Habitat drivers of Barn Swallow (*Hirundo rustica*) feeding behaviour and breeding productivity

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Abstract

Barn Swallows *Hirundo rustica* belong to a declining guild of birds, and much remains unknown about the causes of these declines. Research in Europe has shown that pastures, hay fields, and livestock benefit Barn Swallow populations, and this study aimed to determine whether similar trends are found in a North American context. We studied this in two ways, first, by examining breeding productivity in three different habitats and then by examining how much they fed over certain types of fields. Breeding productivity parameters of swallows were largely similar although there were some differences, with higher fledging success in crop habitat and a higher proportion of intermediate nests in non-agricultural habitat in one of the years, however the overall picture suggests that non-agricultural, crop, and livestock are largely similar to one another, unlike what was found in European studies. Weather and manure management may have a greater impact on breeding productivity and warrant future research. We also found no difference in Barn Swallow feeding over grassland set-aside and cultivated fields, though the insect communities were different.

Keywords: aerial insectivore; agricultural intensification; barn swallow; breeding productivity; grassland; livestock

Dedication

To Claudia, Peter, Bob and Fernanda; thank you is just the beginning of it. Also to Emma, Kiara, Jess, Drulia, Courtney, and Persia, the best friends a person could ever hope for.

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Chapter 1.

Annual variation in breeding phenology and productivity in relation to agricultural habitat in the Barn Swallow *Hirundo rustica*

1.1. Introduction

Recent evidence suggests that aerial insectivore bird populations across North America are in decline, including swallows (Family *Hirundinidae*) that depend on farmland, and that this potentially involves a systematic change related to the birds' insect diet (Environment Canada, 2012; Nebel et al., 2010). However, there is no consensus in the literature about whether or not there are commonalities in the timing, or causes, of aerial insectivore declines (Michel et al., 2015; Smith et al., 2015). Historical changes in the use of the pesticide DDT are implicated in dietary shifts of aerial insectivores to less profitable prey items, suggesting that pesticide use could be driving trends of aerial insectivore decline (Nocera et al., 2012). It has also been suggested that a newer class of pesticides, neonicotinoid pesticides, are linked to declines in insectivorous bird populations (Hallmann et al., 2014). However other evidence suggests that broader changes in climate and weather patterns are driving population declines in some regions, with links between various climate indices and population trend estimates (García-Pérez et al., 2014).

Due to changes in agricultural habitats, and in particular decreases in available pasture via intensification of cultivation of farmland there have been declines of farmland birds (Donald et al., 2006) and of aerial insectivores (Robillard et al., 2012). For Barn Swallows (*Hirundo rustica*) in particular, decreases in livestock numbers and decreases in pasture-dominated livestock production are implicated in population declines (Ambrosini et al., 2012). Evans et al. (2007) compared pasture to cultivated fields and found both more insects and more foraging Barn Swallows on pasture fields. There is also evidence that presence of livestock increases breeding productivity by up to 1.6 chicks per breeding season, both via presence of livestock at the nest site and increased manure heaps in the surrounding habitat (Grüebler et al., 2010). One study found that

presence of livestock buffered against severe declines in abundance of Barn Swallow breeding pairs (Ambrosini et al., 2012), and another found that the larger insects found near livestock led to larger swallow breeding colonies (Orłowski and Karg, 2013). Similarly, a study conducted in Italy found that presence of livestock in the years preceding the data collection predicted Barn Swallow presence on a farm, that swallows laid later at sites with no livestock, and there was a positive correlation between number of cattle and fledging success (Ambrosini et al., 2002).

Evidence for declines in different guilds of aerial insectivores in western North America is generally weaker, and more inconsistent, than that in eastern North America (Nebel et al., 2010). However, available data suggest there have been marked changes in abundance of livestock and in livestock farming practices in the Pacific North West, which could influence population changes in aerial insectivores in this region. Barn Swallow populations have declined by approximately 4.73 percent per year between 1970 and 2015 in British Columbia (Environment and Climate Change Canada, 2017). For example, between 2001 and 2011, cattle numbers in Metro Vancouver decreased 38.0 percent, and horse numbers decreased 19.6 percent (Metro Vancouver, 2014). mirroring a province-wide trend of declines in cattle farming (British Columbia Ministry of Agriculture, 2011). In fact, over this time period there was a 38 percent decrease in the number of beef cattle farms in British Columbia, from 4,177 in 2006 to 2,579 in 2011, with a 29 percent decline in beef cattle numbers (British Columbia Ministry of Agriculture, 2011). In contrast, dairy cow numbers have remained relatively constant, increasing by 1 percent during the same time period (British Columbia Ministry of Agriculture, 2011). In total, 62 percent of crop land in British Columbia is pasture, and although there has been a general trend for an increase in pasture land since 1986, between 2006 and 2011 it decreased by 9 percent (from 1,770,937 hectares to 1,611,657 hectares (British Columbia Ministry of Agriculture, 2011). Therefore, a major change in agricultural land use in BC has involved livestock farming.

In light of these changes in livestock production in British Columbia, the primary goal of this study was to determine whether there are differences in breeding phenology and breeding productivity of Barn Swallows at livestock, crop and non-agricultural sites. Previous work comparing Barn Swallow breeding success in the context of livestock production has largely been conducted in Europe (Ambrosini et al., 2012; Grüebler et al., 2010; Orłowski and Karg, 2013), and ours is the first study to examine trends in a North

American context. Specifically, we compared a) breeding phenology (laying dates for, and proportions of, first, intermediate and second clutches), b) fecundity (mean clutch size, seasonal variation in clutch size), and c) breeding productivity (chick survival, chick quality, fledging success) among sites with livestock, crop sites and non-agricultural sites (e.g. parks). We also attempted to explain seasonal- and year-specific patterns of breeding success in terms of frequency of occurrence of nest mites, predation, and food (insect) availability.

1.2. Methods

Fieldwork was conducted between May – September 2013 and 2014 at 11 different sites in a region of intensively managed agricultural land in southwestern British Columbia, Canada, close to the city of Vancouver (49.07 N, 123.13 W). We found potential breeding sites based on map searches and discussions with local naturalists and selected sites that had at least five nests and fitted the following criteria: a) for livestock sites, horses or cows were present at the site; b) crop sites were surrounded by agricultural land and had no livestock were present within 500 meters of the nest sites, and c) at non-agricultural sites there was no agricultural activity of any sort within at least 500 meters of the nest locations.

We attempted to find four replicates of each site type; non-agricultural sites were rare and only 3 sites were found (Table 1.1), and we visited each one to three times per week to monitor Barn Swallow breeding. We used a specially designed mobile nest camera (Peeper, Daryl Cockle, Vancouver, BC, Canada) to monitor nests. The Peeper consisted of an iPhone camera secured in a holster at the top of an extendable pole and an iPad secured at waist-level in a holster. The iPhone was positioned carefully above the nest with the camera portion of the iPhone above the center of the nest, and wirelessly connected to the iPad via Bluetooth, so that nest contents and activity could be directly observed with minimum disturbance. Using the Peeper, on each visit we recorded a) the presence and number of feathers in the nest cup (an early indication of nesting activity or occupancy); b) the number of eggs (clutch size); c) the number of nestlings (brood size), d) whether feces were present, indicating the birds were once present in the nest, e) whether mites were present and f) any evidence of predation. If mites were found in a nest and the Peeper was contaminated, the peeper was disinfected using tissues and 70 percent ethanol to avoid contaminating other nests. We

estimated the age of any nestlings present based on a Barn Swallow-specific nestling ageing guide (Fernaz et al., 2012). Hatch date was predicted using the penultimate egg plus 14 days, and we visited nests on, or as close to predicted hatch date as possible. Each nest was given a unique number and nest locations were recorded on detailed maps for each site. When the same nest had multiple clutches we labelled these A and B but for subsequent analysis we categorised nests as first, second, and replacement breeding attempts (see below for details). We calculated expected fledge date using hatch date plus 18 days, and visited the nest as close as possible to expected fledge date to determine whether the nest was successful. For 149 nests throughout the breeding season totaled over two years, nestlings were banded at day 9 post-hatching with a numbered Canadian Wildlife Service metal band (Environment Canada banding permit # 10646), we measured body mass, scored body fat and measured tarsus, wing and tail length (Pyle, 1997), and recorded capture date and time.

1.2.1. Insect sampling

In summer of 2013 and 2014 we placed two insect nets per site where possible based on limitations due to farm and other vehicle traffic, property owner preference, physical limitations such as impenetrable surface or water, and limitations due to animal traffic or animal needs. We employed passive wind nets, designed to rotate on a pole in the direction of the wind so that the mouth of the net faced upwind, allowing interception of aerial insects with nets positioned so that the mouth was one meter above the vegetation (Hussell and Quinney, 1985). The ends of the nets contained jars of 70 percent alcohol where the insects were collected at or near sunrise daily, and each sample was labeled and placed a separate vial according to the collection date and the net from which the sample was retrieved. We recorded wind speed for a two-minute period using a digital anemometer at the time of collection (La Crosse Technology, Model # EA-3010U). Data showed that insect abundance estimated for one net was positively correlated with insect abundance from a second net at a given site ($r^2 = 0.44$, P < 0.001), showing that the nets at each site provide a representative sampling of insect abundances.

Arthropod samples were counted and sorted to taxonomic order by pouring contents of a vial into a Petri dish and examining them under a dissecting microscope. Identification of arthropods was completed based on the taxonomic keys and pictoral

guides (American Museum of Natural History, 2017; Iowa State University Department of Entomology, 2017; Johnson and Triplehorn, 2004; Marshall, 2017; University of Queensland, n.d.). Arthropods in poor condition, which we were not able to identify, were counted but not assigned to a taxonomic order, fragments were not counted, and expert entomologists identified intact ones that we could not identify with keys.

1.2.2. Data manipulation and analysis

We obtained some breeding data from 618 nests over two years and three habitat types, and 290 (46.9 percent) nests were assigned as either first or second nests based on field data and nest checks. However, since not all sites/nests were checked daily we had varying levels of certainty with regard to each nest record, e.g. first egg dates, hatch dates or clutch sizes were not always known with certainty (± 1 day or 1 egg) for all nests. We therefore used data from nests with high-quality data to estimate 'missing' data for as many of the remaining 328 nests (53.1 percent) as possible in a step-wise process, i.e. estimated nest order. First, we calculated the mean interval between first egg date and hatching date for a sample of nests were these were both known. Mean interval was 18 days for clutch sizes of 2-4 eggs and 19 days for clutch sizes of 5-6 eggs. We used these values to estimate first egg dates where hatching date but not egg date was known with certainty. We then calculated the range of first egg dates for 'known' first (A), i.e. the first nest recorded at a specific, mapped, nest location and then calculated first egg dates for 'known' second (B) nests where breeding was successful for the first nest (i.e. chicks fledged) and then a second clutch was initiated at that same nest location. We then used the 5th or 95th percentile date (Table 1.2) to assign 'unknown' nests as either first or second nests. Any nest with a first egg date > Anest 95th percentile date or < B-nest 5th percentile date were considered to be 'intermediate' or replacement clutches.

Data manipulation and statistical analysis were conducted using SAS software ("SAS," 2013) and R (R Core Team, 2015).

1.3. Results

1.3.1. Variation in breeding phenology

Total sample sizes for first, intermediate and second nests were n = 106, 95 and 75 for 2013 and n = 157, 68 and 117 for 2014, respectively (though we did not have complete breeding data for all nests). The overall pattern of initiation of egg-laying for all nests varied throughout the season and differed between 2013 and 2014 (Figure 1.1). In each year there was an initial peak of laying at around Julian day 140 (May 20), but in 2014 there was a more defined bimodal distribution with one peak during the first clutch (A) range and one during the second clutch (B) range at about Julian date 195 or July 14. In contrast, for 2013 the bi-modality of egg-laying was not as well-defined, especially for second clutches: in this year there were more nests in the intermediate (I) range (Table 1.3). Comparing the total number of nests assigned as first, second and intermediate clutches among years, there was a significant overall difference in the frequency distribution (X-squared = 16.69, df = 2, p-value = 0.0002). Specifically, there was a higher percentage of intermediate nests in 2013 (34 percent) compared to 2014 (20 percent).

Analysing each year separately, there was a significant difference in the frequency distribution of A, I and B nests between habitats in 2013 (X-squared = 12.1 df = 4, p-value = 0.017), but not in 2014 (X-squared = 1.7 df = 4, p-value = 0.79). In 2013 Crop sites (42 percent A, 28 percent B, 30 percent I) and Livestock sites (41 percent A, 28 percent B, 32 percent I) had similar distributions of clutch types, but Non-Agricultural sites had a different distribution of clutches, with a much higher proportion of intermediate nests (18 percent A, 21 percent B, 61 percent I).

There were data for only n = 2 first clutches in non-agriculture habitat in 2013, which yielded an unbalanced data set for analysis with non-estimable model parameters. We therefore restricted data to assigned first clutches from Crop and Livestock habitats. Egg- laying date did not differ with year or habitat and there was no habitat*year interaction for this sub-sample of nests (p > 0.27 in all cases). Similarly, for intermediate and second clutches there was no effect of year, habitat or a year*habitat interaction on egg-laying dates (p > 0.20 in all cases; using data from all three habitat types).

1.3.2. Clutch size variation

Clutch size declined with laying date in both years, analysing all nests: (2013, F $_{1,228}$ = 6.01, p = 0.015; 2014, F $_{1,296}$ = 38.7, p < 0.001; Fig. 2). However, there was no effect of habitat and no date*habitat interaction for clutch size in either year (P > 0.25 in all cases). Restricting data to first clutches there was a significant year*habitat interaction for clutch size (F_{2,204} = 3,40, p = 0.035) but no effect of year and habitat (p > 0.087 in both cases; controlling for date). Post-hoc analysis with Tukey correction showed that clutch size in non-agricultural habitat was significantly different between 2013 and 2014 (DF = 204, t ratio = -2.89, p = 0.048), but no other pairwise comparisons were significant. For intermediate clutches year, habitat, and year*habitat did not influence clutch size (p > 0.33 in all cases; controlling for date), and for second clutches similar results were found (p > 0.19 in all cases; controlling for date). Clutch size of first nesting attempts was different from second nesting attempts with a mean of 4.5 compared to 4.2 (t = 3.3, DF = 449.9, p = 0.0012).

1.3.3. Variation in breeding productivity and chick quality

For first nests, the proportion of nests successfully fledging at least one chick differed in relation to habitat (logistic regression, Z < 0.89, p < 0.030). The proportion of successful nests was lower, but similar between livestock (74.6 percent of nests fledging 1+ chicks) and non-agricultural (75.0 percent) habitats, whereas in crop habitats more nests successfully fledged at least one chick (85.7 percent). In contrast, for intermediate and second broods proportion of nests fledging at least one chick did not differ among habitats (p > 0.63). Furthermore, the proportion of nests fledging at least one chick did not differ between years or habitat*year for any of the nesting attempts (p > 0.51 in all cases).

When restricting the data to nests that successfully fledged chicks, mean brood size for first broods was independent of year (p = 0.97) and habitat (p = 0.62), but there was a significant habitat*year interaction ($F_{2, 172} = 3.78$, p = 0.030). Mean brood size was lowest in Non-Ag in 2013 (3.0 ± SD 1.4 chicks, but based on only n = 3 nests) and highest in Non-Ag in 2014 (4.5 ± SD 0.7 chicks), though no pair-wise differences were significant at the Tukey-corrected P value of < 0.05. The model does not converge for second broods since there are only 6 that were known to successfully fledge across

three habitat types; both crop and non-agricultural habitat were represented by only one nest, and there was only one nest represented in 2013.

For first broods in 2014, chick mass at 9 days post-hatching did not vary with habitat or brood size (p > 0.37 in all cases; site and nest identity as random factors, date as a covariate). Similarly, for chicks in intermediate broods, measured in both years habitat, year, habitat*year and brood size did not affect chick mass (p > 0.12 in all cases). However, for chicks in second broods there was a difference in chick mass by year ($F_{1.70} = 5.19$, p = 0.026), but no difference with habitat, brood size, or habitat*year (p > 0.13 in all cases). Second brood chicks were heavier in 2013 (17.6 \pm SD 2.6 g) compared with 2014 (16.7 ± SD 3.2 q). Chick mass was positively correlated with tarsus length (r = 0.24) and tail length (r = 0.57), however controlling for body mass there was no effect of year, habitat, brood size or a habitat*year interaction for tarsus length (p > 0.20 in all cases). For tail length year, brood size, and habitat*year had no effect (p > 0.06 in all cases) whereas in second broods habitat had an effect (F2,8 = 7.99, p = 0.012); tails lengths were similar for crop (11.65 ± SD 4.52) and livestock (11.13 ± SD 5.12), and higher for non-agricultural (15.22 ± SD 2.98) habitats. However, post-hoc testing with a Tukey correction factor did not reveal any inter-habitat differences at p < 0.05. For all nesting attempts, chicks with higher mass had higher fat scores (r = 0.34), and this correlation was significant in intermediate and second broods (p < 0.0001). For second broods, year influenced fat scores (F1,70 = 32.19, p < 0.0001), and for all other nesting attempts year, brood size, and habitat were not significant in determining fat scores (p > 0.066 in all cases); mean fat scores were higher in 2013 (3.97± 0.86) compared to 2014 (3.24 \pm 1.65), and fat scores increased with mass.

1.3.4. Variation in potential sources of breeding failure: depredation, mites, and insect availability

The proportion of nests depredated versus not depredated did not differ among years or habitats and there was no habitat*year interaction (logistic regression, p > 0.13 in all cases; Table 1.3). Results are similar when performed on first, intermediate, and second clutches separately (p > 0.44 in all cases). Similarly, the proportion of nests with mites did not vary with habitats, years and the interaction term habitat*year (p > 0.23 in all cases); results did not differ if analyzed separately by clutch type (p > 0.35 in all cases; Table 1.3).

Total number of insects captured per sampling net varied throughout the year and by habitat, with low numbers of insects early in the season (week 1) and higher numbers of insects later in the season (Fig. 3). We compared insect numbers, in relation to year and habitat, in week 4 (17/18 June) when first brood chicks were in the nest and in week 8 when second brood chicks were in the nest. Total number of insects sampled in week 4 was independent of year ($F_{1,17} = 0.63$, p > 0.40) and year*habitat ($F_{2,17} = 0.14$, p > 0.80), but there was a marginally significant effect of habitat ($F_{2,17} = 3.24$, p = 0.074). In the reduced model, without the non-significant interaction habitat was significant ($F_{2,17} = 4.23$, p = 0.037) with number of insects being similar in livestock and crop sites but much lower in non-agricultural sites (Fig. 4). Similarly, total number of insects sampled in week 8 was independent of year ($F_{1,22} = 0.37$, p > 0.50) and year*habitat ($F_{2,22} = 0.01$, p > 0.99), but there was a marginally significant effect of habitat ($F_{2,22} = 3.40$, p = 0.057). In the reduced model, without the non-significant interaction term, habitat was significant s ($F_{2,22} = 3.79$, p = 0.041) with lower numbers of insects per net in non-agricultural site (Fig. 4).

1.4. Discussion

Our main goal in this study was to compare crop, livestock and non-agricultural sites, to determine if there were habitat differences in breeding phenology and productivity in a declining aerial insectivore, the Barn Swallow. We found some evidence for year differences in breeding phenology (timing of egg-laying) but no major differences between livestock and crop habitats. In general, initiation of laying showed a strong bi-modal pattern, reflecting first and second broods, but in 2013 this pattern was less distinct with a greater number of intermediate or replacement broods. Clutch size declined with laying date but there were no year or habitat differences in this relationship. Clutch size was smaller in non-agricultural habitats in 2013 than in 2014, but otherwise clutch size did not differ between non-agricultural, crop and livestock habitats. Similarly, brood size was lower in non-agricultural habitats in 2013 and higher in 2014, but brood size did not differ between non-agricultural, cropl and livestock habitats. Overall, crop habitats had a higher proportion of nests fledging at least one chick in first nesting attempts. Chick mass and size did not vary among habitats for first broods but overall chicks in second broods were heavier and had higher fat scores in 2013 compared with 2014. Finally, there was no annual variation in occurrence of nest

mites or nest predation so these were unlikely to explain annual variation in breeding parameters. We therefore consider, below, alternative explanations: the role of manure management, individual quality, weather and insect availability.

The timing of egg-laying in our study was similar to other sites across North America, with peaks of egg laying in late May to early June for first clutches (Brown and Brown, 1999). Less is known about mean timing of second clutches, but the sites in our study match other studies in terms of the reported inter-clutch interval of approximately 50 days (Brown and Brown, 1999). We found some evidence that timing of egg-laying differed between years; the lack of clear bimodality and larger proportion of intermediate nesting attempts in 2013 could indicate that after failing in their initial nesting attempt. more birds re-nested shortly after, compared to 2014 where there were fewer re-nesting birds. However, there was no statistically-significant difference in fledging success between years for first nesting attempts, which doesn't support this interpretation. It is also possible that first nesting attempts were more spread out in 2013 due to weather effects and/or timing of bird arrival, and the higher number of nests we classified as "intermediate nests" were actually later, first nesting attempts for which there was no second attempt. Barn Swallows are known to spend more energy foraging when conditions are favourable and less when the converse is the case. Thus, it is possible that conditions were less favourable early in 2013 leading to decreased investment in production of young until later, and once past a threshold date, pairs did not produce a second nest. Spring temperature is also known to affect laying date in these birds (Dolenec et al., 2009), so again weather patterns may have played a role in differences in nest phenology between the two years. Dolenec (2009) found that the laying date (date of first egg) was earlier with increasing mean April and May temperature.

Most importantly, we found limited evidence for differences in breeding phenology or proportion of first, intermediate and second broods among livestock and crop and non-agricultural habitats although there was a higher proportion of intermediate nests in non-agricultural habitat in 2013. The lack of difference is consistent with Grüebler et al's (2010) study which reported that livestock presence at the nest site and the number of manure heaps around farms had no significant effect on laying date or the occurrence of multi-broodedness in Barn Swallows in Switzerland.

Clutch size declined with date in our study, a relationship that is well supported for many bird species in the literature (Ambrosini et al., 2006; Safran, 2006; Sicurella et al., 2013). Although in some multi-brooded species clutch size increases and then decreases with time in a humped pattern, in other multi-brooded species there is a consistent linear decline in clutch size like that which we found in Barn Swallows; however there is often considerable individual variation in clutch size for any given date (Williams, 2012). Again, the change in clutch size with date did not differ among habitats and we found little evidence for differences in mean clutch size among habitats. The difference in clutch sizes of first clutches between non-agricultural habitats in 2013 and 2014 is likely an artefact of a small sample size. Grüebler et al. (2010) also found that neither the number of manure heaps within 500 m around the nest, nor livestock presence at the nest site had any significant effect on clutch size. Similarly, there was little evidence for significant variation in breeding productivity, based on brood size comparing non-agricultural, crop and livestock habitats in our study. We did find that non-agricultural habitats had lower brood size in 2013 but higher brood size in 2014, though again this was based on small sample of nests (< 6). This lack of difference in breeding productivity among livestock- and crop habitats in our study, does contrast markedly with similar studies in European Barn Swallows. For example, Grüebler et al (2010) showed that presence of livestock had a positive effect on nestling survival to fledging, but only in multi-brooded, not single, brooded Barn Swallow pairs. Grüebler et al. (2010) estimated that annual nestling productivity increased by 1.6 fledglings if nests were located at high-quality nest sites (i.e. in the presence of livestock) surrounded by high-quality foraging habitats (i.e. large numbers of manure heaps) compared to nests located at low-quality sites with low-quality foraging habitats. Ambrosini et al. (2002) also reported that fledging success declined with the number of cattle per farm at breeding sites in Italy. In our study, crop habitats actually had a higher proportion of nests fledge at least one offspring in the first nesting attempt, perhaps due to superior insect availability early in the season (see Figure 1.3), contrasting with European studies which highlight the importance of habitats with livestock (Grüebler et al., 2010). However, other studies of European populations have also reported positive relationships between occurrence of hayfields and numbers of swallows (Sicurella et al., 2013).

One reason for the higher productivity in livestock habitats reported in other studies might be differences in manure management. In Grüebler et al's (2010) study

there were at least six manure piles within 500 meters of the nest whereas in most of our study sites manure was collected centrally. Quantifying manure management strategies, such as counting number of manure piles or number of droppings/area in a pasture, is a promising avenue of research for determining effects of livestock on Barn Swallows since manure piles (Ambrosini et al., 2012) and pastures are known to produce more insects and support more foraging birds in Europe (Evans et al., 2007). It is also possible that the lack of major habitat differences has to do with other drivers of reproductive success, as a study examining the relative effect of nest site versus individual quality concluded that factors such as the individual quality and the age of the nest itself play a larger role in determining number of young fledged than nest site (including ecological variables), measured by number of young fledged (Safran, 2006). However, this is countered by European research, which shows that there are more young produced in regions with livestock (Grüebler et al., 2010). This leads to the possibility that lack of an effect in Safran's (2006) study was due to smaller differences between habitats than in Grüebler et al's (2010) study, and also each site was considered a habitat, making it a comparison of nest-sites rather than habitats. However, the lack of site/habitat effect mirrors our findings, leading to the possibility that in North America individual quality or nest age drives nesting success more than habitat.

Predation is known to be generally minimal in Barn Swallows, and close to zero in some populations, though on occasion it can be significant such as in one site where one bobcat destroyed more than 40 nests (Brown and Brown, 1999; Møller, 2013). Another factor associated with breeding productivity in Barn Swallows is mite infestation (Brown and Brown, 1999; Saino et al., 2002). In some populations up to half of nests are infested with mites, and presence of mites is known to increase nestling mortality (Brown and Brown, 1999) and decrease clutch size, brood size, number of fledglings and nestling mass (Moller, 1990). In an experimental study Saino et al. (2002) showed that nests with an enlarged brood had larger prevalence and intensity of mite infestation than those with a reduced brood. Nestlings in enlarged broods also had smaller body mass and immune function compared to reduced broods and immune function and feather growth were negatively correlated with per nestling intensity of infestation in enlarged but not in reduced broods. However, in our study we found no evidence that predation or mites can explain differences in survival to fledge, clutch size or brood size, since there were no differences in predation or mite infestation between habitats or years.

We found little evidence for major differences in insect availability between agricultural sites with and without livestock, at least during the critical periods with first and second brood chicks. However, it appears that insect numbers peaked somewhat earlier (at week 2) in agricultural habitats compared to week 7 in livestock habitats (Fig. 3). We did find that number of insects trapped in non-agricultural habitat was very low in both years and across the study period, compared with other habitats, perhaps indicating that the bulk of insects collected by foraging birds were at a higher altitude than the nets, which were one meter above the height of vegetation. Alternatively, birds in these habitats might forage primarily over water or wetland habitats which our nets did not sample. It is also interesting to note that chick mass and fat scores were higher in second broods in 2013, which could be related to the higher insect availability later in the season (see Fig. 4).

The main goal of our study was to investigate effects of habitat, and specifically presence of livestock, on Barn Swallow reproduction. However, one important factor that we did not consider is weather which is known to influence Barn Swallows, e.g. wind speed can determine foraging success (Møller, 2013), large-scale climate indexes like the NAO (North American Oscillation) influencing breeding parameters such as number and quality of offspring in Barn Swallows (Møller, 2002), and spring weather conditions influencing timing of arrival (Dolenec et al., 2009). Irons et al. (2017) found that that two measures of breeding phenology, annual lay and hatch dates, are more strongly predicted by windiness and precipitation than by annual variation in temperature. In May there was more precipitation in 2014 (100.1mm) than 2013 (88.0 mm), whereas in June there was more precipitation in 2013 (57.6 mm) than 2014 (40.1 mm). We would have expected more intermediate nests if conditions were poor early in the season, and if this is the case then June weather could be driving the trend. The time-scale of our study (two years) provide limited power to identify weather or climate effects. However, however future research examining the influence of weather on reproductive breeding parameters such as the number of first and intermediate nests would prove useful in furthering our understanding of Barn Swallow breeding performance. Furthermore, shortterm, but severe, weather events may explain the higher number of intermediate nests we found in 2013 than 2014, and is worth examining further in future studies.

Table 1.1 Geographic coordinates of field sites

Habitat Type	Location	Latitude	Longitude
	Code		
Crop	RS	49.07	-123.15
Crop	SE	49.06	-123.14
Crop	SR	49.09	-123.16
Crop	WW	49.21	-122.99
Livestock	CS	49.13	-123.05
Livestock	JZ	49.08	-123.16
Livestock	SH	49.05	-123.09
Livestock	SI	49.21	-123.18
Non agricultural	CY	49.35	-123.22
Non agricultural	HB	49.38	-123.27
Non agricultural	WI	49.35	-122.65

Table 1.2. Variation in egg-laying date, clutch size and brood size by year and habitat for first, intermediate and second clutches/broods. Values are means ± S.D. with sample sizes in parentheses.

Year	Habitat	Clutch/ Brood	Laying Date (1 = 1 Jan)	Clutch Size	Brood Size
2013	Crop	First	142.1 ± 4.6 (34)	4.5 ± 1.0 (37)	4.3 ± 0.9 (34)
	,	Intermediate	163.8 ± 8.0 (26)	4.4 ± 1.1 (26)	$4.2 \pm 0.8 (25)$
		Second	$189.6 \pm 6.4 (20)$	$4.4 \pm 0.7 (25)$	$4.3 \pm 0.7 (23)$
2013	Livestock	First	143.4 ± 4.7 (49)	4.2 ± 1.2 (61)	4.1 ± 1.0 (53)
		Intermediate	$165.1 \pm 7.7 (49)$	4.1 ± 1.1 (49)	4.1 ± 1.0 (45)
		Second	$192.7 \pm 5.4 (37)$	$4.1 \pm 0.7 (42)$	$4.0 \pm 0.6 (33)$
2013	Non-Agricultural	First	147.5 ± 6.4 (2)	$3.7 \pm 3.7 (6)$	3.0 ± 1.4 (3)
	·	Intermediate	$164.9 \pm 7.6 (20)$	$4.2 \pm 1.0 (20)$	$4.0 \pm 1.0 (20)$
		Second	$195.1 \pm 8.0 (7)$	$4.3 \pm 0.8 (7)$	$4.2 \pm 1.0 (6)$
2014	Crop	First	142.1 ± 6.8 (49)	4.6 ± 0.7 (57)	4.2 ± 0.7 (55)
	·	Intermediate	$163.2 \pm 8.5 (22)$	$4.5 \pm 0.5 (22)$	$4.0 \pm 0.6 (22)$
		Second	191.1 ± 6.3 (30)	$4.1 \pm 0.8 (36)$	$3.8 \pm 0.6 (32)$
2014	Livestock	First	141.7 ± 6.2 (72)	$4.6 \pm 0.7 (83)$	4.1 ± 0.8 (79)
		Intermediate	$165.0 \pm 7.5 (36)$	$4.3 \pm 0.7 (36)$	$3.9 \pm 0.7 (36)$
		Second	$191.7 \pm 7.4 (66)$	$4.2 \pm 0.8 (68)$	$3.9 \pm 0.7 (63)$
2014	Non-Agricultural	First	146.1 ± 4.9 (14)	4.4 ± 1.0 (17)	4.5 ± 0.7 (15)
	-	Intermediate	$162.4 \pm 7.0 (10)$	$4.4 \pm 0.7 (10)$	$3.9 \pm 0.8 (9)$
1		Second	193.5 ± 7.5 (11)	$4.0 \pm 0.8 (13)$	$3.7 \pm 0.7 (10)$

Table 1.3. Variation in percentage of successful nests, nests with mite infestation, and nest with predation by year and habitat for first, intermediate and second clutches/broods.

Year	Habitat	Clutch/ Brood	Successful % (n)	Mites % (n)	Predated (%)
2013	Crop	First	87.1 (31)	5.4 (37)	5.6 (36)
		Intermediate	87.5 (24)	7.7 (26)	11.5 (26)
		Second	NA (0)	4.0 (25)	0.0 (25)
2013	Livestock	First	79.6 (54)	0.0 (63)	15.9 (63)
		Intermediate	91.1 (45)	8.2 (49)	8.2 (49)
		Second	50.0 (2)	2.3 (43)	4.7 (43)
2013	Non-Agricultural	First	40.0 (5)	0.0 (6)	20.0 (5)
	•	Intermediate	89.5 (19)	20.0 (20)	5.0 (20)
		Second	NA (0)	0.0 (7)	0.0 (7)
2014	Crop	First	84.9 (53)	1.8 (57)	12.3 (57)
		Intermediate	81.8 (22)	13.6 (22)	18.2 (22)
		Second	20.0 (5)	2.8 (36)	8.3 (36)
2014	Livestock	First	71.2 (80)	0.0 (83)	19.3 (83)
		Intermediate	77.4 (31)	0.0 (36)	11.1 (36)
		Second	33.3 (9)	1.5 (68)	5.9 (68)
2014	Non-Agricultural	First	86.7 (15)	0.0 (17)	5.9 (17)
	-	Intermediate	77.8 (9)	0.0 (10)	20.0 (10)
		Second	100.0 (1)	0.0 (13)	7.7 (13)

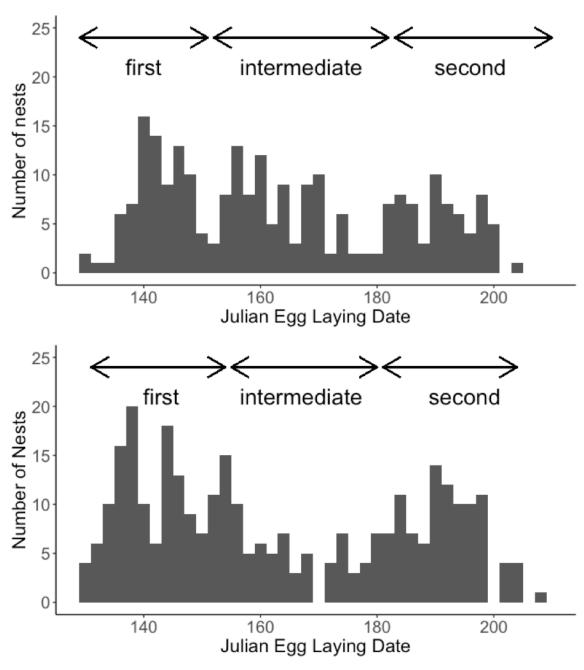
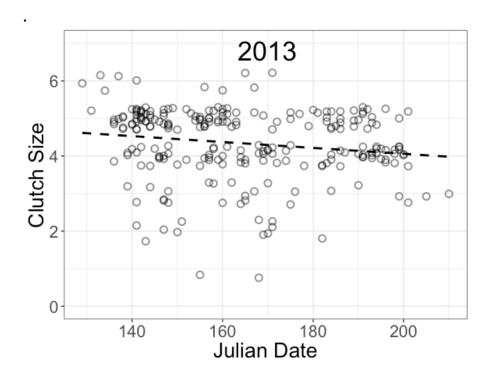


Figure 1.1 Frequency distribution of clutch initiation dates for 2013 (top) and 2014 (bottom). Ranges of first, intermediate, and second clutches are shown at the top of graphs using arrows. Note that in subsequent analyses nests with first egg date before calculated first clutch range were considered first clutches, and nests with first egg date after calculated second clutch range were considered second clutches



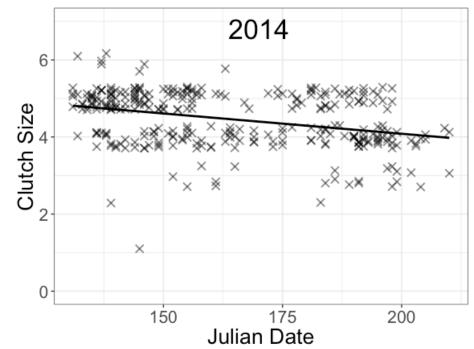


Figure 1.2. Seasonal decline in clutch size with laying date. Circles and dotted line represent 2013 and X's and solid line represent 2014 data; lines are linear models of clutch size by date. Points are jittered along the y axis to avoid overlapping points

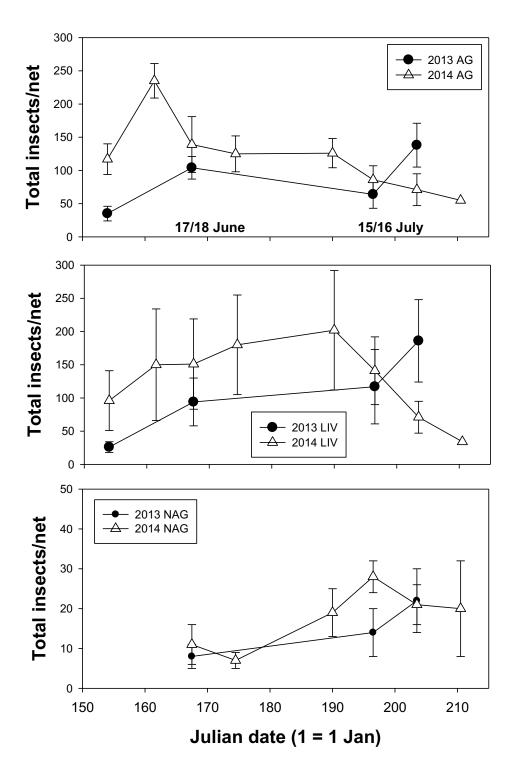


Figure 1.3 Variation in insect abundance by year and habitat. Data are mean ± S.E. total number of insects per net. Dates indicate periods for 1st brood chicks (17/18 June) and 2nd brood chicks (15/16 July).

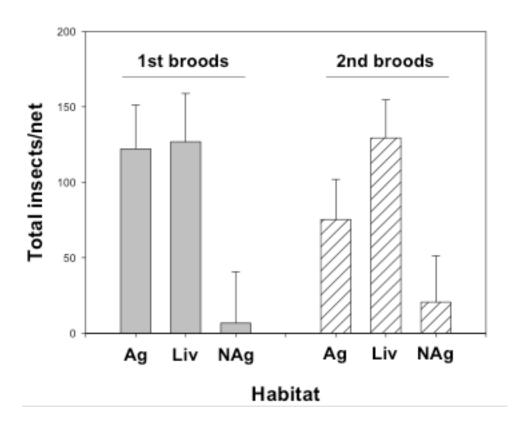


Figure 1.4 Variation in total number of insects per net by habitat (pooling years) during rearing of 1st brood chicks (17/18 June) and 2nd brood chicks (15/16 July). Values are means ± S.E.

Chapter 2. Comparing Barn Swallow foraging and food resources between crop and grassland set-aside fields.

2.1. Introduction

There have been widespread population declines in farmland birds across Europe (Donald et al., 2006) and North America (Conover et al., 2014). Grassland birds are one of the most steeply declining bird groups in North America, with a mean decline in breeding populations of 37 percent between 1968 and 2008 (Sauer and Link, 2011). The Barn Swallow has declined by over 1.5 percent per year in British Columbia, with some estimates of declines of 4.73 annually (Environment and Climate Change Canada, 2017; Sauer et al., 2017). Numerous causes of these population declines have been proposed including a decrease in semi-natural areas between or around agricultural fields (Henderson et al., 2012), afforestation in northeastern North America (Brennan and Kuvlesky, 2005), degradation of range-lands in western North America (Brennan and Kuvlesky, 2005), acute pesticide toxicity (Mineau and Whiteside, 2013), abandonment of agricultural land in eastern Europe (Donald et al., 2002) and change in agricultural policy deterring grassland set-asides (Wretenberg et al., 2007). However, one of the main factors implicated in the decline of many farmland birds is agricultural intensification, (Donald et al., 2006; With et al., 2008), the change in agricultural practices which includes higher nutrient inputs on farmland, larger field sizes, fewer open pastures, simplified crop rotations, increased mechanization and increased use of pesticides and herbicides (Donald et al., 2006; Stoate et al., 2001). In less agriculturally intensive landscapes plant species richness is higher (Kleijn et al., 2009) and a metaanalysis of arthropod richness and abundance in different levels of agricultural intensity found that species richness and abundance of decomposers and predators, though not herbivores, decreases with increasing agricultural intensity (Attwood et al., 2008). It has therefore been suggested that these decreases in plant and arthropod diversity in more agriculturally intensive systems are linked to declines in farmland birds.

One common conservation solution to biodiversity declines is grassland set-aside schemes, in which fields are either planted or allowed to naturally re-vegetate and not harvested for one to more than ten years (Buskirk and Willi, 2004). Originally enacted to combat crop surpluses and to enhance soil quality, there is now a large body of evidence that suggests that grassland set-asides also add to biodiversity in agricultural landscapes (Buskirk and Willi, 2004; Herkert, 2009; Kovács-Hostyánszki and Báldi, 2012). As one example, the Conservation Reserve Program in the United States currently has approximately 100,000 square kilometers in 10-15 year set aside contracts, accounting for 1.0 percent of the land in the United States (United States Department of Agriculture Conservation Reserve Program, 2015). Several similar federal programs in Canada have resulted in establishment of between 2,000 and 4,500 square kilometers of long-term perennial cover, representing 0.30 percent to 0.67 percent of Canada's agricultural land (Agriculture and Agri-Food Canada, 2017; McMaster and Davis, 2001). Between 1992 and 2008 five to fifteen percent of all agricultural land in the European Union was in set aside due to the EU's Common Agricultural Policy ((Kovács-Hostyánszki and Báldi, 2012; Tscharntke et al., 2011). Additionally, smaller programs including voluntary agri-environmental schemes add to the amount of farmland in grassland set-aside unaccounted for by federal programs or EU directives (Hiron et al., 2013). Though there is evidence of the positive effect of grassland set-aside land on plant, arthropod and avian abundance and biodiversity (Buskirk and Willi, 2004), it remains unclear whether such a scheme would be enough to curb large-scale declines of farmland birds. One study in Central Europe reported that grassland set-asides have higher abundance and diversity of birds compared to cultivated fields depending on the feeding guild, with higher diversity and abundance of insectivores but not granivores (Kovács-Hostyánszki and Báldi, 2012). Furthermore, grassland set-asides have been shown to increase population densities of early-succession bird species in an agricultural landscape (Tscharntke et al., 2011), and after three years planted grassland set-asides support similar bird communities to semi-natural grassland., The size of grassland setaside fields corresponds positively with the number of bird territories in an agricultural land matrix (Herzon et al., 2011). A comparison of time-periods with different agricultural policies found that farmland bird populations increased during years when policy favored the establishment of grassland set-asides (Wretenberg et al., 2007). Thus, it appears that grassland set-aside programs can positively influence farmland bird populations by altering the landscape composition of agriculturally productive regions.

Recent evidence suggests that aerial insectivore bird populations across North America are in decline, including swallows that depend on farmland (Family Hirundinidae), potentially involving a systematic change related to the birds' insect diet (Environment Canada, 2012; Nebel et al., 2010). However, there is no consensus in the literature about whether or not there are commonalities in timing of aerial insectivore declines (Michel et al., 2015; Smith et al., 2015). Historical changes in the use of the pesticide DDT were implicated in dietary shifts of aerial insectivores to less profitable prey items, suggesting that pesticide use could be driving trends of aerial insectivore decline (Nocera et al., 2012). A newer class of pesticides, the neonicotinoids, are also linked to declines in insectivorous bird populations (Hallmann et al., 2014). However other evidence suggests that climate and weather patterns are driving population declines in some regions, with links between climate indicies and population trend estimates (Garcia-Perez and Hobson, 2014). It is also possible that habitat changes such as decreases in available pasture via intensification of farmland and the conversion of farmland from livestock to crops may be the main contributing factor, since research comparing pasture to cultivated fields found both more insects and more foraging Barn Swallows on pasture fields (Evans et al., 2007). Research from Denmark shows that there are more insects and more breeding birds in habitats with livestock present (Møller, 2001), mirrored by research in Italy which found that though the response is delayed, more barn swallows breed in areas with livestock present (Ambrosini et al., 2002). A study about Tree Swallows in Quebec found that breeding success was lower in more agriculturally intensive areas, which the researchers attributed to lower food availability (Ghilain and Belisle, 2008). The trend of higher insect abundance and more foraging birds over pasture suggests that less intensive field types such as grassland set-aside fields will support more foraging birds, but this idea remains untested.

In this study, we examined the role grassland set-asides might have in mitigating population declines to a farmland aerial insectivore the Barn Swallow (*Hirundo rustica*) in an agricultural region in southwestern British Columbia, Canada. To do this, we compared aerial insect abundance and community composition and the number of Barn Swallows feeding over grassland set-aside fields and conventionally managed crop fields, during the Barn Swallow breeding season.

2.2. Methods

2.2.1. Study area

This study was conducted from August 15 to 23, 2013 and from May 15 to July 31, 2014 in a region of intensively managed agricultural land in southwestern British Columbia, Canada, south of the city of Vancouver (49.068234, -123.134554). Study fields were located in the district municipality of Delta, 40 percent of which is agricultural land. Grassland set-aside fields were enrolled in a stewardship program with a local non-profit organization, the Delta Farmland and Wildlife Trust, which provides a per acre cost-share payment to farmers participating in the program (Delta Farmland and Wildlife Trust, 2017). Fields enrolled in the program were planted to a mix of five perennial grass species as well as red clover, and left undisturbed for up to four years (Delta Farmland and Wildlife Trust, 2017).

In 2013 we selected four grassland set-aside fields and four potato fields, with fields selected based on field type, location, and farmers' willingness to cooperate. In 2014 we used five grassland set-aside fields and five cultivated fields in matched pairs, with each grassland set-aside field adjacent to or within 500 meters of a cultivated field. In 2014, cultivated fields contained potato (2), vegetable, peas/lettuce and corn crops grassland set-aside fields were re-used. Fields were chosen based on location, availability of a grassland set-aside field, and farmer willingness to cooperate, and once a grassland set-aside field was selected a nearby cultivated one was chosen. (See Table 2.1). Fields were an average of 5.6 hectares, and ranged from 1.9 to 14.8 hectares in size. Fields were sampled in an area with a high density of breeding swallows, with multiple breeding sites within 500 meters of study fields. We measured the vegetation height and estimated the percent cover to the nearest percent in 2014.

2.2.2. Arthropod sampling and identification

In August 2013, we placed three insect nets per field at randomly chosen locations on four grassland set-aside and three potato fields. We were unable to put insect nets on one of the four potato fields because of farm activity. We employed passive wind nets, used for other Swallow studies (Hussell and Quinney, 1985), designed to rotate on a pole in the direction of the wind so that the mouth of the net

faced upwind, allowing interception of aerial insects. Nets were positioned one meter above the vegetation. The ends of the nets contained a jar of 70 percent alcohol where the insects were collected at or near sunrise daily, with each daily sample from each net labeled and placed a separate vial. We measured and recorded wind speed for a two-minute period using a digital anemometer at the time of collection (La Crosse Technology, Model # EA-3010U). Data from other sites during the study showed that insect abundance estimated for one net was positively correlated with insect abundance from a second net at a given site ($r^2 = 0.44$, P < 0.001), showing that the nets at each site provide a representative sampling of insect abundances at that site.

Arthropod samples were counted and sorted to taxonomic order by examining them under a dissecting microscope. Identification of arthropods was completed based on the taxonomic keys and pictoral guides (American Museum of Natural History, 2017; Iowa State University Department of Entomology, 2017; Johnson and Triplehorn, 2004; Marshall, 2017; University of Queensland, n.d.). Arthropods in poor condition, which we were not able to identify, were counted but not assigned to a taxonomic order, fragments were not counted, and expert entomologists identified intact ones that we could not identify with keys.

2.2.3. Counts of foraging Barn Swallows

Ten minute observations were conducted at eight fields in 2013 and ten fields in 2014 using methods similar to Evans et al. (2007), recording the maximum number of Barn Swallows seen foraging over the field by one observer at any point during a ten minute observation. Birds were too far away to distinguish between age class or sex, so the total number of birds was counted. We observed fields from a stepladder to gain a higher vantage point allowing us to observe the entire field. A fifteen meter border around the edge of the field was excluded from the field area during the count to account for edge effects, to ensure that birds were choosing to forage over the field itself and not its edge. Birds were considered to be foraging if their flight patterns were uneven, indicating that swallows were actively foraging for insect prey. Observations were conducted between 08:45 and 14:23 when wind speeds were less than 4.5 m/s. For each observation we recorded observer, field identity, observation time, average 3-minute wind speed, cloud cover to the nearest percent and the maximum number of foraging birds at any point during the observation.

In both 2013 and 2014 fields or matched pairs of fields were visited in a random order each day. In 2013 data collection occurred over an 8-day period in August in which there was no precipitation and the cloud cover ranged from about 1-100 percent, and in 2014 we obtained bird observation data for 20 days throughout the breeding season from May 15-July 31. In 2013 there were more newly fledged birds compared to 2014.

2.2.4. Statistical analysis

All statistical analyses were completed using program R (R Core Team, 2015). To compare arthropods between field types we used total counts per insect order. We computed totals for the five most abundant insect categories, and also categorized each insect order according to their predominant feeding habits, dividing samples into the three feeding guilds of herbivorous, omnivorous or predatory. We then summed up the total number of arthropods per category per field type. We also ran general linear mixed-effects models (GLMM) with a Poisson link to test the effect of other factors such as cloud cover, wind speed and field size (area) on bird counts for the 2013 data and 2014 data using the lme4 package in R (R Core Team, 2015). Model results were tested for over-dispersion and a random factor for each data point was included to account for over-dispersion. GLMMs were performed using a Laplace approximation, and results were tested with Wald Z tests for statistical significance. Other Linear Mixed-Effects Models were performed for vegetation characteristics using the lme function in the nlme package; in that case F values and P values are reported. We analyzed overall diversity (at the level of Order) using the Simpson's Diversity Index (SDI).

2.3. Results

2.3.1. Arthropods in crop vs. grassland set-aside fields

Overall, for all fields in 2013 there was a mean of 13.7 ± 7.8 insects captured per 24-hour sample (range 2-50). There was a mean of 15.1 ± 8.7 insects captured per 24 hours on grassland set-aside fields and 11.4 ± 5.2 insects on potato fields. However, there was no difference in total number of insects among grassland set-aside and potato fields (Z = -1.01, P = 0.31, with net, field and date as random factors). One grassland set-aside field (field 1) had much higher numbers of insects than all other fields (Figure 2.1) and the total number of insects varied among fields for grassland set-aside fields (Z = -1.01).

< -2.87, P < 0.004) but not for potato fields (Z > -1.27, P > 0.21, with net and date as random factors). Total number of insects sampled was correlated with cloud cover (Z = 2.18, P = 0.029) but not wind speed (Z = 0.35, P = 0.72).

The five most abundance insect orders, Coleoptera, Diptera, Homoptera, Hymenoptera and Thysanoptera, together accounted for 97.2 percent of all the arthropods identified. The taxonomic distribution of arthropods in grassland set-aside fields was different from that in potato fields when considering frequency distribution of these dominant five arthropod orders (Chi-square test, χ^2 = 70.27, df = 4, p < 0.01; Figure 2.2). Grassland set-aside fields had a higher percentage of Coleoptera, Diptera and Hymenoptera but fewer Homoptera and Thysanoptera than potato fields. Furthermore, grassland set-aside and potato fields differed in the frequency distribution of arthropods in different feeding guilds (herbivore, omnivore and predator; (χ^2 = 34.394, df = 2, p-value < 0.01; Figure 2.3). Although SDI was slightly lower in grassland set-aside (0.42) than potato fields (0.46) this difference was not significant either including (p = 0.23) or excluding Field 1 (p = 0.78).

In 2014 there was a difference in mean height of vegetation in grassland set-aside versus cultivated fields ($F_{1, 183} = 4.61$, P = 0.03) and no date*habitat interaction (P > 0.8), but there was a highly significant effect of date: vegetation height increased markedly through the season ($F_{1, 183} = 77$, P < 0.0001, Figure 2.4). There was a difference in vegetation cover in grassland set-aside versus cultivated fields ($F_{1, 183} = 55.52$, P < 0.001), as well as a date*habitat interaction (P < 0.001) and an effect of date ($F_{1, 183} = 105.13$, P < 0.001, Figure 2.5). On average, grassland set-aside fields had much higher vegetation cover (95 ± 17 percent) compared with cultivated fields (29 ± 31 percent).

2.3.2. Barn Swallow abundance

In 2013 there was a mean of 4.5 ± 10.3 Barn Swallows per 10-minute observation (range 0 - 55, n = 45) across all fields, with means of 7.21 ± 13.6 birds over Grassland set-aside fields and 1.5 ± 1.7 over potato fields (no difference in time of day of observations for each habitat type, P > 0.08). However, one grassland set-aside field (field 1), the same one with higher arthropod abundance had much higher numbers of foraging Barn Swallows (mean 23.5 birds/10 min) than all other fields (mean 0.3-2.5

birds/10 min; Figure 2.1). The total number of swallows varied among grassland set-aside fields ($F_{3,15} = 6.97$, P = 0.004) but not potato fields ($F_{3,12} = 2.12$, P = 0.15), with date as a random factor.

For this 2013 data we analyzed the relationship between number of foraging swallows observed by habitat (crop vs. grassland set-aside), with field as a random effect, and cloud cover, wind speed and field size (area) as covariates. There was no difference in number of swallows observed by habitat (Z = -1.43, P = 0.15), a marginal effect of wind speed (Z = 1.95, P = 0.052), and no effect of field size (Z = 0.917, P = 0.36) or cloud cover (Z = -1.62, P = 0.11). Furthermore, there was no difference in presence/absence of swallows (observations with 0 or ≥ 1 birds) between grassland setaside fields (17/24 (70.8 percent) observation with ≥ 1 bird) and potato fields (13/21 (61.9 percent), $\chi^2 = 0.40$, P = 0.53). There was a positive relationship between the number of Barn Swallows observed per 10-min observation period and the number of insects captured in a 24-hour period that included the bird count (Z = -4.40, P < 0.001); with wind speed and cloud cover as covariates, and field as random factor). In that model there was no effect of cloud cover (Z = -0.40, P = 0.69) but and there was an effect of wind speed (Z = -2.81, P = 0.0049). However field 1, mentioned earlier, drove the relationship between number of insects and number of birds, being both an outlier for number of insects and number of birds (Figure 2.6); without field 1 the relationship between number of insects and number of birds was not significant (Z = -0.36, P = 0.72).

In 2014 there was a mean of 4.9 ± 1.3 Barn Swallows on cultivated fields and 6.6 ± 1.7 on grassland set-aside fields but this difference was not significant (Z = 1.59, P = 0.12) in a model that included cloud cover (Z = -5.96, P < 0.001, Figure 2.7a), wind (Z = -3.01, P = 0.003), field area (Z = -2.45, P = 0.014, Figure 2.7b), and Julian date (Z = 11.07, P < 0.001, Figure 2.7c), and included field as a random factor. Finally there was no difference in the proportion of observations where at least one foraging swallow was observed over the different field types: cultivated fields 64.3 percent of observations with > 1 bird versus grassland set-aside fields 69.4 percent (χ^2 = 0.38, P = 0.54).

2.4. Discussion

In this study we aimed to determine the role grassland set-aside fields might have in mitigating population declines to a farmland aerial insectivore the Barn Swallow

(*Hirundo rustica*) in an agricultural region in southwestern British Columbia, Canada. We found that grassland set-aside fields had similar arthropod abundances compared with cultivated fields, although there was considerable variation among fields. However, grassland set-aside fields had a different arthropod assemblage compared with potato fields (in 2013), with a higher representation of Coleoptera, Diptera and Hymenoptera but fewer Homoptera and Thysanoptera. Coleoptera were found to be the most common insect taxa found in Barn Swallow food boluses brought to chicks in Poland (Orłowski and Karg, 2011, 2013) suggesting that grassland set-aside fields might provide higher quality foraging habitats than cultivated fields for Barn Swallows.

There were other differences in the insect communities of grassland set-aside fields compared to cultivated fields, with more herbivorous insects and fewer omnivorous or predatory insects on cultivated fields. This matches the findings of Attwood et al. (2008) who found that arthropod richness was significantly higher in areas of less intensive land use for all taxa combined, and for predators and decomposers, although not for herbivorous taxa. Another study also found higher abundance and richness of insects on grassland set-aside fields compared to cropped fields (Kovács-Hostvánszki and Báldi, 2012). Thus, although we found that the overall abundances of prey were comparable between grassland set-aside and cultivated fields, there may be a difference in profitability of prey items for aerial insectivores, especially given more Diptera, Coleoptera, and Hymenoptera in grassland set-aside fields. Data from Eastern Europe shows that the highest number, proportion and total mass of Barn Swallow diets was made up by Coleoptera, Diptera and Hymenoptera (Orłowski and Karg, 2011). Furthermore, in a study comparing the diets of three species of aerial insectivores, Barn Swallows consumed a much higher proportion of Diptera than house martins (Delichon urbicum) or swifts (Apus apus), suggesting a species preference for Diptera prey (Orłowski and Karg, 2013). A study specifically about Diptera abundance on a landscape that has a gradient of agricultural intensity found that less intensive landscapes generally had a higher abundance of Diptera (Paquette et al., 2013). This suggests that grassland set-aside fields might provide higher quality foraging habitat for aerial insectivores such as Barn Swallows.

However, despite differences in vegetation and arthropod diversity we were unable to detect a statistical difference in the number of Barn Swallows foraging above grassland set-aside versus cultivated fields. We did find a number of factors that affected

counts of foraging Barn Swallows: more birds were observed foraging later in the season, on days with lower mean wind speed and cloud cover, and over smaller fields (although effects of wind speed and cloud cover might reflect correlated effects of date).

One of the strongest relationships we found was between number of foraging Barn Swallows and date. More birds were observed later in the season, likely due to an increase in foraging juvenile birds after the first brood had fledged later in the season. This suggests that our observational protocol was able to detect broad differences in number of foraging Barn Swallows. Our average fledge date for the first brood was July 1, which corresponds to the general timing of an increase in Barn Swallows counted on farm fields (Figure 2.8). In some of our models we also found a significant effect of field size on number of foraging swallows that was perhaps counterintuitive: the smaller the field, the more foraging birds were counted. However, Fahrig et al. (2015) also found an increase in biodiversity and abundance of a wide range of taxa, including birds, with decreasing mean crop field size, and they suggested that smaller fields represented a more heterogeneous feeding environment. Fields were bordered by ditches, roads, vegetation, and fences, adding to this hypothesis. We found that as cloud cover increased, the number of foraging birds decreased, which has also been found in other studies of bird activity and cloud cover (Bruni et al., 2014). This could be due to cloudless days being warmer on average, and in a higher temperature environment Barn Swallows may have more energy to spend foraging, or may spend more energy foraging when conditions are favourable (Schifferli et al., 2014). However, it is also likely that this actually reflected an effect of date, with more swallows later in the season when it was more likely less cloudy. Finally, we found a negative effect of wind speed on abundance of foraging swallows in one of two years (2014). Other research indicates that higher wind speeds decrease insect abundance and have negative effects on Barn Swallows counts (Evans et al., 2007; Møller, 2013) which is consistent with the pattern we found.

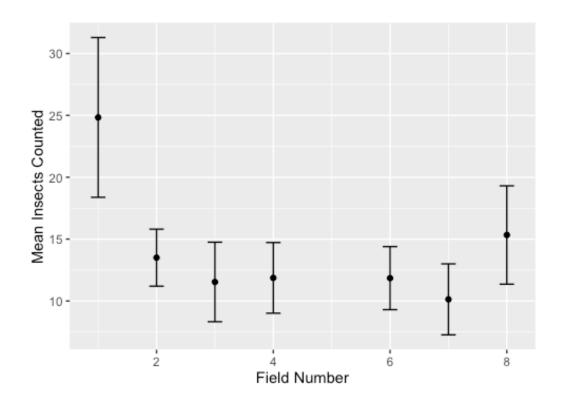
Despite differences in arthropod communities, and marked differences in total number of insects among fields, although not between habitats, and controlling for all potentially confounding factors (date, field size, cloud cover) we were unable to detect a difference in the number of Barn Swallows foraging above grassland set-aside versus cultivated fields. Furthermore, number of insects did not predict the count of foraging birds, perhaps because other factors are more important in driving foraging decisions. Other research has found differences in foraging Barn Swallow abundance over different

field types. One study found that there were more foraging Barn Swallows over pastures than cereal or silage fields (Evans et al., 2007) and another found differences in Barn Swallow abundance over farmland and non-cropped area (Kang, 2013). Thus our findings may reflect a lack of difference between grassland set-aside and potato/cultivated fields or may be due to the variability in our count data and relatively small sample sizes, making it difficult to detect differences between the habitat types.

Based on our research it does not appear likely that grassland set-asides alone can mitigate the local decline in farmland, grassland, or aerial insectivore birds. Despite all the evidence that agricultural intensification causes decreases in ecosystem function (Flohre et al., 2011; Guerrero et al., 2012), and that grassland set-asides increase the abundance of birds, especially insectivore birds (Kovács-Hostyánszki and Báldi, 2012), we did not find any difference in Barn Swallow abundance over grassland set-aside and cultivated fields. Bird feeding behaviour, quantified by 10-minute maximum bird counts, throughout the breeding season in 2014 suggests that prey availability was comparable between the two field types from late May till early August. However it could be that Barn Swallows are not necessarily representative of grassland or farmland birds, so its trend may not be mirrored by other species and feeding guilds. This is similar to feeding guild responses to grassland set-asides in Central Europe due to different habitat preferences such as affinity to bare patches (Kovács-Hostyánszki and Báldi, 2012). Though not significant, mean counts of Barn Swallows were slightly higher in grassland set-aside fields in 2013 than 2014, perhaps because in 2013 data was from an eight-day period near the end of the breeding season, whereas in 2014 data was from throughout the breeding period. The lower number of birds over potato fields in 2013 compared to cultivated fields in 2014 could be due to the fact that in 2013 we only measured bird numbers over potato fields, whereas in 2014 multiple cultivated field types were included, so perhaps potato fields attract fewer feeding Barn Swallows. In both years there were higher, though not significantly different, mean counts on grassland set-aside fields than cultivated/potato fields, suggesting that perhaps there is a difference between the two field types, though with our sample size we were not able to detect it. Our research suggests that weather factors, including wind and cloud cover, may affect foraging behaviour in Barn Swallows. Given this, further examination of the relationship between climate change and Barn Swallow population trends and processes is warranted.

Table 2.1 Field type, size and latitude and longitude of study fields in 2013 and 2014

Year	Field type (habitat)	Field number	Size (Ha)	Latitude	Longitude
2013	Grassland set-aside	1	7.0	49.07	-123.13
2013	Grassland set-aside	2	2.5	49.08	-123.12
2013	Grassland set-aside	3	4.7	49.08	-123.12
2013	Grassland set-aside	4	4.4	49.10	-123.15
2013	Potato	5	6.1	49.07	-123.14
2013	Potato	6	6.7	49.06	-123.12
2013	Potato	7	2.3	49.09	-123.14
2013	Potato	8	6.1	49.08	-123.13
2014	Grassland set-aside	1A	4.6	49.10	-123.15
2014	Potato	1B	6.4	49.09	-123.16
2014	Grassland set-aside	2A	2.3	49.08	-123.12
2014	Vegetables	2B	1.9	49.08	-123.12
2014	Grassland set-aside	3A	7.2	49.07	-123.13
2014	Pea/lettuce	3B	2.6	49.07	-123.13
2014	Grassland set-aside	4A	14.8	49.07	-123.09
2014	Potato	4B	9.8	49.06	-123.08
2014	Grassland set-aside	5A	5.4	49.06	-123.07
2014	Corn	5B	6.2	49.06	-123.07



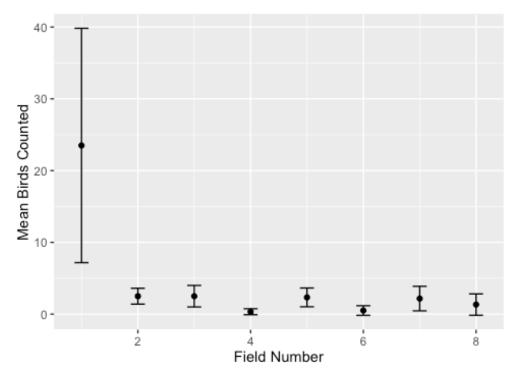


Figure 2.1. Mean number of insects counted (top) and the number of birds counted (bottom) on the same fields in 2013, showing 95% confidence intervals.

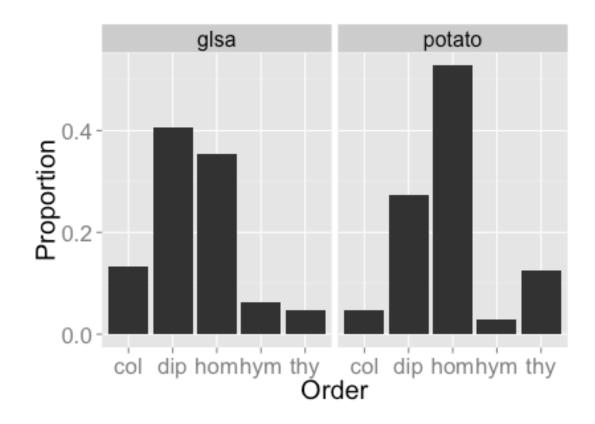


Figure 2.2 Proportion of insects belonging to the five most common insect orders found over grassland set-aside (left) and potato (right) fields; col = Coleoptera, dip = Diptera, hom = Homoptera, hym = Hymenoptera, thy = Thysanoptera.

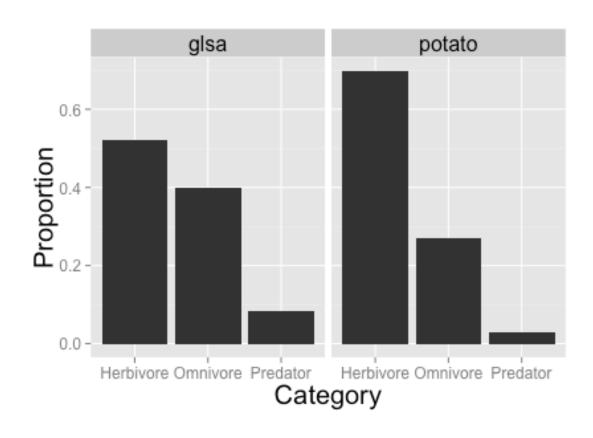


Figure 2.3 Proportion of each feeding guild of insect found on Grassland Setaside (left) and Potato (right) fields

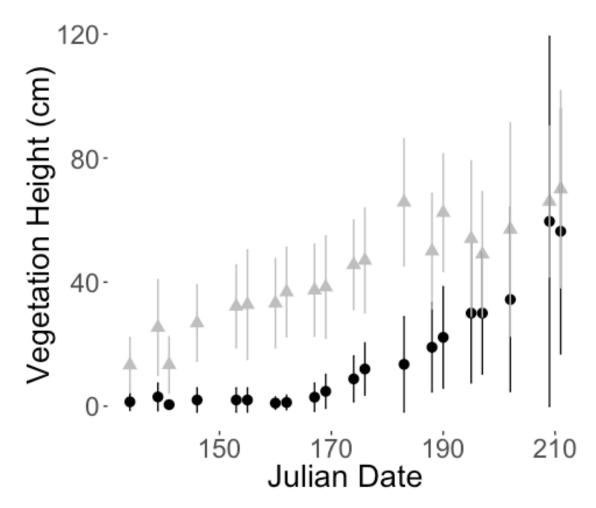


Figure 2.4 Relationship between vegetation height and Julian date, with 95% confidence interval shown. Grey triangles are grassland set-aside fields, and black circles are cultivated fields.

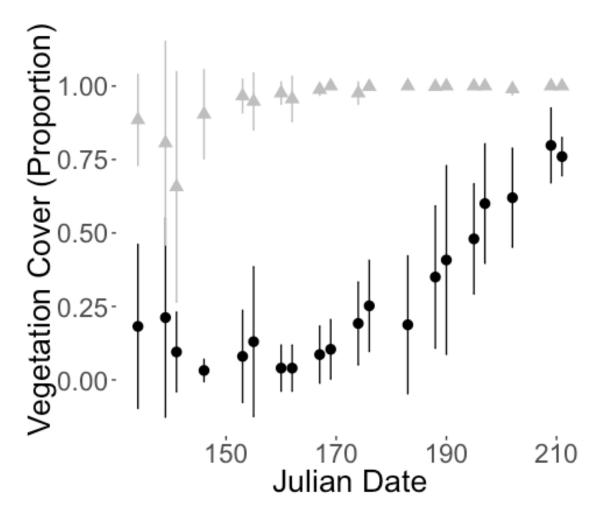


Figure 2.5 Relationship between vegetation cover and Julian date, with standard error shown. Grey triangles are grassland set-aside fields, and black circles are cultivated fields.

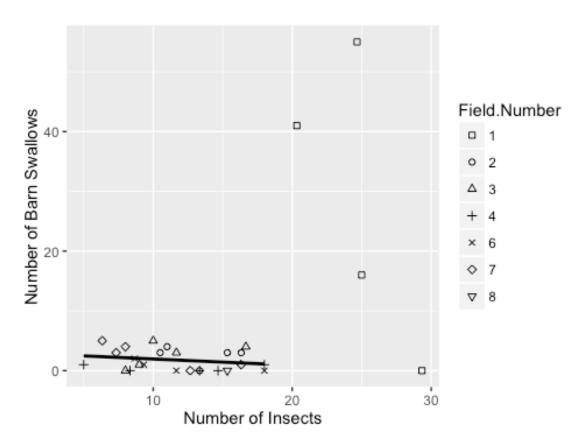


Figure 2.6 Number of insects compared to number of birds, with the linear regression line for fields 2 to 8 shown. Field one, the squares, is driving the trend correlating number of insects to number of birds.

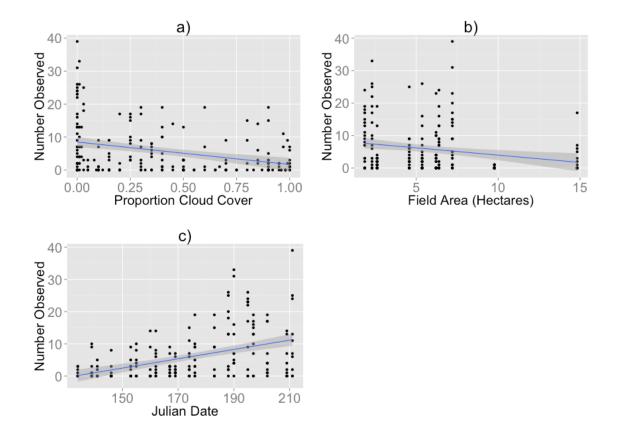


Figure 2.7 Correlation between cloud cover (A), field area (B) and Julian date (C) with number of Barn Swallows observed in 2014.

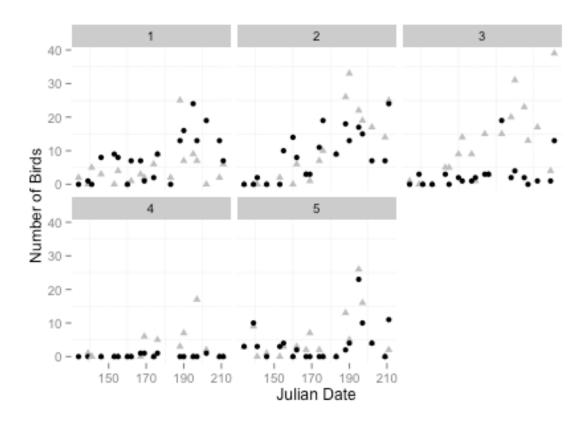


Figure 2.8 Number of Barn Swallows and Julian date, with each pair of fields represented as one panel. Grey triangles are grassland set-aside fields, and black circles are cultivated fields

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