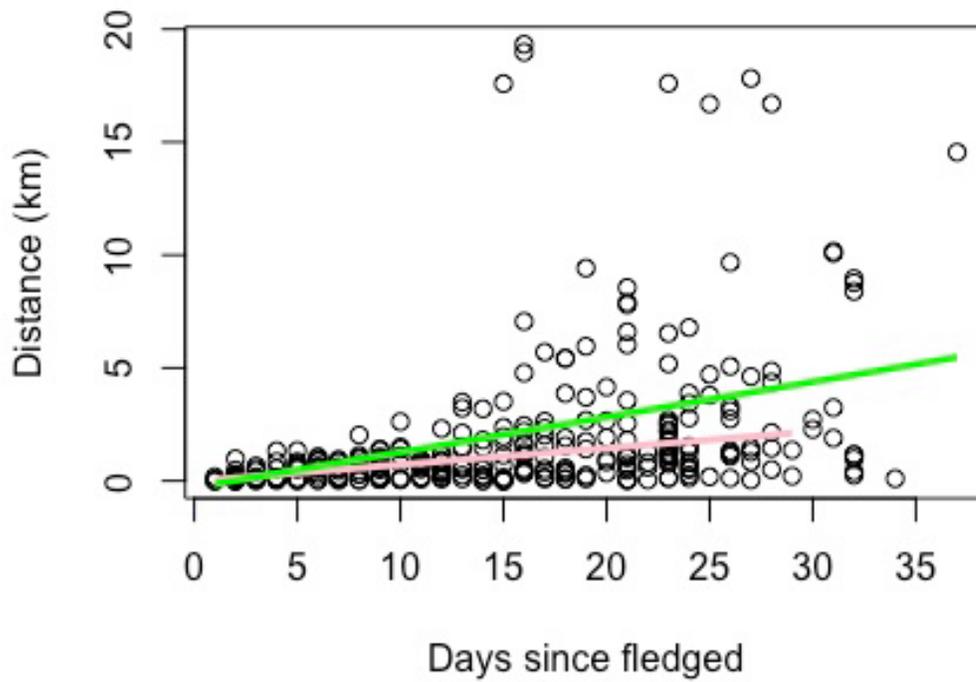


Figure 3.2. The total distance (km) Barn Swallow fledglings travelled by the number of days out of the nest in 2015 (pink line) and 2016 (green line).

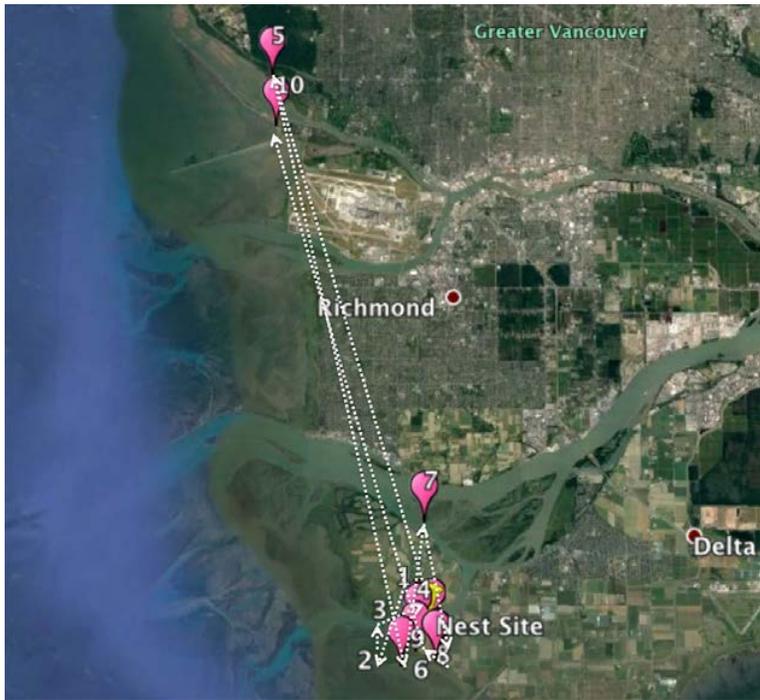
a.



b.



c.



d.



Figure 3.3. Individual tracking locations for tagged Barn Swallow fledglings over the entire tracking period overlaid onto a satellite map. Numbers and arrows identify order each individual fledgling was tracked, starting at the nest site (yellow marker). Blue markers indicate fledglings tagged in 2015 (b,d) and pink markers indicate birds tagged in 2016 (a,c).

Map data © 2016 Google

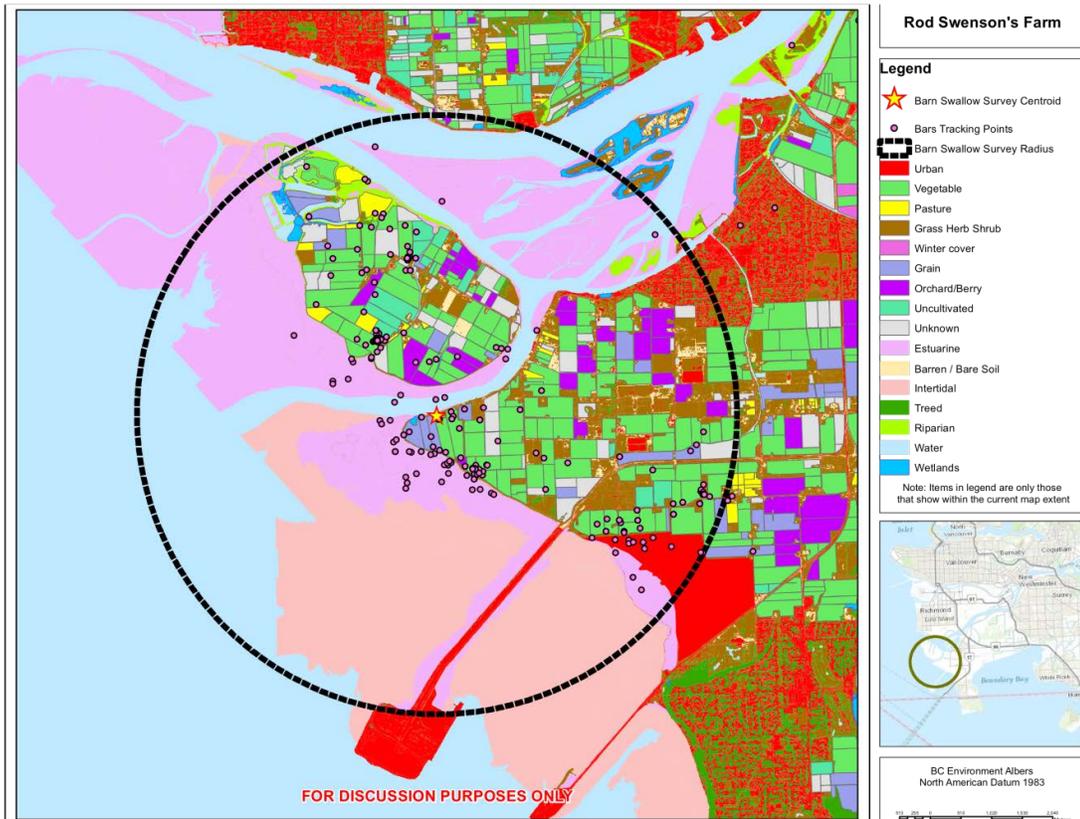


Figure 3.4. Habitat map of one crop site (Rod Swenson's farm) with Barn Swallow location points indicated in pink over two years. The black circle represents the 5 km buffer used to determine available habitat and habitat classes (n=16).

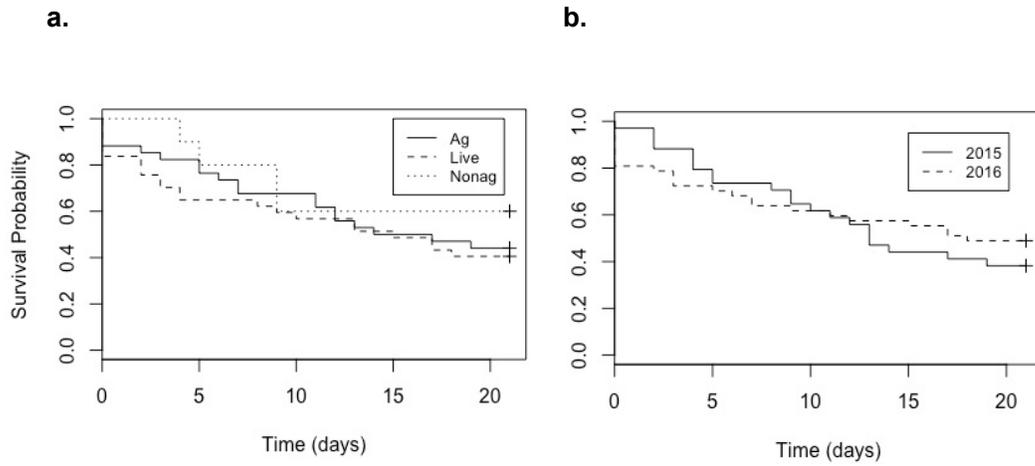


Figure 3.5. Kaplan Meier curve of survival over time (days) showing cumulative survival probability of Barn Swallow fledglings a) born in crop (solid line), livestock (dashed line) and non-agriculture (dotted line) habitats for 2015 and 2016 combined and b) by year (2015 solid line, 2016 dashed line).

Chapter 4. Conclusions

General conclusions

Comparative empirical research on aerial insectivores has been relatively limited to date, and region-specific species variation in population change has therefore been limited to modelling population trajectories from breeding surveys (see Michel et al. 2015). In part, to address this issue, we compared reproductive success and the effect of landscape type (crop, livestock and non-agriculture) and weather on two co-occurring aerial insectivores, Barn Swallows and Tree Swallows in the Pacific Northwest (Chapter 2). We found variation in lay date both between species and across years, but no effect of habitat type. Both Barn Swallows and Tree Swallows bred earlier across the 4 years of our study (2013 was the latest year and 2016 was the earliest), but Tree Swallows bred on average a week earlier than Barn Swallows in each year. However, first egg dates between the two species were very similar and across all 4 years they only laid 1-2 days apart. For first broods, Tree Swallows had larger clutches than Barn Swallows over all years in crop habitat and in livestock habitat in one year, however Barn Swallows were also double-brooded suggesting they may have higher breeding potential which could account for smaller clutches in their first brood. We found few interspecies differences of breeding productivity (fledging success and brood size at fledge). Average temperature during the 4-week pre-laying period, across sites, with species and years pooled, was significantly associated with earlier average lay dates and earlier first egg dates, suggesting both species might adapt similarly to warming temperatures. Overall, we found only minor interspecies differences on the breeding grounds in the lower mainland of British Columbia. Therefore, interspecies variation in population trajectories in this region suggested by Michel et al. (2015), could be driven by differences during migration, on the wintering grounds or different survival rates during the post-fledge period.

Chapter 3 investigated variation in behaviour, quality, survival and habitat use in the post-fledging period in Barn Swallows. The post-fledging period is considered to be one of the most vulnerable life history stages throughout a bird's life cycle (Templeton et al. 2011), which could have large implications for threatened species, such as Barn Swallows (COSEWIC 2011). Therefore, we used radio telemetry to track post-fledging

Barn Swallows in 2015 and 2016, specifically to determine habitat use and survival rates. We found little overall effect of natal habitat on post-fledging behaviour, quality and survival rates, suggesting natal habitat is less important to post-fledglings. Contrary to our predictions, crop habitat was used more than expected based on availability of this habitat type, while fledglings showed no preference for pasture habitat. Selectivity of crop habitat could be due to a higher abundance of insects found along crop field edges, specifically in hedgerows (Evans et al. 2003), or even due to greater protection from predators when roosting. The survival rate of Barn Swallow fledglings over the two years (2015-16) was relatively low (0.44), in comparison to other post-fledgling studies (0.3-0.8; Lloyd and Martin 2015, 0.37- 0.68; Naef-Daenzer and Gruebler 2016), but we found no variable (fledge date, mass, tarsus, year, natal habitat) to explain these low survival rates. Post-fledge habitat could effect survival rates, but this was not tested in our study (due to small sample sizes), and should therefore be a consideration for future research.

There were several limitations within this study; the primary limitation being sample size. For Barn Swallow nests, we generally had a large sample to work with, although some sites had much smaller numbers of active nests, especially the non-agriculture sites. In terms of selecting nestlings to put radio tags on between certain dates (ideally within two weeks), there were some sites that were difficult to obtain adequate samples in some years, particularly due to nest predation (i.e. why Crescent Stables site was not used in 2015). To compensate we had to select nestlings from other sites, ideally with more active nests, and of the same habitat type (i.e. depredated target nest at a livestock site, new nest selected from another livestock site). However, in comparison, Tree Swallow active nest numbers were much smaller overall. In particular, 2013 was a difficult year for sample sizes, as nest boxes had just been set up, so Tree Swallow populations were not fully established. Generally there were enough active nest boxes in agriculture and livestock sites over other years to obtain comparable sample sizes to Barn Swallows, but Tree Swallows rarely used non-agriculture sites (boxes were instead occupied by Violet-green Swallows), which limited comparison in this habitat. In one non-agriculture site where there were plentiful Tree Swallow active nests, bear cubs knocked down 10/10 boxes in 2014, so attempts to re-mount nest boxes in subsequent years were forgone. In addition, nest boxes in non-agriculture were used more by Violet-green Swallows than Tree Swallows, and while this is encouraging for that species, it did not help our study.

Another limitation was that the first year of radio tagging was largely an experimental year (2015). Despite the post-fledging period becoming a more popular life history stage to study, there is less work on swallows, particularly in North America during this phase of the life-cycle. This left us with uncertainty regarding distances the post-fledglings could travel between leaving the nest and 3 weeks post-fledge, and we therefore likely underestimated how far birds flew in 2015 (although European post-fledge Barn Swallows have been suggested to stay relatively close to natal sites; Gruebler et al. 2014). In addition, we had a very limited idea of what type of habitat they would use for foraging, and therefore our search parameters were not entirely standard in the first year. The spatial layout of our study region is quite large, and this forced us to travel sometimes over an hour between sites, and it also limited our ability to track individuals, which may have lead to underestimating distances, and not searching all available habitats for fledglings. However, we tried to compensate for this during our 2016 tracking period, where we eliminated non-agricultural sites, which were the farthest sites.

We were also slightly limited by availability of certain data for the habitat analysis. One of the habitat datasets used for available habitat, was older than desired (Sensitive Ecosystems from 2009), and despite new data being available for this dataset from 2016, it is not available till sometime in the Fall of 2017, after this study has concluded. In addition, radio tower data to better inform last-seen fledgling dates has been on hold for several months due to updates with the MOTUS system. Therefore final sightings of one or two fledglings may change, but it will not likely effect survival rates significantly.

Future studies and conservation recommendations

While our study was one of the first to track post-fledgling swallows in Western Canada, we had relatively small sample sizes, which limited our analysis. Therefore, future studies are necessary to a) increase sample sizes of individual post-fledglings, b) widen survey parameters and follow a continuous survey protocol (only done in one year of our study), and c) set up automated radio towers in closer proximity to a smaller number of sites, to gather the best local data. In addition, our study was only conducted over two years, and more subsequent years of tracking data could elucidate larger

patterns of habitat use, and also help determine causes behind low survival rates in this region.

Although Barn Swallows and Tree Swallows in the lower mainland seem to be fairing well, it is also possible that they are doing poorly in other areas on their breeding grounds. For Barn Swallows, this could be due to a decrease in available nesting habitat, particularly old-style barns and buildings that are open (and easily accessible). Future studies could therefore examine differences in the number of breeding pairs at new and old barns, as well as determining if both Barn Swallow and Tree Swallow abundance has decreased in parts of their breeding range more than others. Future studies should follow suit of this research and conduct more comparative work on aerial insectivores, particularly for species thought to have dissimilar population trajectories (see Michel et al. 2015). Replications of this study in areas where there are thought to be variation in population trajectories could further determine mechanisms driving declines among aerial insectivores (or why some populations appear to be stable or even increasing), such as the effects of poor weather on aerial insect prey, or certain populations not adapting to warming temperatures and climate change.

Further research should also include comparative post-fledging studies using radio telemetry to compare both species during this period, in a system similar to our study, where Tree Swallows and Barn Swallows breed and coexist and have access to the same habitat. As the post-fledging stage is one of the most vulnerable life history stages throughout a birds' life cycle, understanding differences between a relatively stable species and one that is declining could be crucial for understanding population variation among aerial insectivores. In addition, exploring more of the annual life cycle for each species could help improve understanding of different population trajectories and if these are driven by variation in survival during the post-fledging stage, migration or on the wintering grounds. Therefore future studies should also consider using integrated population models, such as in the recent study on Tree Swallows from Weegman et al. (2017), or tracking both species across their annual cycles (i.e. Hobson et al. 2015) and determining survival rates at each life history stage (i.e. Gruebler et al. 2014).

Our findings also have conservation implications, particularly for Barn Swallows. Contrary to European studies on Barn Swallows that have found higher productivity and

greater numbers of foraging adults over pasture (Moller 2001, Ambrosini et al. 2012, Evans et al. 2007), post-fledgling Barn Swallows in the lower mainland of British Columbia foraged over crop habitats non-randomly. Therefore, unlike in Europe, the conversion of arable and pasture fields to crop fields is likely a benefit for Barn Swallows in this region. In addition, maintaining and protecting old wood-style buildings for breeding adults to use as nesting sites around areas in close proximity to crop habitats is an important conservation step. While Barn Swallows will use newer buildings in this region (Boynton, personal observation), barns or other buildings with metal roofs can cause nestlings to overheat in their nests resulting in nestling mortality, which is avoided in older designed buildings (Campbell et al. 1997). Educating the public on the benefits of Barn Swallows in an area and their specific conservation requirements on the breeding grounds (older, open buildings and crop habitat) could also help with the conservation of these species.

References

- Ambrosini, R., A. M. Bolzern, L. Canova, S. Arieni, A. P. Møller, and N. Saino. 2002. The distribution and colony size of barn swallows in relation to agricultural land use. *Journal of Applied Ecology* 39:524–534.
- Ambrosini, R., R. P. Ferrari, R. Martinelli, N. Saino, R. Ambrosini, R. P. Ferrari, R. Martinelli, M. Romano, R. Ambrosini, R. P. Ferrari, R. Martinelli, and M. Romano. 2006. Seasonal, meteorological, and microhabitat effects on breeding success and offspring phenotype in the barn swallow, *Hirundo rustica*. *Ecoscience* 13:298–307.
- Ambrosini, R., D. Rubolini, P. Trovò, G. Liberini, M. Bandini, A. Romano, B. Sicurella, C. Scandolara, M. Romano, and N. Saino. 2012. Maintenance of livestock farming may buffer population decline of the Barn Swallow *Hirundo rustica*. *Bird Conservation International* 22:411–428.
- Arizaga, J., A. Herrero, A. Aldalur, J. Cuadrado, and D. Oro. 2015. Effect of pre-fledging body condition on juvenile survival in Yellow-legged Gulls *Larus michahellis*. *Acta Ornithologica* 50:139–147.
- Attwood, S. J., M. Maron, A. P. N. House, and C. Zammit. 2008. Do arthropod assemblages display globally consistent responses to intensified agricultural land use and management? *Global Ecology and Biogeography* 17:585–599.
- Baker, R. R. 1993. The Function of Post-Fledging Exploration: A Pilot Study of Three Species of Passerines Ringed in Britain. *Scandinavian Journal of Ornithology* 24:71–79.
- Benton, T. G., D. M. Bryant, L. Cole, and H. Q. P. Crick. 2002. Linking agricultural practice to insect and bird populations: A historical study over three decades. *Journal of Applied Ecology* 39:673–687.
- Berkeley, L. I., J. P. McCarty, and L. L. Wolfenbarger. 2007. Postfledging survival and movement in dickcissels (*Spiza americana*): Implications for habitat management and conservation. *The Auk* 124:396–409.
- Boutin, C., K. E. Freemark, and D. A. Kirk. 1999. Farmland birds in southern Ontario: field use, activity patterns and vulnerability to pesticide use. *Agriculture, Ecosystems & Environment* 72:239–254.
- Bowers, K. E., J. L. Grindstaff, S. S. Soukup, N. E. Drilling, K. P. Eckerle, S. K. Sakaluk, and C. F. Thompson. 2016. Spring temperatures influence selection on breeding date and the potential for phenological mismatch in a migratory bird. *Ecology* 97:2880–2891.

- Brown, C. R., and M. B. Brown. 1999. Barn Swallow (*Hirundo rustica*), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: <https://birdsna-org.proxy.lib.sfu.ca/Species-Account/bna/species/barswa>
- Brown, J., and P. Taylor. 2015. Adult and hatch-year Blackpoll Warblers exhibit radically different regional-scale movements during post-fledging dispersal. *Biology Letters* 11:1-4.
- Bryant, D. M. 1975. Breeding biology of house martins *Delichon urbica* in Relation To Aerial Insect Abundance. *Ibis* 117:180–216.
- Campbell, R.W., Dawe, N.K., McTaggart-Cowan, I., Cooper, J.M., Kaiser, G.W., Stewart, A.C., and McNall, M.C.E. 1997. The birds of British Columbia. Vol. 3: Passerines: flycatchers through vireos. Canadian Wildlife Service, Delta, B.C.; BC Ministry of Environment, Lands and Parks, Victoria, B.C.; and University of British Columbia Press, Vancouver, B.C.
- Cohen, E. B., and C. A. Lindell. 2004. Survival, habitat use, and movements of fledgling white-throated robins (*Turdus assimilis*) in a Costa Rican agricultural landscape. *The Auk* 121:404–414.
- Conover, R. R., S. J. Dinsmore, and L. W. J. Burger. 2014. Effects of set-aside conservation practices on bird community structure within an intensive agricultural landscape. *The American Midland Naturalist* 172:61–75.
- COSEWIC. 2011. COSEWIC assessment and status report on the Barn Swallow *Hirundo rustica* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. ix + 37 pp. (www.sararegistry.gc.ca/status/status_e.cfm).
- Dittmar, E. M., D. A. Cimprich, J. H. Sperry, and P. J. Weatherhead. 2014. Habitat selection by juvenile black-capped vireos following independence from parental care. *Journal of Wildlife Management* 78:1005–1011.
- Donald, P. F., R. E. Green, and M. F. Heath. 2001. Agricultural intensification and the collapse of Europe 's farmland bird populations. *Proceedings of the Royal Society of London, Series B* 268:25–29.
- Donald, P. F., F. J. Sanderson, I. J. Burfield, and F. P. J. Van Bommel. 2006. Further evidence of continent-wide impacts of agricultural intensification on European farmland birds , 1990 – 2000. *Agriculture, Ecosystems and Environment* 116:189–196.
- Doxa, A., Y. Bas, M. L. Paracchini, P. Pointereau, J. M. Terres, and F. Jiguet. 2010. Low-intensity agriculture increases farmland bird abundances in France. *Journal of Applied Ecology* 47:1348–1356.

- Dunn, Jenny, C., A. J. Morris, and P. V. Grice. 2017. Post-fledging habitat selection in a rapidly declining farmland bird, the European Turtle Dove *Streptopelia turtur*. *Bird Conservation International* 27:45–57.
- Dunn, P. O., and D. W. Winkler. 1999. Climate change has affected the breeding date of tree swallows throughout North America. *Proceedings of the Royal Society B: Biological Sciences* 266:2487–2490.
- Environment and Climate Change Canada, 2017. North American Breeding Bird Survey - Canadian Trends Website, Data-version 2015. Environment and Climate Change Canada, Gatineau, Quebec, K1A 0H3
- Evans, K. L., R. B. Bradbury, and J. D. Wilson. 2003. Selection of hedgerows by Swallows *Hirundo rustica* foraging on farmland: the influence of local habitat and weather. *Bird Study* 50:8–14.
- Evans, K. L., J. D. Wilson, and R. B. Bradbury. 2007. Effects of crop type and aerial invertebrate abundance on foraging barn swallows *Hirundo rustica*. *Agriculture, Ecosystems and Environment* 122:267–273.
- Fair, J. M., E. Paul, J. Jones, and A. Editors. 2010. Guidelines to the use of wild birds in research. Washington, D.C.: Ornithological Council.
- Fisher, R. J., and S. K. Davis. 2011. Post-fledging dispersal, habitat use, and survival of Sprague's pipits: Are planted grasslands a good substitute for native? *Biological Conservation* 144:263–271.
- Fraser Lowland Agricultural Crop Cover Surveys 1992 – 2015 (Public)* [computer file]. Ducks Unlimited Canada and the Canadian Wildlife Service of Environment and Climate Change Canada. 2017. Available: Environment and Climate Change Canada (Accessed March 2017).
- Fuller, R. 2000. Relationships between recent changes in lowland British agriculture and farmland bird populations: an overview. *Ecology and Conservation of Lowland Farmland Birds* 1950:5–16.
- García-Pérez, B., K. A. Hobson, G. Albrecht, M. D. Cadman, and A. Salvadori. 2014. Influence of climate on annual survival of Barn Swallows (*Hirundo rustica*) breeding in North America. *The Auk* 131:351–362.
- Ghilain, A., and M. Belisle. 2008. Breeding Success of Tree Swallows Along a Gradient of Agricultural Intensification. *Ecological Applications* 18:1140–1154.
- Grimm, A., B. M. Weiß, L. Kulik, J. B. Mihoub, R. Mundry, U. Köppen, T. Brueckmann, R. Thomsen, and A. Widdig. 2015. Earlier breeding, lower success: Does the spatial scale of climatic conditions matter in a migratory passerine bird? *Ecology and Evolution* 5:5722–5734.

- Grüebler, M. U., F. Korner-Nievergelt, and B. Naef-Daenzer. 2014. Equal nonbreeding period survival in adults and juveniles of a long-distant migrant bird. *Ecology and Evolution* 4:756–765.
- Grüebler, M. U., F. Korner-Nievergelt, and J. Von Hirschheydt. 2010. The reproductive benefits of livestock farming in barn swallows *Hirundo rustica*: Quality of nest site or foraging habitat? *Journal of Applied Ecology* 47:1340–1347.
- Grüebler, M. U., M. Morand, and B. Naef-Daenzer. 2008. A predictive model of the density of airborne insects in agricultural environments. *Agriculture, Ecosystems and Environment* 123:75–80.
- Grüebler, M. U., and B. Naef-Daenzer. 2008. Fitness consequences of pre- and post-fledging timing decisions in a double-brooded passerine. *Ecology* 89:2736–2745.
- Hallmann, C. A., R. P. B. Foppen, C. A. M. Van Turnhout, H. De Kroon, and E. Jongejans. 2014. Declines in insectivorous birds are associated with high neonicotinoid concentrations. *Nature* 511:341–343.
- Harris, M. P., and P. Rothery. 1985. The post-fledging survival of young Puffins *Fratercula arctica* in relation to hatching date and growth. *Ibis* 127:243–250.
- Hedgren, S. 1981. Effects of Fledging Weight and Time of Fledging on Survival of Guillemot *Uria aalge* Chicks. *Scandinavian Journal of Ornithology* 12:51–54.
- Hobson, K. A., K. J. Kardynal, S. L. Van Wilgenburg, and G. Albrecht. 2015. A Continent-Wide Migratory Divide in North American Breeding Barn Swallows (*Hirundo rustica*). *PLoS ONE* 10:1–13.
- Hussell, D. J. T., and T. Quinney. 1985. Food abundance and clutch size of Tree Swallows *Tachycineta bicolor*. *Ibis* 129:243–258.
- Irons, R. D., A. H. Scurr, A. P. Rose, J. C. Hagelin, T. Blake, D. F. Doak, R. Ap, H. Jc, T. Blake, D. Df, and D. F. Doak. 2017. Wind and rain are the primary climate factors driving changing phenology of an aerial insectivore. *Proceedings of the Royal Society B* 284:1-8.
- Jackson, A. K., J. P. Froneberger, and D. A. Cristol. 2011. Postfledging survival of eastern bluebirds in an urbanized landscape. *Journal of Wildlife Management* 75:1082–1093.
- Kesler, D. C. 2011. Non-permanent radiotelemetry leg harness for small birds. *Journal of Wildlife Management* 75:467–471.
- King, D. I., R. M. Degraaf, M. Smith, J. P. Buonaccorsi, D. I. King, and U. F. Service. 2006. Special section Habitat selection and habitat-specific survival of fledgling ovenbirds (*Seiurus aurocapilla*). *Journal of Zoology* 269:414–421.

- Land Cover Classification: Public Project Report* [computer file]. Metro Vancouver: Coombes, M., 2010. Available: Environment and Climate Change Canada (Accessed 2012).
- Lloyd, P., and T. E. Martin. 2015. Fledgling survival increases with development time and adult survival across north and south temperate zones. *Ibis* 158:135–143.
- Magrath, R. D. 1991. Nestling Weight and Juvenile Survival in the Blackbird, *Turdus merula*. *Journal of Animal Ecology* 60:335–351.
- McArthur, S. L., A. E. Mckellar, N. J. Flood, and M. W. Reudink. 2017. Local weather and regional climate influence breeding dynamics of Mountain Bluebirds (*Sialia currucooides*) and Tree Swallows (*Tachycineta bicolor*): a 35-year study. *Canadian Journal of Zoology* 277:271–277.
- McCarty, J. P., and D. W. Winkler. 1999. Foraging Ecology and Diet Selectivity of Tree Swallows Feeding Nestlings. *The Condor* 101:246–254.
- Metro Vancouver. 2014. Farming in Metro Vancouver.
- Michel, N. L., A. C. Smith, R. G. Clark, C. A. Morrissey, and A. Keith. 2015. Differences in spatial synchrony and interspecific concordance inform guild-level population trends for aerial insectivorous birds. *Ecography* 38:774-786.
- Møller, A. P. 2001. The effect of dairy farming on barn swallow *Hirundo rustica* abundance, distribution and reproduction. *Journal of Applied Ecology* 38:378–389.
- Møller, A. P. 2002. North Atlantic Oscillation (NAO) effects of climate on the relative importance of first and second clutches in a migratory passerine bird. *Journal of Animal Ecology* 71:201–210.
- Moore, L. C., B. J. M. Stutchbury, D. M. Burke, and K. a Elliott. 2010. Effects of Forest Management on Postfledging Survival of Rose-Breasted Grosbeaks (*Pheucticus ludovicianus*). *The Auk* 127:185–194.
- Morales Fernaz, J., L. Schifferli, and M. U. Gruebler. 2012. Ageing nestling Barn Swallows *Hirundo rustica*: an illustrated guide and cautionary comments. *Ringing and Migration* 27:65-75.
- Naef-Daenzer, B. 2007. An allometric function to fit leg-loop harnesses to terrestrial birds. *Journal of Avian Biology* 38:404–407.
- Naef-Daenzer, B., and M. U. Gruebler. 2014. Effects of radio-tag characteristics and sample size on estimates of apparent survival. *Animal Biotelemetry* 2:1-8.

- Naef-Daenzer, B., and M. U. Grüebler. 2016. Post-fledging survival of altricial birds: Ecological determinants and adaptation. *Journal of Field Ornithology* 87:227–250.
- Naef-Daenzer, B., F. Widmer, and M. Nuber. 2001. Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. *Journal of Animal Ecology* 70:730–738.
- Nebel, S., A. Mills, J. D. McCracken, and P. D. Taylor. 2016. Declines of Aerial Insectivores in North America Follow a Geographic Gradient. *Avian Conservation and Ecology* 5:1-14.
- Nocera, J. J., J. M. Blais, D. V. Beresford, L. K. Finity, C. Grooms, L. E. Kimpe, K. Kyser, N. Michelutti, M. W. Reudink, and J. P. Smol. 2012. Historical pesticide applications coincided with an altered diet of aerially foraging insectivorous chimney swifts. *Proceedings of the Royal Society B: Biological Sciences* 279:3114–3120.
- North American Bird Conservation Initiative Canada. 2012. The State of Canada's Birds, 2012. Environment Canada, Ottawa, Canada 1-36.
- Ockendon, N., D. Leech, and J. W. Pearce-Higgins. 2013. Climatic effects on breeding grounds are more important drivers of breeding phenology in migrant birds than carry-over effects from wintering grounds. *Biology Letters* 9:1-4.
- Orłowski, G., and J. Karg. 2013. Partitioning the effects of livestock farming on the diet of an aerial insectivorous passerine, the barn swallow *Hirundo rustica*. *Bird Study* 60:111–123.
- Paquette, S. R., D. Garant, F. Pelletier, and M. Bélisle. 2013. Seasonal patterns in Tree Swallow prey (Diptera) abundance are affected by agricultural intensification. *Ecological Applications* 23:122–133.
- Paquette, S. R., F. Pelletier, D. Garant, and M. Belisle. 2014. Severe recent decrease of adult body mass in a declining insectivorous bird population. *Proceedings of the Royal Society B: Biological Sciences* 281:1–9.
- Ramstack, J., M. T. Murphy, and M. R. Palmer. 1998. Comparative Reproductive Biology of Three Species of Swallows in a Common Environment. *The Wilson Bulletin* 110:233–243.
- Rappole, J. H., and A. R. Tipton. 1991. New Harness Design for Attachment of Radio Transmitters to Small Passerines. *Journal of Field Ornithology* 62:335–337.
- Robillard, A., D. Garant, and M. Bélisle. 2013. The Swallow and the Sparrow: How agricultural intensification affects abundance, nest site selection and competitive interactions. *Landscape Ecology* 28:201–215.

- Robinson, R. A., R. E. Green, S. R. Baillie, W. J. Peach, and D. L. Thomson. 2004. Demographic mechanisms of the population decline of the song thrush *Turdus philomelos* in Britain. *Journal of Animal Ecology* 73:670–682.
- Sæther, B.-E., and Ø. Bakke. 2000. Avian Life History Variation and Contribution of Demographic Traits To the Population Growth Rate. *Ecology* 81:642–653.
- Schaub, M., T. S. Reichlin, F. Abadi, M. Kéry, L. Jenni, and R. Arlettaz. 2012. The demographic drivers of local population dynamics in two rare migratory birds. *Oecologia* 168:97–108.
- Schwagmeyer, P. L., and D. W. Mock. 2008. Parental provisioning and offspring fitness: size matters. *Animal Behaviour* 75:291–298.
- Sensitive Ecosystem Inventory for Metro Vancouver & Abbotsford 2010-2012* [computer file]. Metro Vancouver: Meidinger, D., Clark, J. and Adamoski, D., 2009. Available: Environment and Climate Change Canada (Accessed 2012).
- Sicurella, B., M. Caprioli, A. Romano, M. Romano, D. Rubolini, N. Saino, and R. Ambrosini. 2014. Hayfields enhance colony size of the Barn Swallow *Hirundo rustica* in northern Italy. *Bird Conservation International* 24:17–31.
- Sim, I. M. W., G. W. Rebecca, S. C. Ludwig, M. C. Grant, and J. M. Reid. 2011. Characterizing demographic variation and contributions to population growth rate in a declining population. *Journal of Animal Ecology* 80:159–170.
- Smith, A. C., M. A. R. Hudson, C. M. Downes, and C. M. Francis. 2015. Change points in the population trends of aerial-insectivorous birds in North America: Synchronized in time across species and regions. *PLoS ONE* 10:1–23.
- Statistics Canada. 2012. 2011 Census of Agriculture: British Columbia Highlights.
- Streby, H. M., and D. E. Andersen. 2013. Movements , cover-type selection, and survival of fledgling Ovenbirds in managed deciduous and mixed coniferous-deciduous forests. *Forest Ecology and Management* 287:9–16.
- Sullivan, K. A. 1989. Predation and Starvation: Age-Specific Mortality in Juvenile Juncos (*Junco phaeotus*). *Journal of Animal Ecology* 58:275–286.
- Taylor, P. D., T. L. Crewe, S. A. Mackenzie, D. Lepage, Y. Aubry, Z. Crysler, C. M. Francis, C. G. Guglielmo, D. J. Hamilton, R. L. Holberton, P. H. Loring, D. R. Norris, J. Paquet, R. A. Ronconi, P. A. Smith, J. Smetzer, L. Welch, and B. K. Woodworth. 2017. The Motus Wildlife Tracking System: A collaborative research network to enhance the understanding of wildlife movement. *Avian Conservation and Ecology* 12:1-11.

- Templeton, C. N., V. A. Reed, S. E. Campbell, and M. D. Beecher. 2012. Spatial movements and social networks in juvenile male song sparrows. *Behavioral Ecology* 23:141–152.
- Turner, A. 2006. *The Barn Swallow*. Berkhamstead, UK: T and A D Poyser.
- Twining, C. W., J. T. Brenna, P. Lawrence, J. R. Shipley, T. N. Tollefson, and D. W. Winkler. 2016. Omega-3 long-chain polyunsaturated fatty acids support aerial insectivore performance more than food quantity. *PNAS* 113:1–6.
- Vega Rivera, J. H., J. H. Rappole, W. J. Mcshea, and C. A. Haas. 1998. Wood Thrush Postfledging Movements and Habitat Use in Northern Virginia. *The Condor* 100:69–78.
- Vitz, A. C., and A. D. Rodewald. 2010. Movements of fledgling Ovenbirds (*Seiurus Aurocapilla*) and Worm-Eating Warblers (*Helmitheros vermivorum*) within and beyond the natal home range. *The Auk* 127:364–371.
- Weegman, M.D., T.W. Arnold, R.D. Dawson, D.W. Winkler and R.G. Clark. 2017. Integrated population models reveal local weather conditions are the key drivers of population dynamics in an aerial insectivore. *Oecologia* 185:199-130.
- White, J. D., and J. Faaborg. 2008. Post-fledging movement and spatial habitat-use patterns of juvenile Swainson's Thrushes. *Wilson Journal of Ornithology* 120:62–73.
- Winkler, D. W., K. K. Hallinger, D. R. Ardia, R. J. Robertson, B. J. Stutchbury and R. R. Cohen. 2011. Tree Swallow (*Tachycineta bicolor*), *The Birds of North America* (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: <https://birdsna-org.proxy.lib.sfu.ca/Species-Account/bna/species/treswa>.