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RESEARCH ARTICLE

Barn Swallow (*Hirundo rustica*) fledglings use crop habitat more frequently in relation to its availability than pasture and other habitat types

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ABSTRACT

Populations of birds that forage on aerial insects have been declining across North America for several decades, but the main causes of and reasons for geographical variation in these declines remains unclear. We examined the habitat use and survival of post-fledging Barn Swallows (*Hirundo rustica*) near Vancouver, British Columbia, Canada, using VHF radio telemetry. We predicted that fledgling Barn Swallows hatched in higher-quality natal habitat (pasture) would fledge at higher quality, stay closest to the nest, disproportionately use higher-quality habitat during the post-fledge stage, and have higher survival rates in the region. Contrary to our predictions, we found that natal habitat (crop, pasture, or non-agriculture) had no effect on fledgling quality or movement distance. Barn Swallow fledglings used crop habitat more frequently in relation to its availability than other habitat types, including pasture. Barn Swallows had low post-fledging survival rates (0.44; 95% CI: 0.35–0.57), which could negatively influence the population trend of the species in this region. While natal habitat had only minor effects, crop habitat appears to be important for fledgling Barn Swallows and, therefore, a decline in this habitat type could have further negative implications for an already declining species.

Keywords: Barn Swallow, habitat use, *Hirundo rustica*, post-fledging, radio-telemetry, survival

Les jeunes de *Hirundo rustica* utilisent l'habitat de cultures plus fréquemment en fonction de sa disponibilité que les pâturages et d'autres types d'habitats

RÉSUMÉ

Les populations d'oiseaux se nourrissant d'insectes volants sont en déclin en Amérique du Nord depuis plusieurs décennies, mais les principales causes de ces déclins et les raisons expliquant la variation géographique de ceux-ci demeurent obscures. Nous avons examiné l'utilisation de l'habitat et la survie des jeunes de *Hirundo rustica* ayant atteint l'envol près de Vancouver, en Colombie-Britannique, au Canada, à l'aide de la télémétrie VHF. Nous avons prédit que les jeunes de cette espèce issus d'un habitat natal de plus grande qualité (pâturage) seraient de meilleure qualité à l'envol, demeureraient plus près du nid, utiliseraient de façon disproportionnée l'habitat de meilleure qualité après l'envol et auraient des taux de survie plus élevés dans la région. Contrairement à ce que nous avions prédit, nous avons constaté que l'habitat natal (cultures, pâturage ou non agricole) n'avait aucun effet sur la qualité des jeunes ou sur la distance de déplacement. Les jeunes utilisaient l'habitat de cultures plus fréquemment en fonction de sa disponibilité que les autres types d'habitats, dont les pâturages. Cette espèce avait des taux de survie faibles après l'envol (0,44; 95 % IC: 0,35-0,57), ce qui pourrait influencer négativement la tendance des populations de cette espèce dans cette région. Alors que l'habitat natal avait seulement des effets mineurs, l'habitat de cultures semble être important pour les jeunes de *H. rustica* et, par conséquent, un déclin dans ce type d'habitat pourrait avoir d'autres conséquences négatives pour cette espèce déjà en déclin.

Mots-clés: après l'envol, *Hirundo rustica*, survie, télémétrie, utilisation de l'habitat

INTRODUCTION

Over the last several decades the avian guild that feeds on flying insects, aerial insectivores, has experienced steep population declines in some parts of North America (Smith et al. 2015, Nebel et al. 2016). Although the drivers of these population declines remain unclear (Spiller and Dettmers 2019), many potential causes have been proposed. These include climate and weather effects (García-Pérez et al. 2014), and many aspects of agricultural intensification that may affect aerial insect abundance including changing crop types and amounts (Paquette et al. 2013, Stanton et al. 2018) and insecticide use (Nocera et al. 2012, Hallmann et al. 2014). In areas with highly intensive agriculture practices, such as areas with crop fields, insect abundance is lower than in native vegetation (Attwood et al. 2008). Agricultural land use and farming practices have shifted dramatically in the last several decades toward greater intensification (Conover et al. 2014) with an increase in crop field sizes causing a decrease in the availability of non-crop habitat, such as hedgerows and native vegetation strips (Boutin et al. 1999). Prairie grasslands and pasture have slowly been converted to row crops, allowing for increased crop production (Boutin et al. 1999) but less diverse agricultural landscapes, leading to a decrease in food supply for farmland birds through reductions in seed and insect prey (Fuller 2000, Stanton et al. 2018). Higher numbers of insects have been found over pasture compared to cereal fields, suggesting a greater benefit of pasture for species such as aerial insectivores (Evans et al. 2007). Ultimately, these agricultural changes will affect how species make use of the available habitat throughout their life cycle.

Juvenile survival, particularly in the immediate post-fledging period, is a major contributor to population growth rate and population trends in some species, and may be related to age-dependent habitat use (Sæther and Bakke 2000, Robinson et al. 2004, Sim et al. 2011, Schaub et al. 2012). Thus, greater mortality during this important life stage may contribute to aerial insectivore population declines by negatively impacting population growth (Grüebler et al. 2014). Changes to available habitat through agricultural intensification have implications not only for adult birds, but juveniles as well. Juvenile birds can display differences in habitat use compared with adults, particularly during the post-fledging stage (the period after nestlings have left the nest for the first time, prior to migration or dispersal). For example, fledglings of some species, such as Blackpoll Warblers (*Setophaga striata*), display exploratory behavior and different habitat use than adults prior to fall migration (Brown and Taylor 2015). Fledgling Eastern Bluebirds (*Sialia sialis*) utilize a greater amount of forest than breeding adults (Jackson et al. 2011), and fledgling Ovenbirds (*Seiurus aurocapilla*) select greater vegetation cover compared to adults (King et al. 2006). Fledglings may also select habitat that differs from their natal habitat, as seen in Black-capped Vireos (*Vireo atricapilla*; Dittmar et al. 2014). Prior to dispersal, White-throated Robin (*Turdus assimilis*) fledglings select forest over their natal agriculture habitat (Cohen and Lindell 2004). The high level of within- and between-species variation of adult and fledgling habitat use highlights the importance of focusing on all life stages, particularly the less understood post-fledging stage.

In addition to variation in habitat use between adults and juveniles, there can also be significant differences in survival between the two different life stages, particularly during the breeding season. Until recently, the post-fledging stage was one of the least understood periods in avian life cycles because it is one of the most difficult stages to observe. However, recent advancements in radio-tracking technology have increased the ability to track juveniles in the post-fledging period, increasing the understanding of survival rates and habitat use during this life stage (King et al. 2006).

The Barn Swallow (*Hirundo rustica*) is a common and widespread aerial insectivore that breeds across North America and winters in Central and South America (Brown and Brown 2019). Similar to other aerial insectivores, Barn Swallow populations are declining in parts of their range and are listed as “Threatened” in Canada (Government of Canada 2017). While reasons for these population declines are not clear, Barn Swallows commonly nest and forage in agricultural habitats and could therefore be negatively impacted by aspects of agriculture intensification that may reduce available foraging habitat or aerial insect populations.

Higher numbers of foraging Barn Swallows are found in pastures (fields where livestock graze) compared to crop fields (Evans et al. 2007), and Grüebler et al. (2010) showed that the presence of pasture increases productivity and nestling survival for double-brooded Barn Swallows, indicating that pasture is a high-quality habitat. Post-fledging survival of Barn Swallows has been studied in Europe (Grüebler and Naef-Daenzer 2008, Grüebler et al. 2014), and in Ontario, Canada (Evans et al. 2019), but to our knowledge there has been no research that also focused on post-fledging habitat use. Furthermore, habitat use studies for Barn Swallows have focused on adults, and it is not known if Barn Swallow fledglings use habitat similarly.

We explored Barn Swallow post-fledging habitat use and survival in a declining population in a predominantly agricultural area. For the purposes of this study, we defined habitat use as use of different land cover types. We hypothesized that (1) if natal habitat is important to Barn Swallow fledglings, then it will have an effect on fledgling behavior (distance from the nest), quality, and survival; and (2) Barn Swallow fledglings will preferentially use the highest-quality foraging habitat. We predicted Barn Swallows hatched in higher-quality pasture habitat will (1) fledge at higher quality (higher mass, longer tarsi, and wing chord at fledging), (2) have earlier fledge dates, (3) stay closest to the nest (have the shortest maximum distances), (4) use high-quality pasture habitat disproportionately relative to its availability, and (5) have the highest survival rates compared to fledglings using other habitat types in the post-fledging period.

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. There were 11 study sites representing 3 habitat types: agriculture with crop (hereafter "crop," *n* = 4); agriculture with livestock, including both cows and horses (hereafter "pasture," *n* = 4); and non-agriculture (hereafter "non-agriculture"; a park, a marina, and a municipal works yard, *n* = 3). All sites were surrounded to a radius of 300 m with their assigned habitat type.

Nest Monitoring

We checked Barn Swallow nests twice a week from May 4 to August 6 in 2015 (*n* = 258) and May 2 to August 10 in 2016 (*n* = 230). Barn Swallows nested on or in barns, old sheds, or other buildings. We recorded the date on which the first egg of a clutch was laid (lay date), clutch size, hatch date, brood size (best estimate closest to fledging), and if a nest fledged (1 = at least one nestling fledged, 0 = no nestlings fledged). We determined the hatch date (day 0) of nestlings using an 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) and known average fledging age for our study sites, which was also 21 days (range: 18–23) over 2 yr (*n* = 14). Nests were considered to have fledged young if the nest was empty, and nestlings were day 18 or older with no signs of predation (i.e. broken nest, blood, dead nestlings). We assumed that nests fledged on the day following the last day they were observed in the nest. Nest siblings were assumed to have fledged on the same day (Turner 2006).

Radio Telemetry

We used radio telemetry to track the habitat use and survival of Barn Swallow fledglings (defined as birds up to 21 days after leaving the nest) in 2015 and 2016. We affixed radio transmitters to 35 nestlings in 2015 (LOTEK Picopip Ag379 VHF radio transmitters, battery life of ~29 days and range of ~1 km) and 48 nestlings in 2016 (LOTEK digitally coded nano-tag NTQB-2 radio transmitters, battery life of ~33 days, ~5.0 s burst interval rate and range of ~1 km). In 2015 we selected 12 nestlings from pasture sites, 12 from crop sites, and 11 from non-agriculture sites. In 2016, because of logistics (non-agricultural sites were distant from other sites), radio transmitters were only put on nestlings from crop (*n* = 23) and pasture (*n* = 25) sites. One or two nestlings per nest were randomly selected and fitted with radio-transmitters 15 days post-hatching (range day: 14–17) (Grüebler and Naef-Daenzer 2008). We used leg-loop harnesses to attach radio transmitters (0.35–0.42 g; Rappole and Tipton 1991) with a non-permanent harness (Kesler 2011). Harnesses were fitted based on an allometric function from Naef-Daenzer (2007) for European Barn Swallows and adjusted accordingly once radio transmitters were fitted to nestlings. Radio transmitters plus harnesses weighed less than 0.6 g, which is <5% of average nestling body weight (Fair et al. 2010). Measurements were taken by two observers in 2015, and one of those same observers in 2016. We measured tarsus to the nearest 0.05 mm, wing chord and tail length to the nearest 0.5 mm, and mass to the nearest 0.5 g of each nestling equipped with a radio tag.

Fledglings were tracked for ~1 mo after fledging using hand-held receivers, 3-element folding YAGI antennae (2015, 2016), and automated MOTUS radio towers (2016). We attempted to locate each individual fledgling a minimum of 1–2 times per week (mean: 5 locations per bird). We conducted scanning surveys in 2015, searching for fledglings initially at nest sites (*n* = 10) and then we used data from eBird sightings (https://ebird.org) and personal observations to track fledglings. In 2016 we conducted standardized surveys once a week for each site (*n* = 8) in addition to surveys, guided by automated radio tower data (see below) and 2015 habitat and location data. Each week standardized surveys were conducted at (1) each nest site and (2) at an additional 3–4 points spaced out evenly and in each cardinal direction around the nest site (dependent on topography). Surveys away from the nest site were conducted in the same directions, but at increasing distances from the nest site with each week fledglings were out of the nest (500 m, first week; 1 km, second week; 2 km, third week; 3 km, fourth week). We surveyed for 2 min with the antennae directed in each cardinal direction twice for 15 s. If a tagged bird was detected during a survey, it was pursued on foot to obtain a visual sighting of the bird.

We tracked individual fledglings based on their radio signal, and each location point was assigned a confidence level based on the strength of the radio signal and, if possible, a visual observation of a group of Barn Swallows, fledgling Barn Swallow, or an individual with a radio transmitter. Location points with low confidence rankings (signal strength lower than 20 and gain below 80) were not used in analyses. 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, resulting in a location point for that bird. Additional information recorded for each location point included time, date, ID number, and habitat type (e.g., crop field where crop type was identified in 2015 and 2016).

In 2016 an automated MOTUS radio tower system (Taylor et al. 2017), consisting of 4 towers, was erected (towers between 6 and 7 m high) in Ladner and Richmond, British Colombia. The towers were 8–20 km apart and encompassed the study area. 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). Three towers had a range of ~1–2 km with the fourth having a greater range of 5–10 km. Towers were erected before nestlings were equipped with radio transmitters and were used to locate tagged birds after leaving their natal site and to increase hand-held tracking efficiency, as well as to confirm fates (dead or alive) of individuals during analysis.

Post-fledging Habitat Use

To analyze post-fledging habitat use, we calculated the percent available and percent use of each habitat class per individual location point. Available habitat was calculated by creating a buffer around each individual bird location point and calculating the proportion of each habitat class within that buffer using ArcGIS (ESRI, Redlands, California, USA). Increased fledgling movement away from the nest was addressed by splitting habitat use into 2 different time periods, days 1–6 and day ≥7, based on information from this study and from European Barn Swallows (Naef-Daenzer and Grüebler 2014) showing that fledglings start to move farther from nest sites after 6 days, and following similar methods as Dunn et al. (2017). Buffers for each time period were calculated separately as the average distance between location points for each individual. We calculated a 0.33 km buffer for the first period (days 1–6) and a 3.56 km buffer for the second period (day ≥7). We calculated used habitat as the percentage of observed bird locations by habitat across all locations per individual. We calculated available habitat as the average percentage of each habitat type in each location buffer across all locations per individual. To determine habitat types, a digital map was created for each location based on several different landcover datasets; a crop cover dataset (Fraser Lowland Agricultural Crop Cover Surveys [Public]; Ducks Unlimited Canada et al. 2017), the Sensitive Ecosystems Inventory dataset (Sensitive Ecosystem Inventory for Metro Vancouver & Abbotsford 2010–2012, 2009; http://www.metrovancouver.org/data), the Metro Vancouver Land Cover Classification dataset (Land Cover Classification: Public Project Report 2010; http://www.metrovancouver.org/data), 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 onto one map allowed us to determine differences in crops and pasture fields, as well as incorporating important marsh and urban habitat around each location, because 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 used 9 broad habitat classes: marsh (wetlands, riparian, estuary, intertidal), crops (vegetable crop, grain crop, fruit crop, winter cover crop), pasture (pasture fields and fallow fields), barren (uncultivated fields, which encompasses bare and harvested fields), water, grass (mostly lawns and shrubs), trees, unknown, and urban (buildings, including greenhouses). Location points for each individual fledgling were overlaid onto each habitat map to identify habitat used by each tagged bird in comparison to habitat availability. 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).

Statistical Analysis

Modeling and statistical analysis was performed in RStudio 1.0.136 (RStudio Team 2016) with program R 3.5.2 (R Core Team 2018). Results are reported as means with standard deviation.

Effect of natal habitat and year on fledgling quality, fledge date, and behavior. We used linear mixed effects models, linear regression, and Pearson's correlation tests to determine if natal habitat had an effect on fledgling quality (mass, tarsus, wing chord, brood size), fledge date, or fledgling behavior (maximum distance or the farthest distance each fledgling traveled from the nest). Brood size was included as a measure of quality as it has been shown as an indicator of apparent post-fledging survival (Styrsky et al. 2005). Due to measuring some nestlings at different ages ($n = 19$), we tested for an effect of nestling age on mass, wing chord, and tarsus using Pearson correlation *t*-tests. We initially tested for heterogeneity among these potential covariates by natal habitat and year using one-way ANOVA and Welch's 2-sample *t*-tests. Based on these preliminary analyses, we ran an initial set of linear mixed-effects models to determine if there was an effect of natal habitat (crop, pasture, non-agriculture) and year on fledgling quality and maximum distance from the nest. We used maximum distance as the main effect, nest location and nest ID as nested random effects to control for pseudoreplication (multiple nests per site and multiple nestlings per nest were used), and year, natal habitat, tarsus, mass, fledge date, and wing chord were used as covariates where appropriate. We ran a second set of linear mixed-effects models, with an interaction between year and natal habitat (without non-agricultural hatched nestlings), to determine if there was variation in fledgling quality or behavior between years in crop and pasture natal habitat. We used linear regressions to examine the effect of nestling mass on maximum distance fledglings traveled and the maximum fledge date (greatest number of days a fledgling found outside of the nest). We further tested for an effect of fledgling behavior, using a Pearson's correlation test, to examine the effect of overall distance (total location points for each fledgling) from the nest and number of days since birds fledged, between years and within each year (2015, 2016) separately.

Post-fledging habitat use. To test our prediction that fledglings use pasture habitat more than it is available, we compared used to available habitat with a parametric compositional analysis using the ADEHABITAT package and *compana* function (Calenge 2006). We separated the post-fledging habitat use period into days 1–6 and days ≥7 to account for increased fledgling movement over time away from the nest. Used and available habitat types were calculated as the proportions of used and available total area, with totals summing to 1. Any zero values in the matrices were replaced with 0.0001 value, and we repeated the analysis with additional values (i.e. 0.00001) to determine if there was an effect of this value, as this arbitrary number can influence results (Dunn et al. 2017). Compositional analysis assumes independence of data points; however, our data violate this assumption where we have 2 individuals tagged from the same nest (Aebischer et al. 1993). Therefore, we removed data location points where nest siblings were found together, although there were few cases where this occurred (n = 10 of total n = 289). We did not use a 2-level spatial analysis approach recommended by Aebischer et al. (1993) because habitat selection at the home range or site level was by adult Barn Swallows, not the fledglings studied, and individuals were too mobile to quantify a home range (Dittmar et al. 2014).

Post-fledging survival. To determine if natal habitat, or fledgling quality or behavior variables, had an effect on post-fledging survival we ran Cox proportional hazard models to day 21 using radio-tracking data. We selected day 21 based on European Barn Swallow fledgling data from Naef-Daenzer and Grüebler (2014) where fledglings generally do not 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 date of the last confirmed sighting where a fledgling was alive. 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 transmitter, the location of the transmitter did not change for 3 days or more, or a transmitter was found damaged with feathers. Kershner et al. (2004) suggested fledglings were dead if their tag location did not change for 3 days or more. Furthermore, there was a year bias (5 events occurred in 2015, 1 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 transmitter 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. In addition, fledglings that disappeared in 2016 were never detected by the automated radio towers after their last hand-tracking detection, suggesting fledglings died rather than emigrated away from their natal sites. The same pattern was seen in European Barn Swallow fledglings within 3 weeks of fledging (Naef-Daenzer and Grüebler 2014).

Prior to fitting data for survival models, we examined the relationships between variables of interest, including mass, tarsus, fledge date, natal habitat, and year. We explored adding habitat used after fledging into the survival analysis as a variable of interest. However, there were very few location points across habitats for most of the fledglings that did not survive because they disappeared early in the tracking period, soon after fledging. Therefore, we had insufficient data because there were not enough "use" location points for this analysis. We examined 2 sets of survival models using the *coxph* command and *survival* package in R 2.38 (Therneau 2015). 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. In both cases we started with the most complex models and used a stepwise procedure to eliminate variables from the models to illustrate the effects of natal habitat and year on survival. Significance was assessed using likelihood ratio tests (Fox and Weisberg 2018). We present the statistics associated with dropping the term of interest from the final or null model (if all terms were dropped; Table 1). Kaplan-Meier plots were used to illustrate natal habitat and year effects on survival to 21 days of age.

RESULTS

Over both years we deployed 83 radio transmitters and confirmed that 82 of these birds fledged. We attempted to track 35 fledglings in 2015 (11 from non-agricultural sites, 12 from crop sites, and 12 from pasture sites) and 47

TABLE 1. Model output from the top 1-variable Cox proportional hazard models of fledgling Barn Swallow survival to post-fledge day 21 (n = 81).

Variable	Effect size (likelihood ratio)	95% CI	χ^2	P
Tarsus	2.61	0.43–1.10	2.61	0.11
Year	0.4	0.46–1.49	0.40	0.53
Natal habitat	1.15	0.60–2.07	1.15	0.56
Fledge date	0.01	0.94–1.07	0.0056	0.94
Mass	0	0.87–1.16	0	1.0

fledglings in 2016 (22 from crop and 25 from pasture sites). Seventy-two (87%) were successfully tracked for 2–37 days, and 289 fledgling location points for birds tracked outside of the nest were recorded over both years (mean of 5 locations per bird). Ten (12%) of the fledglings were not detected after leaving the nest (1 in 2015, 9 in 2016) and were assumed to have died.

Effect of Natal Habitat and Year on Fledgling Quality, Fledge Date, and Behavior

Chick 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 based on our data, which suggest mass decreased linearly with age while wing chord increased linearly. The best-fit line (linear for both mass and wing), slope, and intercept of each was calculated and adjusted to the median age (day 15). We found no relationship between age-adjusted mass and tarsus ($F < 0.01$, df = 1 and 79, $P = 0.99$) 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.

Comparing within year (2015) across all natal habitats, fledglings hatched in non-agriculture habitats had smaller tarsi (11.3 ± 1.0 mm) than fledglings hatched in either agricultural type (crop: 11.9 ± 0.6 mm; pasture: 11.6 ± 0.7 mm; $F_2 = 3.74$, $P = 0.028$). However, 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 ($F_2 = 1.87$, $P = 0.16$). Natal habitat had a significant effect on fledge date ($F_2 = 6.41$, $P = 0.0026$), where fledglings hatched in non-agriculture habitats ($n = 11$) fledged at a later date (July 1 ± 4.3 days) than fledglings hatched in both crop ($n = 34$; June 27 ± 3.7 days) and pasture ($n = 37$; June 27 ± 4.0 days) habitats. Non-agricultural fledglings stayed within 5 km of their nests, compared to agriculture fledglings, which traveled just under 20 km (Figure 1).

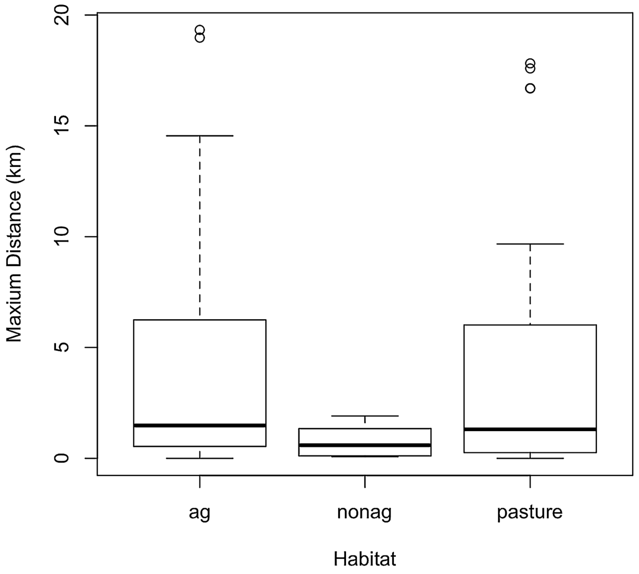

FIGURE 1. Maximum distance Barn Swallow fledglings traveled away from their nest by day 21 post-fledge in 2015 and 2016 by natal habitat (ag = crop habitat, $n = 35$; pasture = livestock habitat including cows and horses, $n = 37$; nonag = non-agriculture habitat including a park, marina and works yard, $n = 11$). Box plot represents the first and third quartiles, bolded lines represent the median and whiskers represent upper and lower limits.

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

For linear mixed-effects models with maximum distance as the dependent variable and including 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.

We further examined how fledgling quality (mass) affected fledge date and fledgling behavior and found mass had no effect on fledge date ($F = 2.05$, df = 1 and 79, $P = 0.157$), maximum distance fledglings traveled from the nest ($F = 0.46$, df = 1 and 73, $P = 0.50$) or the maximum number of days since fledge that birds were located ($F < 0.01$, df = 1 and 73, $P = 0.97$). The overall distance fledglings traveled was positively correlated with the number of days since they fledged for both years ($t_{373} = 9.40$, $P < 0.001$, $r = 0.44$; Figure 2). However, several individuals showed movements that appeared to be exploratory, while others gradually increased their distance from the nest as they aged.

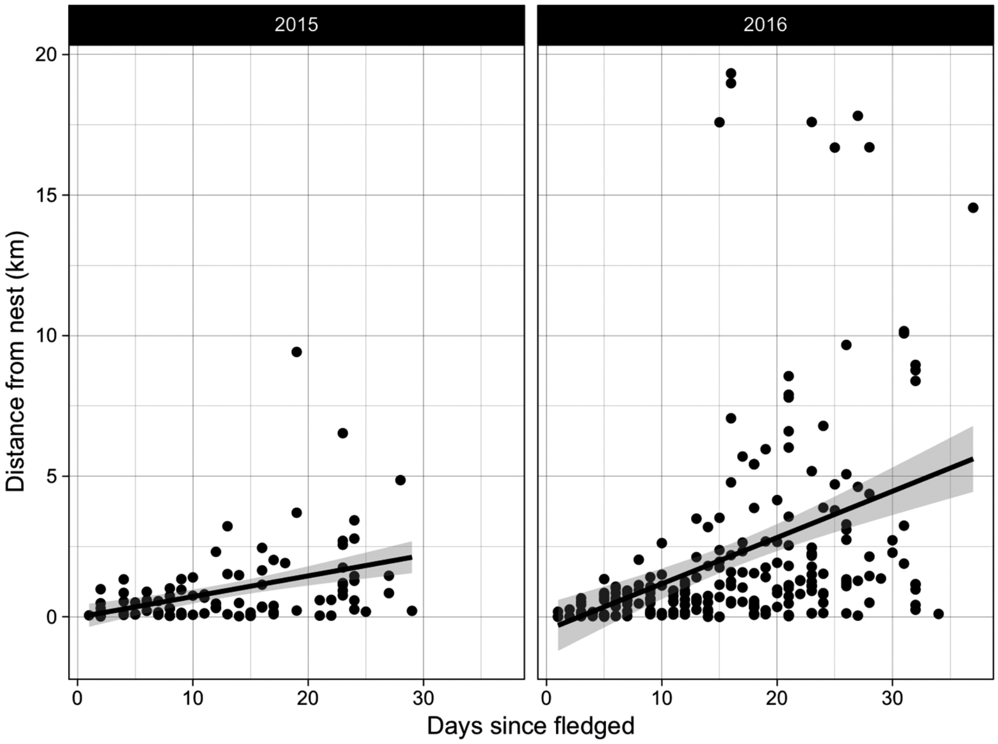

FIGURE 2. The total distance (km) Barn Swallow fledglings traveled from the nest by the number of days out of the nest in 2015 (n = 123) and 2016 (n = 252). The equation of the lines was fitted by linear regression (2015: $y = -0.011x + 0.07$; 2016: $y = -0.29x + 0.16$) with 95% confidence intervals.

Post-fledging Habitat Use

When we compared habitat types used by each individual to those available to each individual, fledglings did not use habitat types in proportion to their availability (Wilk's Lambda < 0.01, df = 8, $P < 0.01$), suggesting habitat use was not random. Habitat use was ranked as follows: crop > marsh > grass > pasture > urban > water > barren > unknown > tree (Figure 3). Crop habitat was used significantly more than all other lower-ranked habitat types (36% of habitat used was crop; 22% of habitat available was crop), including the second-ranked marsh habitat (Table 2). Marsh habitat was used significantly more than all other habitat types except crop (20% of habitat used was marsh; 27% of habitat available was marsh; Table 2).

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 confirmed depredated, likely by an accipiter, with only feathers, a leg with a band, and the intact radio transmitter found, 5.2 km from its nest, killed between 9 and 17 days post-fledge.

Survival probability to day 21 post-fledge over both years was 0.44 (95% CI: 0.35–0.57), calculated using a Kaplan-Meier curve. Survival probabilities did not vary significantly between fledglings hatched in different natal habitats or between fledglings tagged in different years, although there were nonsignificant trends toward higher survival probabilities in non-agricultural habitat (Figure 4A), and in 2016 (Figure 4B).

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 1). 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 2 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 fledgling quality (mass, tarsus, wing chord, brood size) or behavior (fledge date,

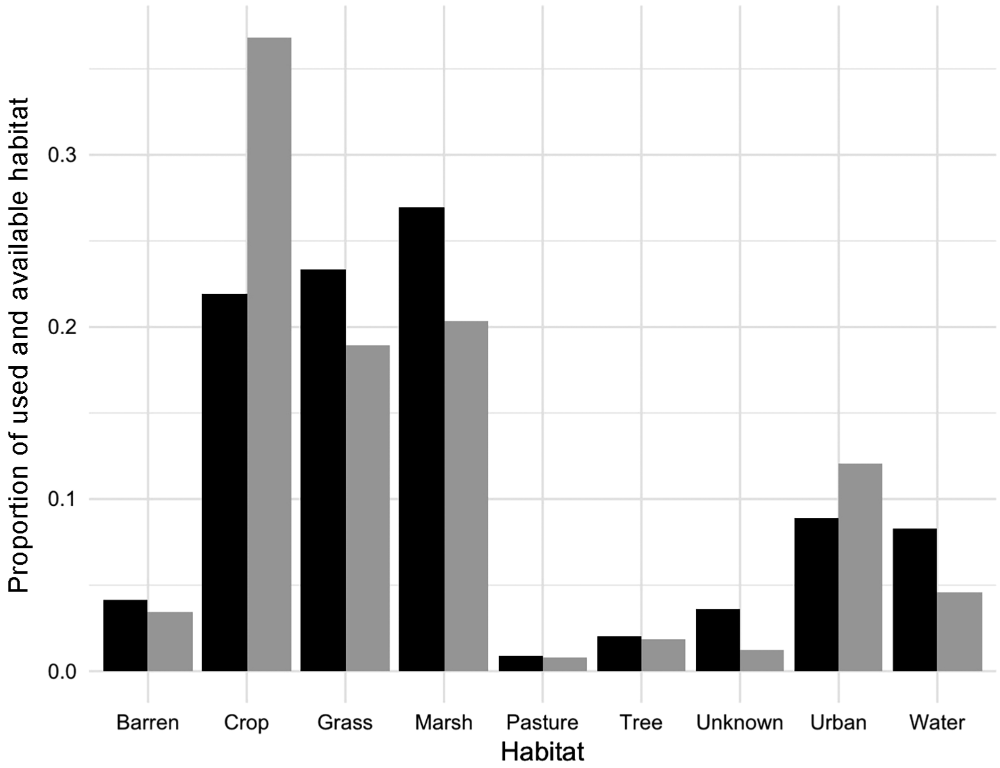

FIGURE 3. The proportion of available habitat (black bars) calculated as the proportion of area within a buffer around each individual fledgling location, compared to used habitat (gray bars) of fledgling Barn Swallows ($n = 61$) for 9 different habitat classes.

TABLE 2. Ranking matrix (*t* values in bold, $P < 0.05$) for comparison of used habitat to available habitat of fledgling Barn Swallows in crop ($n = 30$) and pasture ($n = 31$) natal sites from 2015 to 2016. Positive values indicate habitat in the row is used over habitat in the column.

	Crop	Barren	Pasture	Tree	Unknown	Grass	Urban	Water	Marsh
Crop		**5.19**	**5.72**	**5.48**	**7.54**	**2.66**	**3.26**	**5.16**	**2.78**
Marsh	**−2.78**	**2.08**	**1.82**	**2.04**	**4.14**	−0.05	1.00	**2.28**	**–**
Grass	**−2.66**	**1.87**	**1.78**	**1.95**	**3.84**	–	0.99	**2.06**	0.05
Pasture	**−5.72**	0.49	**–**	0.47	**3.42**	**−1.78**	−0.35	0.90	**−1.82**
Urban	**−3.26**	0.73	0.35	0.62	**2.79**	−0.99	–	1.01	−1.00
Water	**−5.16**	−0.35	−0.90	−0.59	**1.88**	**−2.06**	−1.01	–	**−2.28**
Barren	**−5.19**	–	−0.49	−0.15	**2.28**	**−1.87**	−0.73	0.35	**−2.08**
Unknown	**−7.54**	**−2.28**	**−3.42**	**−2.87**	**–**	**−3.84**	**−2.79**	**−1.88**	**−4.14**
Tree	**−5.48**	0.15	−0.47	–	**2.87**	**−1.95**	−0.62	0.59	**−2.04**

maximum distance traveled from the nest). We found that fledglings used crop habitat more than it was available and more than any other habitat available, including pasture. Across 2 years, the probability of post-fledging survival over a 21-day period was relatively low (0.44) in comparison to other altricial (Naef-Daenzer and Grüebler 2016) and northern temperate species (Lloyd and Martin 2015). However, survival was independent of other potential explanatory variables, specifically fledge date, tarsus, mass, year, and natal habitat. Overall, our results suggest that natal habitat had no effect on post-fledging survival, 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 fledgling quality as measured by mass, brood size, and wing chord prior to fledging or in maximum distance fledglings traveled in the post-fledging period. However, a later fledge date and shorter tarsi were found 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. In addition, a later fledge

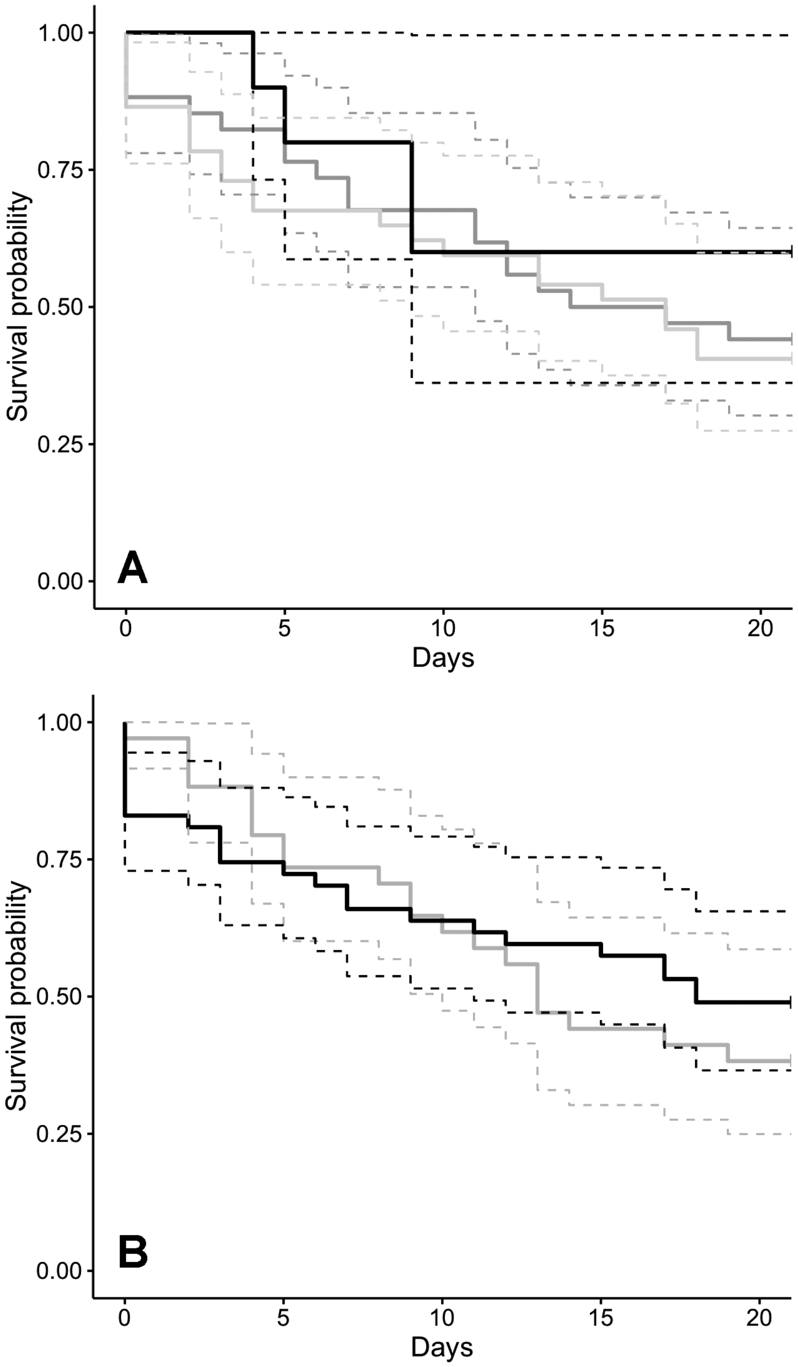

FIGURE 4. Kaplan-Meier curve of survival over time (solid lines) showing cumulative survival probability of Barn Swallow fledglings with 95% upper and lower confidence intervals (dashed lines) (**A**) hatched in crop (*n* = 12; dark gray line), pasture (*n* = 11; light gray line), and non-agriculture (*n* = 3; black line) habitats for 2015 and 2016 combined and (**B**) by year (2015 gray line, 2016 black line).

date is likely explained by non-agriculture sites having an overall slightly later breeding season (approximately a week later) observed over a 4-yr period, likely due to higher altitudes of non-agriculture sites (C. K. Boynton, personal observation).While there was no significant difference in maximum distance traveled, perhaps due to small sample size, it was striking that non-agriculture fledglings only traveled maximum distances of 5 km away from the nest site, compared to both crop and pasture fledglings, which traveled 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 besides smaller tarsi that fledglings hatched in non-agriculture habitats were low quality as there was no difference between mass, wing chord, or brood size across natal habitats.

Our results 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, Cohen and Lindell 2004; Dickcissels [*Spiza americana*], Berkeley et al. 2007; Eastern Bluebirds, Jackson et al. 2011; Grasshopper Sparrows [*Ammodramus savannarum*], Streby and Andersen 2013). We also found that Barn Swallow fledglings are highly mobile during the post-fledge stage, especially in comparison to other fledgling altricial songbirds during this period. For example, 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 >1 km in 24 days (Streby and Andersen 2013), compared to several of our tagged fledglings, which reached distances of 19 km at 16 days post-fledge. Movement away from natal sites is also indicative of exploratory behavior in the post-fledging stage. White and Faaborg (2008) defined exploratory movement as movement greater than 300 m 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 and Rodewald 2010). Several of our tagged Barn Swallows demonstrated exploratory behavior, moving several kilometers away from the natal area, or staying under 1 km, but then subsequently returning to the natal site. Other individuals showed gradual movement away from the natal site, but remained relatively close regardless. Similar exploratory movements have been seen in fledgling Wood Thrush (*Hylocichla mustelina*; Vega Rivera et al. 1998) and Blackpoll Warblers (Brown and Taylor 2015), and is potentially a common post-fledge behavior for migrants. Exploratory movement has also been described as fledglings visiting unfamiliar terrain (Baker 1993), which is comparable with exploratory behavior of our fledglings that were located over “novel” habitats not used for breeding, such as marsh and water.

Fledgling Barn Swallows used crop habitat more than it was available. While the proportion of crop habitat that is available across the study area is quite high (22%), marsh covers a slightly greater area (27%), but we found Barn Swallows did not use this habitat as much as crop habitat (Figure 3). Barn Swallow fledglings also foraged less in pasture habitat, contrary to our predictions, although pasture was only a small proportion of overall area in our study area. Barn Swallow fledglings could be using crop habitats during the post-fledging period because there is a higher proportion of aerial insects in the boundary edges of hedgerows bordering on crop fields, in comparison to pasture fields (Evans et al. 2003). Fritch et al. (2017) showed that an exclusion of grazing increases invertebrate abundance and richness in field margins, which could partially explain why Barn Swallow fledglings use crop habitat over pasture habitat. Crop rotation between years is common in this region, which could provide a larger diversity of prey for fledglings leading to crop habitat usage, and as adult Barn Swallows are shown to be less selective in prey type than other aerial insectivores, such as Tree Swallows (*Tachycineta bicolor*), it is possible fledglings have a similarly broad diet (Brown and Brown 2019, McClenaghan et al. 2019). Crop habitat is used more than pasture by White-throated Robins during the post-fledge period (Cohen and Lindell 2004) and perhaps provides more benefits than just prey for fledglings, such as protection from predators during roosting, as some of our location points were roosting points. In addition, adult North American Barn Swallows use similar habitat to fledglings in our study and are often found foraging in open areas, specifically fields and meadows during the breeding season (Brown and Brown 2019). Similar habitat use between adults and fledglings has been shown in European Turtle-Doves (*Streptopelia turtur*; Dunn et al. 2017) and a similar pattern between UK fledgling and adult Barn Swallows has been suggested (Evans et al. 2007).

Agricultural intensity is implicated in the population decline of aerial insectivores (Paquette et al. 2013, Stanton et al. 2018), but the selection for crop habitat by fledgling Barn Swallows in our region suggests not all types of agriculture are necessarily detrimental. Crop fields in this region are heterogeneous and are often composed of a series of smaller mixed crop fields (approximately 0.5–20 ha), in comparison to other regions of the country, which are more associated with increased agricultural intensity and large fields of monoculture crops, such as in Manitoba or Saskatchewan (Statistics Canada 2016). A similar pattern of heterogeneity in crop fields, including smaller field sizes and higher crop diversity, is related to increased activity of bats, suggesting higher insect abundance (Monck-Whipp et al. 2018). Common crops planted in the study region that contribute to crop diversity include berries, potatoes, peas, beans, corn, alfalfa, and barley. A variety of pesticides are recommended for use on the crops in the study area, although field-level details are not available (Government of British Columbia 2017). However, crop fields in this area are currently undergoing crop conversion toward more intensive monocultures of berry fields, specifically blueberries, as well as greenhouses. For example, the amount of land occupied by greenhouses in the major portion of our study area has increased from 21 ha in 1995 to 271 ha in 2018, which could reduce the availability and diversity of aerial insect prey available for Barn Swallows during an already critical and vulnerable life period (Ducks Unlimited Canada 2019).

We found no evidence that high-quality natal habitat (i.e. pasture) based on previous research on European

Barn Swallows from Evans et al. (2003, 2007), Grüebler et al. (2010), and Orłowski and Karg (2013), had any effect on post-fledging survival, indicating this type of habitat is less important for Barn Swallows in our study area during the post-fledging stage. In Europe, aerial insect abundances are higher over pasture (Evans et al. 2007) and in the presence of livestock (Grüebler et al. 2010, Orłowski and Karg 2013), 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-fledging Barn Swallows and our data suggest fledglings do not follow this same pattern, especially as the total number of insects at pasture sites has been shown to be higher than crop sites (W. Boynton et al., personal communication). We would expect that if pasture habitat is vital to fledgling Barn Swallows, those hatched in pasture habitat would stay close to the natal site for the duration of the post-fledging period before migrating. Conversely, fledglings hatched in non-pasture habitats should have higher maximum distances if they moved preferentially to forage in pasture habitats. However, fledglings hatched in pasture habitat exceeded distances from the nest of 15 km, similar to those hatched in crop habitat, whereas fledglings hatched in non-agriculture did not travel greater than 5 km from their natal site, however these differences were not significant.

The estimated survival of Barn Swallow fledglings in our study was similar (0.44) to that reported for fledgling Barn Swallows in Ontario (0.42; Evans et al. 2019). However, their survival was calculated across an 8-week period, compared to our 3-week period, which would suggest that survival in our region could be much lower if this mortality rate continued over 8 weeks. Based on the Ontario data, and 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 and 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 and 0.68 as being 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, at least in part, by low survival of fledglings. Furthermore, Breeding Bird Survey data for this region show a declining trend of −4.92% year^{-1} for Barn Swallows from 1970 to 2017 (Smith et al. 2019). 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 was found to be independent of fledgling mass in several species, including Dickcissels (Berkeley et al. 2007) and Yellow-eyed Juncos (*Junco phaenotus*; Sullivan 1989) as well as non-passerines such as Atlantic Puffins (*Ratercula arctica*; Harris and Rothery 1985), so the relationship between mass and survival is not a taxa-wide pattern (Magrath 1991, Schwagmeyer and Mock 2008).

In Common Murre (*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 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-fledging habitat use, because most mortality occurred soon after fledging, limiting the number of locations available to compare habitat use of those that survived vs. those that did not. It is therefore possible post-fledging habitat could be driving low survival rates in our study area (Berkeley et al. 2007, Fisher and Davis 2011). Despite post-fledging Barn Swallows using crop fields more than they were available in our study area, these fields could be producing lower-quality aerial insects, creating an ecological trap where fledglings are not able to obtain high enough nutrients from their prey to survive. Weather could also negatively impact survival of post-fledglings as abundance of Barn Swallow prey (aerial insects) 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 transmitter signal picked up thereafter, which points more directly to predation as predators often destroy transmitters (Naef-Daenzer et al. 2001), so mortality due to weather or starvation is less likely a factor in our study. If there is a wide suite of predators using crop fields, such as Sharp-Shinned Hawk (*Accipiter striatus*), Cooper's Hawk (*A. cooperii*), or Merlin (*Falco columbarius*), which are found in our study area, then predation may be the driver of lower survival rates.

While our study was the first to track fledgling swallows in western Canada, a portion of our analysis was limited by small sample sizes. Further research is needed to increase sample sizes of individual fledglings, specifically to examine if used habitat affects survival rates, as this was a limitation of our study. Because our research indicates Barn Swallow fledglings in this region have relatively low survival rates, further research is needed on this period, and for other aerial insectivore species, which may be experiencing similarly low post-fledging survival, potentially causing population declines.

Overall, we found only minor effects of natal habitat on both fledgling quality and behavior. Also, contrary to our predictions, we found that Barn Swallow fledglings use crop habitat more than pasture. Therefore, if crop fields undergo a decline or transformation through agricultural intensification and crop conversion, Barn Swallow fledgling survival could be negatively affected. This could have several implications for conservation of this species, currently listed as Threatened under the Species at Risk Act in Canada (Government of Canada 2017). If low juvenile survival in the post-fledge stage is driving population declines in this species, protection of post-fledge habitat could be critical. As crop habitat appears important for fledgling Barn Swallows after they leave the nest, conversion of this habitat type, creating a more homogeneous landscape could have further negative implications for an already declining species.

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Data depository: Analyses reported in this article can be reproduced using the data provided by Boynton et al. (2020).

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