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Landscape-level effects of agricultural intensification on the condition and diet of nestling Barn Swallows (*Hirundo rustica*)

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Abstract

Farmland bird populations have experienced declines with increasing agricultural intensification for which the leading hypothesis is a reduction of prey insects. This may be especially relevant for aerial insectivores whose primary diet is flying insects. For this thesis, I examined nestling body condition and used stable isotopes ($\delta^{13}C$, $\delta^{15}N$) and fecal DNA barcoding to determine the diet of a farmland breeding aerial insectivore, the Barn Swallow (*Hirundo rustica*), within an agro-ecosystem in Southern Ontario, Canada. Nestling body condition was positively affected by agricultural intensification, but all benefits were lost by the pre-fledging stage and with no effect on productivity. Stable isotopes indicated that nestling diet was derived from within agro-ecosystems. While nestling diet breadth was negatively affected by agricultural intensification, I found evidence for a robust dipteran diet unaffected by landscape. My results provide little evidence of long-term negative repercussions to breeding within agriculturally intense landscapes for the Barn Swallow.

Keywords: agricultural intensification, Barn Swallow, *Hirundo rustica*, aerial insectivore, body condition, diet, DNA barcoding, nestling, row crop, stable-isotopes.

Co-Authorship Statement

This thesis was conceived and designed by Jackson W. Kusack with the help of Keith A. Hobson from Western University and Environment and Climate Change Canada and Greg W. Mitchell from Environment and Climate Change Canada. Fieldwork was primarily conducted by Jackson W. Kusack with the help of Dean R. Evans, Greg W. Mitchell, and Michael D. Cadman of the Canadian Wildlife Service. All analyses and writing were done by Jackson W. Kusack. Dr. Keith Hobson and Dr. Greg Mitchell assisted writing by providing feedback and edits. Any resulting publications will be published with Keith A. Hobson, Greg W. Mitchell, Dean R. Evans, and Michael D. Cadman.

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Table of Contents

List of Tables

List of Figures

List of Appendices

List of Abbreviations

AAFC – Agriculture and Agri-Food Canada

AIC - Akaike information criterion

BLAST - Basic local alignment search tool

BOLD – Barcode of Life Database

BWB III – Bowhead whale baleen

C – Carbon

°C – Degrees Celsius

^{13}C – Carbon-13

$\delta^{13}C$ – Stable-carbon isotopes

C_3 - C_3 carbon fixation pathway

C_4 – C_4 carbon fixation pathway

CAM – Crassulacean acid metabolism carbon fixation pathway

CO_2 – Carbon dioxide gas

COI - Cytochrome c oxidase I

COSEWIC – Committee on the Status of Endangered Wildlife in Canada

DNA – Deoxyribonucleic acid

ECCC – Environment and Climate Change Canada

g - grams

GLMM – Generalized linear mixed effect model

LMM – Linear mixed effect model

mm, m, km – millimeters, meters, kilometers

N – Nitrogen

N_2 – Nitrogen gas

$\delta^{15}N$ – Stable-nitrogen isotopes

NABCI – North American Bird Conservation Initiative

NMDS – Non-metric multidimensional scaling

OLS – Ordinary least squares

PCR - Polymerase chain reaction

PERMANOVA – Permutational multivariate analysis of variance

PGM – Personal Genome Machine

QMR – Quantitative magnetic resonance

SD – Standard deviation

SE – Standard error

UK – United Kingdom

USA – United States of America

VPDB – Vienna Pee Dee Belemnite

Chapter 1

General introduction

1.1. Agricultural intensification

Agro-ecosystems are human-modified communities specialized for the cultivation of food, feed, fibre, and medicinal products. These ecosystems include all biotic (e.g., wildlife, plants, crops, livestock) and abiotic (e.g., agrochemicals, soil, irrigation) components, as well as their interactions, that occur within cultivated landscapes, but are not strictly constrained to cultivated fields as they also describe the surrounding areas that are affected by agricultural land use. Currently, there are 379 and 67 million hectares of agricultural land in the USA and Canada respectively (Stanton et al. 2018). Overall, the amount of land used for agriculture has remained relatively stable since the rapid conversion in the early 1900s (Stanton et al. 2018), but intensification has introduced a shift towards specialization and optimization of agricultural production away from small-scale farming practices and towards large-scale, highly industrialized, homogenous farming systems (Matson et al. 1997). These systems are characterized by high yielding row crops, large quantities of inorganic fertilizer and pesticides, mechanization, early planting and harvest, and a lack of crop rotations (Robinson & Sutherland 2002). These landscapes are structurally and ecologically simplified through removing hedgerows, woodlots, and wetlands resulting in larger fields with a reduced number of crop types (Robinson & Sutherland 2002; Benton et al. 2003; Tscharntke et al. 2005).

Agriculture is considered one of the greatest threats to biodiversity worldwide (Benton et al. 2003; Green et al. 2005; Tscharntke et al. 2005), but responses to agricultural land use changes vary in intensity across taxa (Burel et al. 1998, 2004). For plants, single-crop monocultures represent a drastic reduction in diversity within fields, but studies examining field margins show functional diversity is not reduced compared to natural and semi-natural environments (Flynn et al. 2009). Similarly, carabid beetles show no reduction in species richness in areas of high agricultural intensification, but species composition changes to favour smaller and mobile species (Burel et al. 2004). This is not the case for all taxa, as some groups experience marked negative effects, such as birds and mammals, for which functional diversity is reduced with increasing agricultural intensification (Flynn et al. 2009). Investigating the effects of intensification on each organism, and understanding its ecology, is important when examining these complex ecological relationships, as specific mechanisms of intensification may affect certain taxa more than others.

Insects, which range from beneficial pollinators to crop-damaging pests, provide a diverse group to examine these effects. For example, hedgerow density is positively correlated with flying insect availability, as dense hedgerows provide shelter from wind (Lewis 1969; Burel et al. 2004, Grüebler et al. 2008). Additionally, the presence of natural or semi-natural habitat patches surrounding agricultural fields has also been shown to positively affect species richness in wild bees, carabid beetles, hoverflies, true bugs, and spiders (Hendrickx et al. 2007). Agricultural intensification encompasses many land-use changes that may be implemented in tandem or independently; therefore, it is difficult to disentangle the effects of independent components of these landscapes. While landscape structure (e.g., connectivity, field size, semi-natural field margins) and agricultural practice (e.g., crop type, pesticide amount, harvest timing) are independent, the effects on insects are closely tied and can be additive (Schweiger et al. 2005; Hendrickx et al. 2007). Overall, a metanalysis of 259 studies that presented data on arthropod sampling found that arthropod richness and abundance were lower in areas of agricultural land use compared to semi-natural areas (Attwood et al. 2008).

Similar effects are seen in breeding birds. For example, the decline in Bobolinks (*Dolichonyx oryzivorus*) in northern Illinois has been correlated to the loss of grass crops (e.g., alfalfa, hay), where they nest, to the production of row crops (Herkert 1997). For Bobolinks, breeding success is also tied to the timing of harvest and increased mechanization, as harvest causes high mortality of nestlings and eggs (Bollinger et al. 1990). While breeding birds still occupy agro-ecosystems, these habitats may be of lower quality as the conversion of natural habitats to agriculture has reduced global carrying capacity for avian populations has been by an estimated 20-25% (Gaston et al. 2003). Furthermore, these effects are not always direct, as many studies report indirect effects on the reproductive success of breeding birds, such as altered physiology, body condition, or parental care (reviewed in Stanton et al. 2018). Understanding how various components of agricultural intensification affect farmland birds is integral to the management and conservation of farmland bird populations.

In North America, 57 species associated with farmland have declined since the 1960s (Stanton et al. 2018). These negative population trends are mirrored in Great Britain, where 13 species have experienced average population declines of 30% (Siriwardena et al. 2002). These trends have been related in part to the intensification of agricultural practices (Donald et al. 2001, 2006). Insect populations are experiencing worldwide declines (Potts et al. 2010; Fox et al. 2014; Hallmann et al. 2017), and agricultural intensification is proposed to be one of the primary drivers (Benton et al. 2002; Ollerton et al. 2014). Parallel declines in both insect and bird populations with changes in agricultural intensification suggest that declines in insect abundance may be contributing to declines in farmland birds (Benton et al. 2002). This effect may be especially relevant for obligate insectivores, in which long-term dietary shifts have been observed (Nocera et al. 2012; English et al. 2018).

1.2. Aerial insectivores

Avian aerial insectivores are a polyphyletic guild which are highly specialized to catch and eat prey during flight. This guild, which includes swallows and martins (Hirundinea), swifts (Apodidae), and nightjars (Chordeilinae and Caprimulginae), is experiencing declines worldwide. In North America, this severity is species- and region-specific (Michel et al. 2016) but is generally the most negative in the northeastern region of North America (Nebel et al. 2010). Effects of climate (García-Pérez et al. 2014), land-use changes (Ghilain & Bélisle 2008), and pesticides (Hallmann et al. 2014) may be contributing, but to date no single driving force has been identified despite spatial and temporal synchrony in declines within this guild (Smith et al. 2015). Despite little empirical evidence, it is generally thought that the cause of these declines is a reduction in insect prey availability (Nebel et al. 2010; Nocera et al. 2012), although other studies suggest diet alone is not responsible (Imlay et al. 2017). It is possible that local environmental factors are contributing to a decline in prey insect abundance, through the mechanism of increased agricultural land-use intensity.

Farmland breeding aerial insectivores in North America include the Barn Swallow (*Hirundo rustica*), Cliff Swallow (*Petrochelidon pyrrhonota*), Purple Martin (*Progne* *subis*), and Tree Swallow (*Tachycineta bicolor*), all of which use human-made structures for nesting. Of these species, Barn Swallows have experienced the most severe population declines (Sauer et al. 2017) and are currently listed as Threatened in Canada by the Species at Risk Act and the Committee on the Status of Endangered Wildlife (COSEWIC 2011). Since 1970, Ontario populations have declined by an estimated 2.56% per year, cumulating in a total loss of 66% as of 2012 (Heagy et al. 2014). Historically, Barn Swallows built their cup-shaped mud nests on the walls of natural caves, but now almost exclusively use large open structures such as barns, bridges, and culverts as nesting locations (Brown & Brown 1999). Barn Swallows nest semi-colonially, and often in sympatry with other colonial aerial insectivorous species such as Cliff Swallows (Samuel 1971).

Barn Swallows are widespread in North America and all other continents except for Antarctica (Brown & Brown 1999), with six recognized subspecies that fall into two well-supported clades; North American/Asia and Europe/Middle East (Dor et al. 2010). Despite its global distribution, the bulk of research on breeding biology and behaviour has been done on the European subspecies (*H. r. rustica*) and there is a need for additional research investigating populations in North America. The Nearctic-Neotropical subspecies *Hirundo rustica erythrogaster* breeds across North America and migrates to Central and South America to over-winter.

1.3. Food availability

Prey availability can directly affect reproductive output. For example, supplementing food to breeding Song Sparrows (*Melospiza melodia*) resulted in larger clutch sizes and subsequently more young fledging from the nest (Arcese & Smith 1988). In another example, Pied Flycatchers' (*Ficedula hypoleuca*) with increased access to food during the nesting period fledged more young (Siikamäki 1998). Finally, synchrony between the timing of breeding in Great Tits (*Parus major*) and the peak abundance of caterpillar populations resulted in more fledged young (Visser et al. 2006).

Food availability has been shown to affect nestling body mass and condition both in the lab (Lacombe et al. 1994; Konarzewski et al. 1996; Searcy et al. 2004) and in the wild (Siikamäki 1998; Visser et al. 2006). This is important because condition at the time of fledging condition is a strong predictor of post-fledging and annual survival (Naef-Daenzer et al. 2001; Mitchell et al. 2011; Jones et al. 2016). There are currently two hypotheses that link better condition to greater survival (reviewed in Maness & Anderson 2013). The first is the 'body-reserve advantage' hypothesis, proposes that heavier juvenile birds would have a better probability of survival than lighter individuals, as larger fat stores would reduce the impact of low food availability for recently fledged and inexperienced young (Lack 1966). Young with greater fat stores furthermore have a lower risk of predation, due to a reduced need to forage and they beg less during the parental care period (Naef-Daenzer et al. 2001). The second, the 'size advantage' hypothesis, postulates that overall size confers an advantage during physical competition for resources (Garnett 2008). Regardless of the mechanism, pre-fledging condition relates directly to increased survival.

1.4. Body condition

Critical to describing relationships between nestling quality and direct and indirect measures of food availability is clearly defining nestling condition. While nestling body mass is an easily obtained measure of nestling condition, it is a simplistic measure as it fails to account for differences in structural size between individuals. Body condition indices attempt to estimate fat content based on non-destructive morphometric measurements such as size, mass, and shape (e.g., wing chord, tarsus length, bill length, tail length, and body length in birds) all measures of structural size (Labocha & Hayes 2012). Alternatively, condition can be measured directly by measuring fat stores via destructive sampling or the use of specialized equipment such as quantitative magnetic resonance instruments (QMR; Guglielmo et al. 2011). Despite known limitations of condition indices (see Green 2001; Peig & Green 2009, 2010), they are widely applied in the field and are one of the only methods to approximate the energy and nutrient stores of an individual without invasive sampling. Some studies of adult swallows have approximated body condition using only body mass (Møller et al. 2005), while others use the residuals from an ordinary least squares regression of body mass on a cube structural measurement (e.g., keel[3]; Galeotti et al. 1997). Research investigating nestling body condition uses similarly variable methods, as the ratio of cube root body mass to tarsus length (Saino et al. 1997) and body mass and length measurements analyzed separately have been used to approximate body condition in swallows (Saino et al. 1999). Alternatively, adult body condition, as a defined index, has been avoided altogether by using linear models and including a structural measurement as a covariate to account for the effect of structural size on mass (Saino et al. 2015). A similar technique has been applied to body condition in nestlings (de Ayala et al. 2006). By including structural size as a predictor in a body mass model, it allows the model to account for the variation in body size, without having to define a specific condition index.

1.5. Diet

Diet studies in adult aerial insectivores are difficult because observing foraging bouts yields little quantitative taxonomic information. Early studies examined stomach contents to determine the diet of seven North American swallow species by quantifying different prey insect proportions in the diet (Beal 1918). Such studies have shown that adult aerial insectivores eat from a broad range of orders including Coleoptera, Diptera, Ephemeroptera, Hemiptera, Hymenoptera, Isoptera, Lepidoptera, Mecoptera, Odonata, and Orthoptera (Beal 1918; Johnston 1967). Very little is known about the diet of nestlings of aerial insectivores, and most studies are from Europe (e.g., Sand Martin *Riparia*; Waugh 1979; House Martin *Delichon urbicum*, Common Swift *Apus*, Barn Swallow *Hirundo rustica rustica*; Orłowski & Karg 2011, 2013). The few North American studies have primarily focused on Tree Swallows and have emphasized the importance of Diptera of aquatic-origin prey such as Nematocera (Quinney & Ankney 1985; McCarty & Winkler 1999; Mengelkoch et al. 2004; Michelson et al. 2018).

The fact that provisioned food is brought directly to the young is an advantage for measuring nestling diet. If delivery of food to nestlings is interrupted, prey items intended to be delivered to a nestling can be identified before digestion (e.g., McCarty & Winkler 1999). Sampling methods include the use of a small ligature that is placed around a nestling’s neck to prevent swallowing (e.g., Turner 1982; Mengelkoch et al. 2004), or artificial nestling puppets (McCarty & Winkler 1991, 1999), but while methods like these allow for complete taxonomic identification and quantification, these methods can be invasive and provide information about a single feeding event only. Incorporating multiple methods towards the identification of diets can allow for additional information that is inaccessible by examining diet using only one technique (Nielsen et al. 2017).

1.5.1 Fecal analysis

Feces can provide insights into ingested diet, by visually through inspecting remains of prey body parts (e.g., Bryant 1973; Orłowski & Karg 2011, 2013) or through DNA barcoding to identify prey DNA (reviewed in Valentini et al. 2009). The latter is a powerful tool that utilizes the mitochondrial gene *cytochrome c oxidase I* (COI) as a species-specific genomic profile (Hebert et al. 2003a, 2003b), that is compared to a comprehensive database of barcode profiles such as the Barcode of Life Databases, for taxonomic identification (Barcode of Life Databases, BOLD; Ratnasingham & Hebert 2007). Within ornithology, DNA barcoding of diet has been largely restricted to seabirds (Deagle et al. 2007, 2010; Bowser et al. 2013; but see Joo & Park 2012), but has been used in songbirds to identify pest insects or to avian predators of a known pest species, rather than provide information about diet (Karp et al. 2014; King et al. 2015). More directly relevant to aerial insectivores, fecal DNA barcoding has been utilized in several studies on the diet of bats, which has allowed for the identification of prey insects (e.g., Clare et al. 2009; Zeale et al. 2011; Long et al. 2013). Despite the potential to add to current knowledge of nestling diet, there are only a handful of published studies, all within the last five years, using these methods to investigate nestling diet composition (Jedlicka et al. 2013, 2016; Trevelline et al. 2016, 2018a, 2018b) and none have been done on aerial insectivorous species.

1.5.2 Stable-isotopic analysis

Stable-isotope measurements can be used effectively to assess course info about diet over various periods of temporal integration (Hobson & Clark 1992a). Ratios of heavy to light isotopes of common elements (e.g., $^{13}C/^{12}C$, $^{15}N/^{14}N$), stored within consumer tissues, can provide predictable information on the ultimate source of a consumer's diet (reviewed in Peterson & Fry 1987 and Fry 2006). These ratios are typically expressed in delta (δ) notation, as parts per thousand (‰) deviation from the primary standards, atmospheric air ($\delta^{15}N$) and Vienna Pee Dee Belemnite (VPDB, $\delta^{13}C$):

$$\delta^{Heavy}X = [(R_{sample} / R_{standard}) - 1] \times 1000; \text{ where } R = {}^{Heavy}X / {}^{Light}H$$

Changes in stable-isotope ratios between prey and tissue, or isotopic discrimination, can be affected by numerous processes such as the type of diet, tissue, consumer species and nutritional condition and so predicting isotopic discrimination in any given situation often requires detailed experimentation (e.g., Hobson & Clark 1992a, 1992b; Bearhop et al. 2002; Hobson & Bairlein 2003). For example, feathers are an inert tissue, meaning there is virtually no isotopic turnover or exchange with the body once grown; therefore, the stable-isotopic composition of feathers can be used to provide information on diet during feather growth (Hobson & Clark 1992a). In the case of nestlings, feathers are representative of the entire nestling growth period up until sampling.

Carbon and nitrogen stable isotopes are most commonly used in dietary studies, as they change predictably between dietary sources and consumer tissues. The most common uses of carbon stable-isotope ratios ($\delta^{13}C$) have been to differentiate general diet source via plant photosynthetic pathway (i.e., C_3, C_4 or Crassulacean acid metabolism, Tieszen & Boutton 1989). Differences in $\delta^{13}C$ values in plants are due to different fractionation during C_3 and C_4 photosynthetic pathways, causing a bimodal distribution of $\delta^{13}C$ values (Tieszen & Boutton 1989). Atmospheric values of $\delta^{13}C$ in CO_2 average around -7.7‰, while plant tissues are more depleted in ^{13}C at average values of -27‰ in C_3 plants and -12‰ in C4 plants (Tieszen & Boutton 1989). But even before fractionation during the photosynthetic pathway, relative differences in water-use efficiency can change $\delta^{13}C$ values within plant tissues by affecting stomatal conductance of CO_2, enriching $\delta^{13}C$ values for CO_2 within the leaf thus enriching products of photosynthesis (Marshall et al. 2007). Carbon has also been used to differentiate between carbon sources such as upland vs. aquatic sources, where differences between $\delta^{13}C$ values in aquatic and terrestrial plants are driven by differences in carbon uptake during photosynthesis (France 1995), and marine vs. terrestrial sources, in which differences in $\delta^{13}C$ values between phytoplankton and terrestrial plants are driven by carbon source (i.e., dissolved carbonate or CO_2) (Hobson & Sealy 1991). Carbon fractionation due to plant photosynthetic pathways provides a unique opportunity within agricultural systems as most crops are C_3 (e.g., soybeans, wheat) and corn is the only C_4 crop that is widely grown in Southern Ontario. Furthermore, with agricultural intensification there is a trend towards large monocultures (e.g., corn, soybeans, wheat) allowing for potential determination of foraging preference within corn fields versus other crops or natural areas, based on these distinct $\delta^{13}C$ values.

Nitrogen stable-isotope ratios ($\delta^{15}N$) show a step-wise enrichment (more ^{15}N) with increasing trophic level, making $\delta^{15}N$ values a reliable measure of relative trophic position (Hobson & Welch 1992; Hobson et al. 1994; Boecklen et al. 2011).

Alternatively, $\delta^{15}N$ values can also be used to differentiate between different environments with contrasting nitrogen cycling and inputs (e.g., Hobson 1999). Over the past century, production and agricultural use of nitrogen-based fertilizer has increased exponentially, culminating in over-reliance on anthropogenic fixation of nitrogen (Vitousek et al. 1997). A growing body of evidence suggests that anthropogenic nitrogen inputs, specifically in agriculture, are affecting consumer diets as several studies have shown correlations between increased $\delta^{15}N$ values in agricultural or anthropogenically influenced landscapes (Hobson 1999; Girard et al. 2012). These correlations are not limited to direct agricultural land cover types, as these trends have also been found in non-target areas through runoff into ocean systems (Møller et al. 2018) and wetland systems (Hebert & Wassenaar 2001; Anderson & Cabana 2005, 2006). Synthetic fertilizers derived from atmospheric N_2 have ratios close to 0‰ and fertilizer derived from animal sources ranges from 10-25‰ (Hebert & Wassenaar 2001) but yearly tilling of the soil leads to higher $\delta^{15}N$ values in agricultural landscapes due to ammonification (Kendal 1998). In agricultural systems, it is difficult to identify the main source of anthropogenic nitrogen given multiple possible inputs (e.g., inorganic fertilizer, livestock, sewage; Anderson & Cabana 2006). Nevertheless, $\delta^{15}N$ values are expected to be higher in more agriculturally intense landscapes that rely on anthropogenic sources of nitrogen. Observations of higher N inputs affecting $\delta^{15}N$ values also speak to the possible challenge of identifying trophic foraging levels in agricultural systems and suggest the need to investigate isotope signatures in prey when possible.

1.6. Objectives

The objectives of my thesis were to evaluate the effects of agricultural intensification on nestling Barn Swallows raised in agro-ecosystems, specifically focusing on nestling condition and diet. I tested the overall hypothesis that agriculturally intense landscapes are detrimental to Barn Swallow nestlings as they have reduced insect abundance and richness, leading to lower body condition. The study is presented in two chapters (Chapters 2 and 3), using data collected in the summers of 2016/2017 at 22 Barn Swallow breeding colonies surrounding Guelph, Ontario (43.55° N, 80.25° W). In Chapter 2, I investigated the landscape-level effects of agricultural intensity on nestling condition and success. My objectives were to determine the landscape-level effect of agricultural land use on (1) nestling condition during the growth period, (2) nestling condition pre-fledging, (3) nestling growth, and (4) fledging success. I predicted that all condition, growth and success measures would be lower in nestlings raised in areas of high agricultural intensity compared to less intense landscapes because of lower food availability. In Chapter 3, I investigated the landscape-level effects of agricultural land use on Barn Swallow nestling diet. My objectives in this chapter were to use stable isotopes within nestling feathers to determine if nestlings were (1) being provisioned from agriculturally intense landscapes and to use DNA barcoding of nestling fecal matter to determine (2) whether diet composition was negatively affected by intensification. I predicted nestling feathers would have more positive $\delta^{13}C$ values in landscapes with an increased proportion of corn and more positive $\delta^{15}N$ values in landscapes with a greater proportion of row crop. Second, I predicted that diet breadth would be reduced due to reduced prey insect availability given reduced insect habitat diversity, and prey items found within nestling diet would be representative of agricultural land use.

1.7. Literature cited

Anderson C, Cabana G. 2005. $\delta^{15}N$ in riverine food webs: effects of N inputs from agricultural watersheds. Canadian Journal of Fisheries and Aquatic Sciences **62**:333–340.

Anderson C, Cabana G. 2006. Does $\delta^{15}N$ in river food webs reflect the intensity and origin of N loads from the watershed? Science of The Total Environment **367**:968–978.

Attwood S, Maron M, House A, Zammit C. 2008. Do arthropod assemblages display globally consistent responses to intensified agricultural land use and management? Global Ecology and Biogeography **17**:585–599.

Arcese P, Smith JNM. 1988. Effects of population density and supplemental food on reproduction in Song Sparrows. Journal of Animal Ecology **57**:119–136.

Beal FEL. 1918. Food habits of the swallows: a family of valuable native birds. US Department of Agriculture Bulletin **619**:1–28.

Bearhop S, Waldron S, Votier SC, Furness RW. 2002. Factors that influence assimilation rates and fractionation of nitrogen and carbon stable isotopes in avian blood and feathers. Physiological and Biochemical Zoology **75**:451–458.

Benton TG, Bryant DM, Cole L, Crick HQP. 2002. Linking agricultural practice to insect and bird populations: a historical study over three decades. Journal of Applied Ecology **39**:673–687.

Benton TG, Vickery JA, Wilson JD. 2003. Farmland biodiversity: is habitat heterogeneity the key? Trends in Ecology and Evolution **18**:182–188.

Boecklen WJ, Yarnes CT, Cook BA, James AC. 2011. On the use of stable isotopes in trophic ecology. Annual Review of Ecology, Evolution, and Systematics **42**:411–440.

Bollinger EK, Bollinger PB, Gavin TA. 1990. Effects of hay-cropping on eastern populations of the Bobolink. Wildlife Society Bulletin **18**:142–150.

Bowser AK, Diamond AW, Addison JA. 2013. From puffins to plankton: a DNA-based analysis of a seabird food chain in the northern Gulf of Maine. PLOS ONE **8**:e83152.

Brown CR, Brown MB. 1999. Barn Swallow (*Hirundo rustica*). The Birds of North America Online. Available from http://bna.birds.cornell.edu/BNA/account/Barn_Swallow.html.

Bryant DM. 1973. The factors influencing the selection of food by the House Martin (*Delichon urbica* (L.)). Journal of Animal Ecology **42**:539–564.

Burel F, Baudry J, Butet A, Clergeau P, Delettre Y, Le Coeur D, Dubs F, Morvan N, Paillat G, Petit S, Thenail C, Brunel E, Lefeuvre J-C. 1998. Comparative biodiversity along a gradient of agricultural landscapes. Acta Oecologica **19**:47–60.

Burel F, Butet A, Delettre Y, de La Peña NM. 2004. Differential response of selected taxa to landscape context and agricultural intensification. Landscape and Urban Planning **67**:195–204.

Clare EL, Fraser EE, Braid HE, Fenton MB, Hebert PD. 2009. Species on the menu of a generalist predator, the eastern red bat (*Lasiurus borealis*): using a molecular approach to detect arthropod prey. Molecular Ecology **18**:2532–2542.

COSEWIC. 2011. COSEWIC assessment and status report on the Barn Swallows (*Hirundo rustica*) in Canada. Committee on the Status of Endangered Wildlife in Canada. Available from http://registrelep-sararegistry.gc.ca/document/default_e.cfm?documentID=2288.

de Ayala RM, Martinelli R, Saino N. 2006. Vitamin E supplementation enhances growth and condition of nestling Barn Swallows (*Hirundo rustica*). Behavioral Ecology and Sociobiology **60**:619–630.

Deagle BE, Chiaradia A, McInnes J, Jarman SN. 2010. Pyrosequencing faecal DNA to determine diet of little penguins: is what goes in what comes out? Conservation Genetics **11**:2039–2048.

Deagle BE, Gales NJ, Evans K, Jarman SN, Robinson S, Trebilco R, Hindell MA. 2007. Studying seabird diet through genetic analysis of faeces: a case study on macaroni penguins (*Eudyptes chrysolophus*). PLoS One **2**:e831.

Donald PF, Green R, Heath M. 2001. Agricultural intensification and the collapse of Europe’s farmland bird populations. Proceedings of the Royal Society of London B: Biological Sciences **268**:25–29.

Donald PF, Sanderson FJ, Burfield IJ, van Bommel FPJ. 2006. Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990–2000. Agriculture, Ecosystems & Environment **116**:189–196.

Dor R, Safran RJ, Sheldon FH, Winkler DW, Lovette IJ. 2010. Phylogeny of the genus *Hirundo* and the Barn Swallow subspecies complex. Molecular Phylogenetics and Evolution **56**:409–418.

English PA, Green DJ, Nocera JJ. 2018. Stable isotopes from museum specimens may provide evidence of long-term change in the trophic ecology of a migratory aerial insectivore. Frontiers in Ecology and Evolution **6**:14.

Flynn DFB, Gogol-Prokurat M, Nogeire T, Molinari N, Richers BT, Lin BB, Simpson N, Mayfield MM, DeClerck F. 2009. Loss of functional diversity under land use intensification across multiple taxa. Ecology Letters **12**:22–33.

Fox R, Oliver TH, Harrower C, Parsons MS, Thomas CD, Roy DB. 2014. Long-term changes to the frequency of occurrence of British moths are consistent with opposing and synergistic effects of climate and land-use changes. Journal of Applied Ecology **51**:949–957.

France R. 1995. Critical examination of stable isotope analysis as a means for tracing carbon pathways in stream ecosystems. Canadian Journal of Fisheries and Aquatic Sciences **52**:651–656.

Fry B. 2006. Stable isotope ecology. Springer.

Galeotti P, Saino N, Sacchi R, Møller AP. 1997. Song correlates with social context, testosterone and body condition in male Barn Swallows. Animal Behaviour **53**:687–700.

García-Pérez B, Hobson KA, Albrecht G, Cadman MD, Salvadori A. 2014. Influence of climate on annual survival of Barn Swallows (*Hirundo rustica*) breeding in North America. The Auk **131**:351–362.

Garnett MC. 2008. Body size, its heritability and influence on juvenile survival among Great Tits, *Parus major*. Ibis **123**:31–41.

Gaston KJ, Blackburn TM, Goldewijk KK. 2003. Habitat conversion and global avian biodiversity loss. Proceedings of the Royal Society of London B: Biological Sciences **270**:1293–1300.

Ghilain A, Bélisle M. 2008. Breeding success of Tree Swallows along a gradient of agricultural intensification. Ecological Applications **18**:1140–1154.

Girard J, Baril A, Mineau P, Fahrig L. 2012. Foraging habitat and diet of Song Sparrows (*Melospiza melodia*) nesting in farmland: a stable isotope approach. Canadian Journal of Zoology **90**:1339–1350.

Green AJ. 2001. Mass/length residuals: measures of body condition or generators of spurious results? Ecology **82**:1473–1483.

Green RE, Cornell SJ, Scharlemann JP, Balmford A. 2005. Farming and the fate of wild nature. Science **307**:550–555.

Grüebler MU, Morand M, Naef-Daenzer B. 2008. A predictive model of the density of airborne insects in agricultural environments. Agriculture, Ecosystems & Environment **123**:75–80.

Guglielmo CG, McGuire LP, Gerson AR, Seewagen CL. 2011. Simple, rapid, and non-invasive measurement of fat, lean, and total water masses of live birds using quantitative magnetic resonance. Journal of Ornithology **152**:S75–S85.

Hallmann CA, Foppen RP, van Turnhout CA, de Kroon H, Jongejans E. 2014. Declines in insectivorous birds are associated with high neonicotinoid concentrations. Nature **511**:341–343.

Hallmann CA, Sorg, M, Jongejans E, Siepel H, Hofland N, Schwan H, Stenmans W, Müller A, Sumser H, Hörren T, Goulson D, de Kroon H. 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. PLOS ONE **12**:e0185809.

Heagy A, Badzinski D, Bradley D, Falconer M, McCracken J, Reid RA, Richardson K. 2014. Recovery strategy for the Barn Swallow (*Hirundo rustica*) in Ontario. Ontario Recovery Strategy Series. Prepared for the Ontario Ministry of Natural Resources and Forestry, Peterborough, Ontario. Available from http://files.ontario.ca/environment-and-energy/species-at-risk/mnr_sar_rs_brn_swl_en.pdf.

Hebert CE, Wassenaar LI. 2001. Stable nitrogen isotopes in waterfowl feathers reflect agricultural land use in western Canada. Environmental Science & Technology **35**:3482–3487.

Hebert PDN, Cywinska A, Ball SL. 2003a. Biological identifications through DNA barcodes. Proceedings of the Royal Society of London B: Biological Sciences **270**:313–321.

Hebert PDN, Ratnasingham S, de Waard JR. 2003b. Barcoding animal life: cytochrome c oxidase subunit 1 divergences among closely related species. Proceedings of the Royal Society of London. Series B: Biological Sciences **270**:S96–S99.

Hendrickx F, Maelfait J, Van Wingerden W, Schweiger O, Speelmans M, Aviron S, Augenstein I, Billeter R, Bailey D, Bukacek R. 2007. How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. Journal of Applied Ecology **44**:340–351.

Herkert JR. 1997. Bobolink *Dolichonyx oryzivorus* population decline in agricultural landscapes in the Midwestern USA. Biological Conservation **80**:107–112.

Hobson KA. 1999. Stable-carbon and nitrogen isotope ratios of songbird feathers grown in two terrestrial biomes: implications for evaluating trophic relationships and breeding origins. The Condor **101**:799–805.

Hobson KA, Bairlein F. 2003. Isotopic fractionation and turnover in captive Garden Warblers (*Sylvia borin*): implications for delineating dietary and migratory associations in wild passerines. Canadian Journal of Zoology **81**:1630–1635.

Hobson KA, Clark RG. 1992a. Assessing avian diets using stable isotopes I: turnover of 13C in tissues. The Condor **94**:181–188.

Hobson KA, Clark RG. 1992b. Assessing avian diets using stable isotopes II: factors influencing diet-tissue fractionation. The Condor **94**:189–197.

Hobson KA, Piatt JF, Pitocchelli J. 1994. Using stable isotopes to determine seabird trophic relationships. Journal of Animal Ecology **63**:786–798.

Hobson KA, Sealy SG. 1991. Marine protein contributions to the diet of Northern Saw-whet Owls on the Queen Charlotte Islands: a stable-isotope approach. The Auk **108**:437–440.

Hobson KA, Welch HE. 1992. Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}C$ and $\delta^{15}N$ analysis. Marine Ecology Progress Series **84**:9–18.

Imlay TL, Mann HAR, Leonard ML. 2017. No effect of insect abundance on nestling survival or mass for three aerial insectivores. Avian Conservation and Ecology **12:**19.

Jedlicka JA, Sharma AM, Almeida RP. 2013. Molecular tools reveal diets of insectivorous birds from predator fecal matter. Conservation Genetics Resources **5**:879–885.

Jedlicka JA, Vo A-TE, Almeida RPP. 2016. Molecular scatology and high-throughput sequencing reveal predominately herbivorous insects in the diets of adult and nestling Western Bluebirds (*Sialia mexicana*) in California vineyards. The Auk **134**:116–127.

Johnston RF. 1967. Seasonal variation in the food of the Purple Martin *Progne subis* in Kansas. Ibis **109**:8–13.

Jones TM, Ward MP, Benson TJ, Brawn JD. 2016. Variation in nestling body condition and wing development predict cause-specific mortality in fledgling Dickcissels. Journal of Avian Biology **48**:439–447.

Joo S, Park S. 2012. Identification of bird species and their prey using DNA barcode on feces from Korean traditional village groves and forests (maeulsoop). Animal Cells and Systems **16**:488–497.

Karp DS, Judson S, Daily GC, Hadly EA. 2014. Molecular diagnosis of bird-mediated pest consumption in tropical farmland. SpringerPlus **3**:630.

Kendall C. 1998. Tracing nitrogen sources and cycling in catchments. Pages 519–576 in J. McDonnell, editor. Isotope Tracers in Catchment Hydrology. Elsevier, Amsterdam.

King RA, Symondson WOC, Thomas RJ. 2015. Molecular analysis of faecal samples from birds to identify potential crop pests and useful biocontrol agents in natural areas. Bulletin of Entomological Research **105**:261–272.

Konarzewski M, Kowalczyk J, Swierubska T, Lewonczuk B. 1996. Effect of short-term feed restriction, realimentation and overfeeding on growth of Song Thrush (*Turdus philomelos*) nestlings. Functional Ecology **10**:97–105.

Labocha MK, Hayes JP. 2012. Morphometric indices of body condition in birds: a review. Journal of Ornithology **153**:1–22.

Lack D. 1966. Population Studies of Birds. Clarendon Press, Oxford.

Lacombe D, Bird DM, Hibbard KA. 1994. Influence of reduced food availability on growth of captive American Kestrels. Canadian Journal of Zoology **72**:2084–2089.

Lewis T. 1969. The distribution of flying insects near a low hedgerow. Journal of Applied Ecology **6**:443–452.

Long BL, Kurta A, Clemans DL. 2013. Analysis of DNA from feces to identify prey of Big Brown Bats (*Eptesicus fuscus*) caught in apple orchards. The American Midland Naturalist **170**:287–297.

Maness TJ, Anderson DJ. 2013. Predictors of juvenile survival in birds. Ornithological Monographs **78**:1–55.

Marshall JD, Brooks JR, Lajtha K. 2007. Sources of variation in the stable isotopic composition of plants. Stable isotopes in ecology and environmental science **2**:22–60.

Matson PA, Parton WJ, Power AG, Swift MJ. 1997. Agricultural intensification and ecosystem properties. Science **277**:504–509.

McCarty JP, Winkler DW. 1991. Use of an artificial nestling for determining the diet of nestling Tree Swallows. Journal of Field Ornithology **62**:211–217.

McCarty JP, Winkler DW. 1999. Foraging ecology and diet selectivity of Tree Swallows feeding nestlings. The Condor **101**:246–254.

Mengelkoch JM, Niemi GJ, Regal RR. 2004. Diet of the nestling Tree Swallow. The Condor **106**:423–429.

Michel NL, Smith AC, Clark RG, Morrissey CA, Hobson KA. 2016. Differences in spatial synchrony and interspecific concordance inform guild-level population trends for aerial insectivorous birds. Ecography **39**:774–786.

Michelson CI, Clark RG, Morrissey CA. 2018. Agricultural land cover does not affect the diet of Tree Swallows in wetland-dominated habitats. The Condor **120**:751–764.

Mitchell GW, Guglielmo CG, Wheelwright NT, Freeman-Gallant CR, Norris DR. 2011. Early life events carry over to influence pre-migratory condition in a free-living songbird. PLOS ONE **6**:e28838.

Møller AP, Mousseau T, Milinevsky G, Pelko A, Pysanets E, Szép T. 2005. Condition, reproduction and survival of Barn Swallows from Chernobyl. Journal of Animal Ecology **74**:1102–1111.

Møller AP, Laursen K, Hobson KA. 2018. Retrospectively analysing condition in historical samples of birds. Journal of Zoology **305**:188–195.

Naef-Daenzer B, Widmer F, Nuber M. 2001. Differential post-fledging survival of Great and Coal Tits in relation to their condition and fledging date. Journal of Animal Ecology **70**:730–738.

Nebel S, Mills A, McCracken JD, Taylor PD. 2010. Declines of aerial insectivores in North America follow a geographic gradient. Avian Conservation and Ecology **5**:1.

Nielsen JM, Clare EL, Hayden B, Brett MT, Kratina P. 2017. Diet tracing in ecology: method comparison and selection. Methods in Ecology and Evolution **2017**:1–14.

Nocera JJ, Blais JM, Beresford DV, Finity LK, Grooms C, Kimpe LE, Kyser K, Michelutti N, Reudink MW, Smol JP. 2012. Historical pesticide applications coincided with an altered diet of aerially foraging insectivorous Chimney Swifts. Proceedings of the Royal Society B: Biological Sciences **279**:3114–3120.

Ollerton J, Erenler H, Edwards M, Crockett R. 2014. Extinctions of aculeate pollinators in Britain and the role of large-scale agricultural changes. Science **346**:1360.

Orłowski G, Karg J. 2011. Diet of nestling Barn Swallows *Hirundo rustica* in rural areas of Poland. Open Life Sciences **6**:1023–1035.

Orłowski G, Karg J. 2013. Diet breadth and overlap in three sympatric aerial insectivorous birds at the same location. Bird Study **60**:475–483.

Peig J, Green AJ. 2009. New perspectives for estimating body condition from mass/length data: the scale mass index as an alternative method. Oikos **118**:1883–1891.

Peig J, Green AJ. 2010. The paradigm of body condition: a critical reappraisal of current methods based on mass and length. Functional Ecology **24**:1323–1332.

Peterson BJ, Fry B. 1987. Stable isotopes in ecosystem studies. Annual Review of Ecology and Systematics **18**:293–320.

Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE. 2010. Global pollinator declines: trends, impacts and drivers. Trends in Ecology & Evolution **25**:345–353.

Quinney TE, Ankney CD. 1985. Prey size selection by Tree Swallows. The Auk **102**:245–250.

Ratnasingham S, Hebert PDN. 2007. BOLD: the Barcode of Life Data system (http://barcodinglife.org). Molecular Ecology Notes **7**:355–364.

Robinson RA, Sutherland WJ. 2002. Post-war changes in arable farming and biodiversity in Great Britain. Journal of Applied Ecology **39**:157–176.

Saino N, Calza S, Ninni P, Møller AP. 1999. Barn Swallows trade survival against offspring condition and immunocompetence. Journal of Animal Ecology **68**:999–1009.

Saino N, Calza S, Møller AP. 1997. Immunocompetence of nestling Barn Swallows in relation to brood size and parental effort. Journal of Animal Ecology **66**:827–836.

Saino N, Romano M, Romano A, Rubolini D, Ambrosini R, Caprioli M, Parolini M, Scandolara C, Bazzi G, Costanzo A. 2015. White tail spots in breeding Barn Swallows *Hirundo rustica* signal body condition during winter moult. Ibis **157**:722–730.

Samuel DE. 1971. The breeding biology of Barn and Cliff swallows in West Virginia. The Wilson Bulletin **83**:284–301.

Sauer JR, Niven DK, Hines JE, Ziolkowski J DJ, Pardieck KL, Fallon JE, Link WA. 2017. The North American breeding bird survey, results and analysis 1966 - 2015. Version 2.07.2017. USGS Patuxent Wildlife Research Center, Laurel, MD.

Schweiger O, Maelfait JP, Wingerden W, Hendrickx F, Billeter R, Speelmans M, Augenstein I, Aukema B, Aviron S, Bailey D, Bukacek R, Burel F, Diekötter T, Dirksen J, Frenzel M, Herzog F, Liira J, Roubalova M, Bugter R. 2005. Quantifying the impact of environmental factors on arthropod communities in agricultural landscapes across organizational levels and spatial scales. Journal of Applied Ecology **42**: 1129–1139.

Searcy WA, Peters S, Nowicki S. 2004. Effects of early nutrition on growth rate and adult size in Song Sparrows *Melospiza melodia*. Journal of Avian Biology **35**:269–279.

Siikamäki P. 1998. Limitation of reproductive success by food availability and breeding time in Pied Flycatchers. Ecology **79**:1789–1796.

Siriwardena GM, Baillie SR, Buckland ST, Fewster RM, Marchant JH, Wilson JD. 2002. Trends in the abundance of farmland birds: a quantitative comparison of smoothed Common Birds Census indices. Journal of Applied Ecology **35**:24–43.

Smith AC, Hudson M-AR, Downes CM, Francis CM. 2015. Change points in the population trends of aerial-insectivorous birds in North America: synchronized in time across species and regions. PLOS ONE **10**:e0130768.

Stanton RL, Morrissey CA, Clark RG. 2018. Analysis of trends and agricultural drivers of farmland bird declines in North America: a review. Agriculture, Ecosystems & Environment **254**:244–254.

Tieszen LL, Boutton TW. 1989. Stable carbon isotopes in terrestrial ecosystem research. Pages 167–195 in P. W. Rundel, J. R. Ehleringer, and K. A. Nagy, editors. Stable Isotopes in Ecological Research. Springer New York.

Trevelline BK, Latta SC, Marshall LC, Nuttle T, Porter BA. 2016. Molecular analysis of nestling diet in a long-distance Neotropical migrant, the Louisiana Waterthrush (*Parkesia motacilla*). The Auk **133**:415–428.

Trevelline BK, Nuttle T, Hoenig BD, Brouwer NL, Porter BA, Latta SC. 2018a. DNA metabarcoding of nestling feces reveals provisioning of aquatic prey and resource partitioning among Neotropical migratory songbirds in a riparian habitat. Oecologia **187**:85–98.

Trevelline BK, Nuttle T, Porter BA, Brouwer NL, Hoenig BD, Steffensmeier ZD, Latta SC. 2018b. Stream acidification and reduced aquatic prey availability are associated with dietary shifts in an obligate riparian Neotropical migratory songbird. PeerJ **6**:e5141.

Tscharntke T, Klein AM, Kruess A, Steffan-Dewenter I, Thies C. 2005. Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. Ecology Letters **8**:857–874.

Turner A. 1982. Optimal foraging by the swallow (*Hirundo rustica*, L): prey size selection. Animal Behaviour **30**:862–872.

Valentini A, Pompanon F, Taberlet P. 2009. DNA barcoding for ecologists. Trends in Ecology & Evolution **24**:110–117.

Visser ME, Holleman LJM, Gienapp P. 2006. Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. Oecologia **147**:164–172.

Vitousek PM, Aber JD, Howarth RW, Likens GE, Matson PA, Schindler DW, Schlesinger WH, Tilman DG. 1997. Human alteration of the global nitrogen cycle: sources and consequences. Ecological Applications **7**:737–750.

Waugh D. 1979. The diet of Sand Martins during the breeding season. Bird Study **26**:123–128.

Zeale MR, Butlin RK, Barker GL, Lees DC, Jones G. 2011. Taxon-specific PCR for DNA barcoding arthropod prey in bat faeces. Molecular Ecology Resources **11**:236–244.

Zink RM, Pavlova A, Rohwer S, Drovetski SV. 2006. Barn Swallows before barns: population histories and intercontinental colonization. Proceedings of the Royal Society B: Biological Sciences **273**:1245–1251.

Chapter 2

Landscape-level effects of agricultural intensification on the condition of nestling Barn Swallows (*Hirundo rustica*)

2.1. Introduction

Farmland bird populations in both North America and Europe have shown marked declines with shifts towards specialization of agricultural production away from small-scale farming practices and towards highly industrialized agriculture (Murphy 2003; Donald et al. 2001, 2006). These changes involve the use of high yielding row crops (e.g., corn, soybeans), increasing agro-chemical inputs, mechanization, and increasing field sizes (Matson et al. 1997). Many grassland, shrubland and aerial insectivorous bird species occupy agro-ecosystems and to various degrees have adapted to historic agricultural practices (Murphy 2003). However, the more recent shift to intensive farming practices has resulted in simplified agro-ecosystems characterized by habitat homogeneity and reduced trophic complexity and there is renewed concern about the effects of agricultural intensification on farmland birds (Murphy 2003; Wilson et al. 2017; Stanton et al. 2018).

In North America, aerial insectivores, or birds which almost exclusively forage on the wing, are showing the steepest population declines of any group of birds (NABCI 2016; Sauer et al. 2017; Stanton et al. 2018). The severity of these declines are species- and region-specific (Michel et al. 2016) but are generally the most negative in the northeastern region of North America (Nebel et al. 2010). A proposed mechanism for populations declines in aerial insectivores is the reduction of prey insect abundance

(Nebel et al. 2010; Nocera et al. 2012) as insect abundance and richness are both negatively affected by agricultural practices (Hendrickx et al. 2007; Grüebler et al. 2008). In a metanalysis, Attwood et al. (2008) found that arthropod richness and abundance were lower in areas of high-intensity agricultural land use. Parallel declines between both insect and bird populations with increasing agricultural intensification in Europe, are consistent with this theory (Benton et al. 2002). Furthermore, stable-isotopic evidence indicates long-term dietary shifts in insectivorous birds, possibly driven by changes in insect community composition, theorized to be attributable to pesticides (Nocera et al. 2012; English et al. 2018).

Food availability during the breeding period can directly affect both clutch size and the number of young successfully fledging (Arcese & Smith 1988; Siikamäki 1998; Reynolds et al. 2003; Visser et al. 2006), but these measures broadly fail to address individual nestling condition. During the post-fledging period, the period between fledging and autumn migration, nestlings in better condition at the time of fledging are more likely to survive (Naef-Daenzer et al. 2001; Vitz & Rodewald 2011; Mitchell et al. 2011; Jones et al. 2016; Evans et al. unpub ms.). One hypothesis for this pattern is that young in better condition at fledging have greater fat reserves or possibly face reduced predation if individuals in better condition can afford to be more vigilant while foraging or can be more discriminating about foraging habitats (Lack 1966; Maness & Anderson 2013).

Nestling body mass has been related to food availability both in the wild (Siikamäki 1998; Visser et al. 2006) and in lab-raised young (Konarzewski et al. 1996; Searcy et al. 2004). In the Yellowhammer (*Emberiza citronella*), mean nestling condition was positively correlated with insect abundance, which was depressed in areas of pesticide applications (Hart et al. 2006). Corn Buntings (*Miliaria calandra*) showed a similar response where insect abundance was negatively correlated with the amount of pesticides and positively correlated with nestling condition (Brickle et al. 2000). While this shows that agricultural practices can have indirect effects on nestlings, to date studies investigating these effects on aerial insectivores in North America have been limited to a single species where they found negative effects of agricultural land use on fledging success but did not examine individual nestling condition (Tree Swallows *Tachycineta bicolor*; Ghilain & Bélisle 2008).

The Barn Swallow (*Hirundo rustica*) is a long-distance migratory aerial insectivore that commonly breeds within agricultural landscapes, typically using barn structures for nesting habitat (Brown & Brown 1999). This species has experienced severe population declines over the past several decades (Sauer et al. 2017) and is currently listed as Threatened in Canada, by the Committee on the Status of Endangered Wildlife (COSEWIC 2011) and the Species at Risk Act. Over the same period, Ontario populations have declined by more than 2% per year, cumulating to a total loss of 66% as of 2012 (Heagy et al. 2014). Barn Swallows breeding in Southern Ontario, along with the rest of northeastern North America, are showing steeper population declines compared with the rest of their breeding range (Nebel et al. 2010; Michel et al. 2016). My objective was to determine the landscape-level effects of agricultural intensification on the condition, growth, and fledging success of nestling Barn Swallows in this region. I applied a scale of effect analysis to determine the most appropriate scale or context (i.e., the buffer size or radius within which landscape is measured) for each measure of condition, growth, and success (e.g., Ricketts et al. 2001; Steffan-Dewenter et al. 2002; Holland et al. 2004). To evaluate nestling condition, I focused on condition during the linear growth period (hereafter ‘nestling condition’), condition just before leaving the nest (hereafter ‘pre-fledging condition’), and the change in mass between these two periods (hereafter ‘nestling growth’). Nestling growth follows a non-linear trend, in terms of mass, where mass increases linearly from day 1 (~2.21 g) to 13 (~21.29 g) where mass peaks and subsequently drops slightly before fledging at day 19 - 20 (Fernaz et al. 2012). To assess overall reproductive output, I also measured the number of young that survived to leave the nest (hereafter ‘fledging success’). I hypothesized that nestlings raised within agriculturally intense landscapes would have lower performance due to reduced availability of aerial insects. I predicted (1) nestling condition, (2) pre-fledging condition, (3) nestling growth, and (4) fledging success would be lower in individuals raised in landscapes composed of greater proportions of row crop.

2.2. Methods

2.2.1 Study species and sites

I conducted fieldwork at 22 breeding colonies in 2016 and 2017 near Guelph, within or near Wellington county in southwestern Ontario (43.55° N, 80.25° W; Figure 2.1). I worked at the same colonies in both years, except one colony (GL; see Appendix A. Summary tables Table A1, for a list of site codes and coordinates) that was lost after 2016 and one colony (VV) which was added in 2017. This county represents a rural landscape characterized by a mixture of agricultural crops, pasture, and natural areas. In North America, Barn Swallows nest semi-colonially, using flat vertical surfaces as placement for their cup-shaped mud nests, making open barn structures ideal nesting

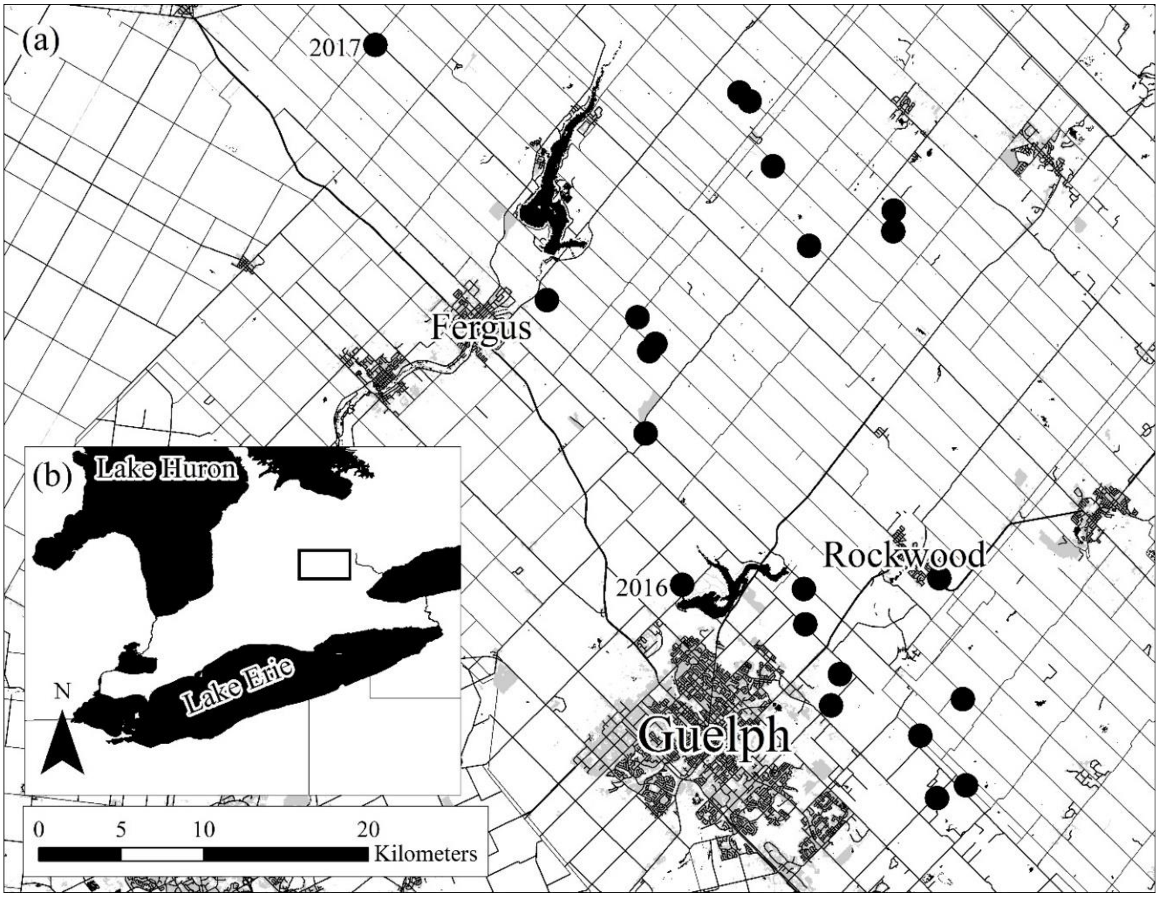


Figure 2.1. Location of Barn Swallow breeding colonies (points, n = 22) in Wellington and surrounding counties (a) within southern Ontario (b), Canada in 2016 and 2017. Sites labelled with a specific year were only included in the analyses for the labelled year. See Appendix A. Summary tables; Table A1. for specific latitudes and longitudes of sites.

habitat (Brown & Brown 1999). Barn Swallows exhibit bi-parental care and are predominantly double-brooded, with their first brood starting in May and the second broods fledging in late August (Brown & Brown 1999). Clutch sizes for Barn Swallows range from three to seven (Brown & Brown 1999).

2.2.2 Monitoring and sampling

Colonies were first visited in early May of each year followed by weekly visits, to establish nest locations and clutch initiation (mean initiation date in 2017 was 27 May brood one; 12 July brood two). Once clutch initiation was determined, nests were monitored at least once a week to record the timing of the penultimate egg laid as the onset of incubation, after which timing of hatch was predicted to be 13 days later (Brown & Brown 1999). Nests were revisited a few days earlier than the estimated hatch day and every few days afterwards to determine hatch day as accurately as possible. Hatch day was considered day zero. For any nests, particularly in 2016, when I was unable to reliably record actual hatch day, nestlings were aged based on feather tract development and feather shaft emergence, relying on expert opinion (M. Cadman pers. obs.; for detailed developmental ageing methods used see Fernaz et al. 2012). In 2017, I assigned hatch day by visiting nests at least once every second day. If a nest was found partially hatched, hatch day was assigned as that day, as an entire brood generally hatches within 24 hours (Brown & Brown 1999). If the nest was found fully hatched, nestlings were examined for signs of recent hatch. These included eggshell remaining in the nest, nestling limbs still curled into the shape of the egg rather than relaxed, and wet feather tufts. If the nestlings did not appear to have hatched within the last few hours, the previous day was assigned as hatch day. Following this protocol, I determined hatch day within 24 hours, for 309 of 385 clutches that hatched. If hatch day was missed, hatch day was retroactively determined based on the development of the nestlings, as in 2016. Late first broods and second broods were found by examining all empty nests at each site once a week to identify newly established clutches.

All nests were visited between day six and ten after hatching, ideally targeting day eight, during which nestlings were banded with a uniquely numbered United States Geological Survey aluminum leg band. For each nestling, I documented mass, age and wing length (i.e., length from the wrist joint to the longest primary, while bent at rest, hereafter ‘wing’) to assess nestling condition during the exponential growth period. I banded 2558 nestling Barn Swallows across 22 sites in 2016 and 2017 (n = 1187 and n = 1372, respectively). Two sites, each for only one year, were excluded from the analyses. The first site (OL 2016, n = 22 nestlings) was excluded due to high predation rates, leading to a whole colony failure, and the second (FL 2017, n = 96 nestlings) was excluded due to infrequent visits relating to landowner permission to access the site. Of the included sites, measurements were taken between day six and day 10 for 2452 nestlings, and at day eight for 1833 nestlings (day eight nestlings: n = 547 in 2016, n = 1286 in 2017). A subset of nests were revisited at day 15 to assess pre-fledging condition, where the above morphometric measurements were also taken. Day 15 was chosen for the final measure of a nestling’s quality as it is the last day that nestlings can be handled without high risk of premature fledging (M. Cadman, pers. obs.). Pre-fledging measurements were taken for 784 nestlings (n = 364 in 2016, n = 420 in 2017). To nestling assess growth, paired morphological measurements between nestlings at day eight and day 15 were available for 603 nestlings (n = 188 in 2016, n = 415).

After sampling at day 15, young were expected to fledge within 4 - 5 days, as average fledging age in Barn Swallows is 19 - 20 days (Brown & Brown 1999). Nests were ideally revisited within one week after the estimated fledging date (i.e., day 20) to determine fledging success, but not all nest could be revisited within this period. As nestling mortality is very low in other populations (< 5 % of total nestlings, reported in Ambrosini & Saino 2010; Saino et al. 2017), it is assumed that any nest that survives to day 10 is successful and the number of young fledged is the same number as the last check. I followed these criteria as a broad measure of fledging success but instead chose day eight as my lowest acceptable age for assumed fledging success. I monitored 847 active Barn Swallow broods in 2016 and 2017 (excluding the dropped sites), of which 687 survived until hatch. These nests were used for subsequent fledging success modelling. An additional five nests were dropped from all analyses due to missing data, and 30 nests were dropped from fledging success models because I was unable to revisit the nests. Of the retained nests, 435 were first broods (199 in 2016, 236 in 2017) and 217 were second broods (109 in 2016, 108 in 2017).

2.2.3 Landscape

Landscapes surrounding my focal barns were classified by cover types known to provide potential foraging habitat for adult Barn Swallows (Evans et al. 2007), which generally forage below 10 meters over open habitat (Brown & Brown 1999). I used two land cover categories, the first being agricultural row crop and the second being natural grassland and pasture (hereafter ‘forage’). Land cover types were classified from annual crop inventory maps available from Agriculture and Agri-food Canada (AAFC 2017). Annual crop inventory maps are comprised of 30 m × 30 m raster cells, populated via remote sensing imagery. Corn, soybeans, winter wheat, and summer wheat were combined into row crop while pasture, forage, and grassland were combined into forage. While Barn Swallows use anthropogenic structures for nesting (Brown & Brown 1999), urban habitats were not included in any analyses because they comprised such a low proportion of land cover across sites (0.045 ± 0.053 within 1000 m of all sites). Also, despite the potential biological significance of insects originating in wetlands and water to nestling Barn Swallows (e.g., Twining et al. 2016), both land cover variables were excluded from all analyses due to low proportion across sites (0.0055 ± 0.02 within 1000 m within of all sites). While row crop proportion is a measure of landscape structure, for the purposes of my analysis it is used as a proxy for agricultural intensity, where landscapes characterized by higher amounts of row cropping represent more intensively managed agricultural landscapes. Conversely, forage represents semi-natural land cover, which is associated with less intensively managed landscapes. All landscape data were visualized, processed, and exported using ESRI ArcMap 10 (ESRI 2011). Concentric buffers (n = 20) spanning from 100 m to 2000 m centred on each colony were used to measure the proportion of each land cover class of interest at each scale.

2.2.4 Statistics

All statistical analyses were performed using RStudio Version 1.0.136 and R version 3.3.1 statistical software (RStudio Team 2015; R Core Team 2016). To determine the scale of effect for each response variable and each land cover variable, a single linear mixed effect model (LMM) or generalized linear mixed effect model (GLMM) was fit for each land cover type at each nested scale (radii 100 m to 2000 m, by 100 m) for each response of interest (nestling condition, pre-fledging condition, growth rate, fledging success). Random effects were nest location and site, except in fledging success models where nest location was not relevant. All scale-of-effect models were fit using maximum likelihood. The best model was determined as the model with the lowest Akaike information criterion (AIC) value, even in the case of more than one competitive model (i.e., within 2.0 AIC of the strongest model; Burnham & Anderson 2002). Scale of effect analyses were performed for each year separately, and for the two years combined, where year was added as a fixed effect.

To test whether nestlings were in worse condition in more agriculturally intense landscapes, I used separate LMMs with (1) nestling mass during the growth period and (2) pre-fledging mass as response variables (R package lme4; Bates et al. 2015). Mixed effect models were used due to the nested structure of my sampling design to account for the random effects of nest location and site (individual nested within nest location nested within site). As structurally larger birds were expected to have greater mass, unrelated to energy stores, wing and wing^2 were added as fixed terms in all mass models to account for the effect of structural size on mass (e.g., nestlings: de Ayala et al. 2006; adults: Saino et al. 2015). The effect of landscape scale was first assessed, then measures of row crop and forage proportion were included at the most appropriate scale. Fixed effects of (i) date (day of the year), (ii) year, (iii) brood size (number of young at time of sampling), and (iv) colony size (maximum number of active nests in the first brood) were added to account for seasonal fluctuations in food availability and parental investment, differences in food availability between years likely owing to weather, intra-nest competition for food among siblings, and possible density-dependent effects on food availability (Lack 1966), respectively. Two-way interactions between year and land cover were included to account for the possibility of year-dependent effects of landscape on nestling condition, as agricultural crops can change between years. Based on preliminary data visualizations, curvilinear terms for date and brood size were also included.

To test whether nestling growth was reduced in more agriculturally intense landscapes, I modelled the growth across the landscape using a LMM with the change in mass between day eight and 15 as the response. Nestlings were included in this model only if they were exactly eight days old in this model. Change in wing length, along with the curvilinear (Δ wing^2) term, were added as fixed effects to control for the change in structural size. Other than this change, model structure was identical to the condition models. The effect of landscape scale was first assessed, then measures of row crop and forage proportion were included at the most appropriate scale, along with year interaction terms.

To test whether fledging success was reduced in more agriculturally intense environments, I used a GLMM with a Poisson distribution. Model structure was identical to the nestling mass models but included the number of young fledged as the model response and did not include a measure of brood size. Fixed effects of (i) row crop amount, (ii) forage amount, (iii) date, (iv) year, and (v) colony size were included in the model for the same reasons described above. For GLMM models, measures of date and colony size were standardized. Interaction terms between each respective land cover type and year were included, along with a curvilinear term for date.

For all models, interaction terms and curvilinear terms were removed if they were not significant because their inclusion could affect the interpretation of lower-order terms. P-values for all mixed-effects models were estimated using parametric bootstrapping (R package pbkrtest; Halekoh & Højsgaard 2014). If interaction terms were found to be significant, p-value estimation for lower order terms via parametric bootstrapping was not possible. After assessment of interaction terms and higher order terms, effects from the best model were modelled using restricted maximum likelihood as this has been shown to produce less biased parameter estimates and standard errors (Pinhero & Bates 2000).

2.3. Results

2.3.1 Landscape

General landscape composition within 100 m of sites was primarily row crop and forage. Row crop proportion averaged 0.20 ± 0.29 (0.18 ± 0.26 in 2016 and 0.21 ± 0.32 in 2017, n = 22) and forage 0.68 (0.70 ± 0.25 in 2016 and 0.67 ± 0.30 in 2017, n = 22). Some sites contained no row crop within 100 m while some were entirely row crop (see Appendix A. Summary tables; Table A1). The same was true for forage amount. Proportion of row crop within 100 m surrounding barns did not change across the two years of study (two-tailed paired t-test; t = -1.17, n = 22, p-value = 0.26). There were also no differences in percent forage between the two years (two-tailed paired t-test; t = 1.24, n = 22, p-value = 0.23).

2.3.2 Landscape effects

Nestling mass was significantly related to both wing and wing^2, indicating that my measures of structural size adequately control for the effect of size on mass (Table 2.1; see Appendix C. Relationship between nestling mass and structural size; Figure C1).

Table 2.1. Linear mixed effect model results for Barn Swallow nestling (day 6 - 10) mass (n = 2452) measured at colonies near Guelph Ontario (nests = 475, sites = 22), in the breeding seasons of 2016 and 2017. The global model included fixed effects of proportion of row crop, proportion of forage, wing, wing^2, brood size, colony size, date, and year, and random effects of nest location, and site. Dropped terms are noted by dashes (-).

	Nestling Mass			
	Coefficient	SE	t value	p-value
Intercept	2.84	0.83	3.43	-
Wing	0.72	0.03	28.03	< 0.001
Wing^2	-0.0055	0.00035	-15.69	< 0.001
Brood Size	-0.70	0.18	-3.88	< 0.001
Brood Size^2	0.058	0.022	2.63	< 0.001
Colony Size	0.0031	0.0069	0.45	0.78
Date	-0.017	0.0016	-10.36	< 0.001
Date^2	-	-	-	-
Year	-0.61	0.25	-2.43	
Row crop (100 m)	1.54	0.46	3.35	< 0.01
Year * Row crop	-	-	-	-
Forage (100 m)	0.077	0.51	0.15	
Year * Forage	1.086	0.35	3.06	< 0.01

There was a positive linear relationship between row crop and nestling condition (LMM; sites = 22, nests = 475, n = 2452; Table 2.1 and Figure 2.2). The relationship between nestling condition and row crop as well as forage was strongest at a spatial extent of 100 m (see Appendix B. Scale of effect figures for nestling condition; Figure B1). Mean nestling mass was 16.73 g ± 2.3 and mean wing length was 35.49 mm ± 5.6 (n = 1833; for year-specific statistics see Appendix A. Summary tables; Table A2). Nestling mass increased with forage amount, but the strength of the relationship was stronger in 2017 compared to 2016 (Table 2.1). Nestling condition was negatively associated with the day of the year, where nestlings from later broods were in worse condition as the season progressed (Table 2.1). Finally, nestling condition decreased as brood size increased initially and then increased again as clutch size increased (Table 2.1). There was no detectable relationship between nestling condition and colony size (Table 2.1).

Like nestling mass, pre-fledging mass increased was significantly related to wing and wing^2 (Table 2.2; see Appendix C. Relationship between nestling mass and structural size; Figure C2). However, unlike nestling mass, pre-fledging condition was not related to either row crop or forage (LMM; sites = 20, nests = 179, n = 784; Table 2.2 and Figure 2.3). Again, pre-fledging condition varied most strongly with row crop and forage proportion at the 100 m extent (see Appendix B. Scale of effect figures for nestling condition; Figure B2). Mean pre-fledging mass was 20.11 g ± 1.8 and wing length was 73.53 mm ± 5.1 (n = 784; for year-specific statistics see Appendix A. Summary tables; Table A2). Pre-fledging condition increased with date, but the rate of increase slowed as the season progressed (Table 2.2). Pre-fledging condition was higher in 2017 compared to 2016 (Table 2.2). Pre-fledging condition decreased with increasing brood size

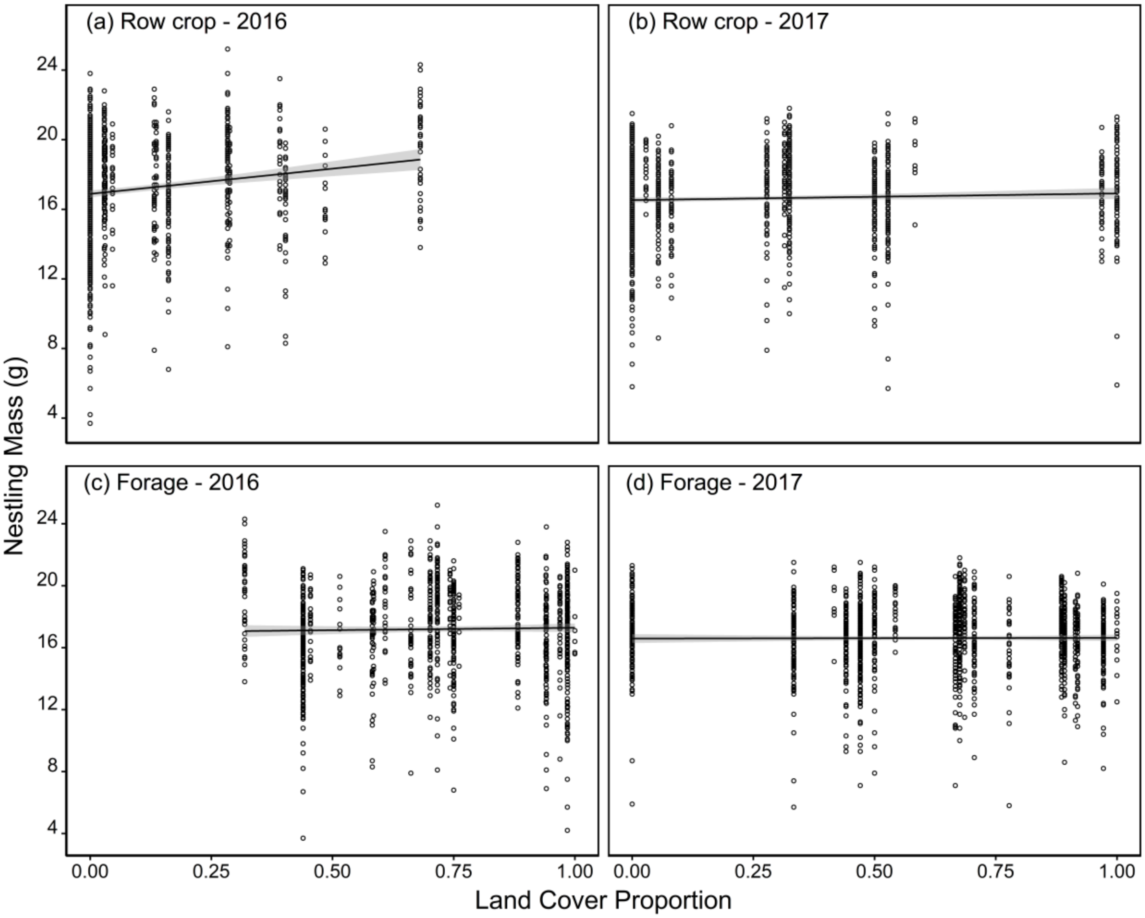


Figure 2.2. Scatterplot of Barn Swallow nestling (day 6–10) mass (n = 2452), measured at colonies near Guelph Ontario (nests = 475, sites = 22), in the breeding seasons of 2016 and 2017, plotted against row crop proportion (a-b) and proportion of forage (c-d) within 100 m of the site. Plots are separated by year (a,c – 2016, b,d – 2017). Line with shaded area indicates linear relationship and standard error.

Table 2.2. Linear mixed effect model results for Barn Swallow pre-fledging (day 15) mass (n = 784) measured at colonies near Guelph Ontario (nests = 179, sites = 20), in the breeding seasons of 2016 and 2017. The global model included fixed effects of proportion of row crop, proportion of forage, wing, wing^2, brood size, colony size, date, and year, and random effects of nest location, and site. Dropped terms are noted by dashes (-).

	Pre-fledging Mass			
	Coefficient	SE	t value	p-value
Intercept	-92.97	14.59	-6.37	-
Wing	1.49	0.14	10.97	< 0.001
Wing^2	-0.0098	0.00096	-10.27	< 0.001
Brood Size	-0.23	0.10	-2.23	< 0.01
Brood Size^2	-	-	-	-
Colony Size	0.022	0.018	1.20	0.63
Date	0.55	0.13	4.15	< 0.05
Date^2	-0.0013	0.00033	-4.09	< 0.05
Year	0.56	0.21	2.66	< 0.05
Row crop (100 m)	2.10	1.20	1.75	0.24
Year * Row crop	-	-	-	-
Forage (100 m)	1.09	1.24	0.88	0.82
Year * Forage	-	-	-	-

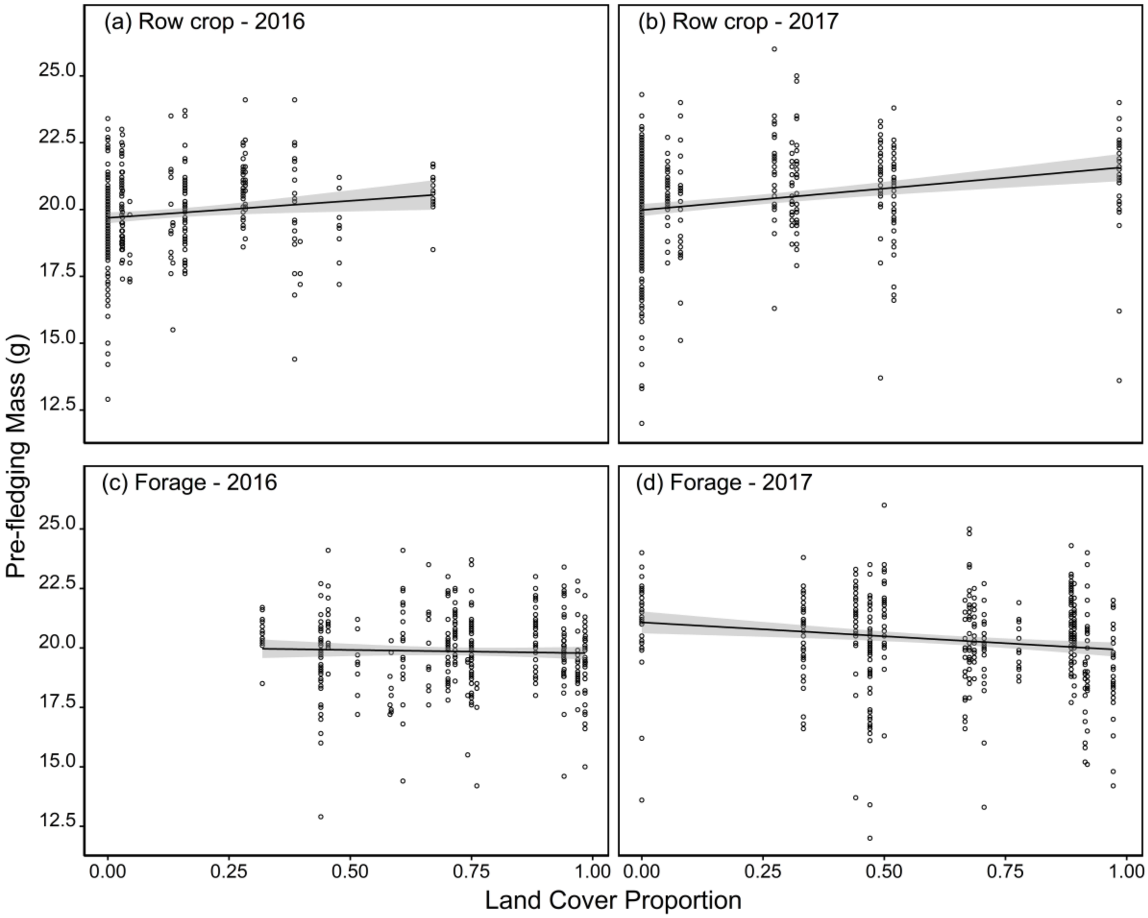


Figure 2.3. Scatterplot of Barn Swallow pre-fledging (day 15) mass (n = 784) measured at colonies near Guelph Ontario (nests = 179, sites = 20), in the breeding seasons of 2016 and 2017, plotted against row crop proportion (a-b) and proportion of forage (c-d) within 100 m of the site. Plots are separated by year (a,c – 2016, b,d – 2017). Line with shaded area indicates linear relationship and standard error.

(Table 2.2), indicating that nestlings were in worse condition when they were in larger broods. No relationship was found between colony size and pre-fledging condition (Table 2.2).

Nestling growth showed no relationship with row crop or forage proportion (LMM; sites = 19, nests = 134, n = 603; Table 2.3 and Figure 2.4). Nestling growth varied most strongly with row crop and forage proportion at the 300 m extent, but there were many competitive models (see Appendix B. Scale of effect figures for nestling condition; Figure B3). Nestling growth increased with date and year, but there was no relationship with either clutch size or colony size (Table 2.3).

Fledging success showed no relationship with row crop or forage proportion (GLMM; sites = 22, n = 552; Table 2.4 and Figure 2.5). There was no significant scale of effect with respect to both row crop and forage, as all models were competitive, but the strongest model used a buffer radius of 2000 m (see Appendix B. Scale of effect figures for nestling condition; Figure B4). Mean fledging success was 4.01 ± 1.3 young per nest (for brood specific and year specific statistics see Appendix A. Summary tables; Table A2). Fledging success decreased with date (Table 2.4). There was no effect of year or colony size on fledging success (Table 2.4).

2.4. Discussion

I predicted Barn Swallow nestlings raised in landscapes with more row crops would be in worse condition, have lower growth rates, and suffer reduced fledging success, because agricultural intensification can negatively affect insect availability (Attwood et al. 2008). Contrary to my predictions, and to previous studies on farmland birds (Brickle et al.

Table 2.3. Linear mixed effect model results for Barn Swallow nestling growth (change in mass between day 8 and 15) (n = 603) measured at colonies near Guelph Ontario (nest = 134, sites = 19), in the breeding seasons of 2016 and 2017. The global model included fixed effects of proportion of row crop, proportion of forage, Δ wing, brood size, colony size, date, and year, and random effects of nest location, and site. Dropped terms are noted by dashes (-).

	Nestling Growth (Δ Mass)			
	Coefficient	SE	t value	p-value
Intercept	-13.89	2.29	-6.06	-
Δ Wing	0.29	0.030	9.84	< 0.001
Δ Wing^2	-	-	-	-
Brood Size	-0.012	0.16	-0.072	0.93
Brood Size^2	-	-	-	-
Colony Size	-0.0024	0.015	-0.16	0.87
Date	0.029	0.0060	4.90	< 0.001
Date^2	-	-	-	-
Year	0.87	0.27	3.29	< 0.01
Row crop (300 m)	0.22	0.96	0.23	0.81
Year * Row crop	-	-	-	-
Forage (300 m)	-0.59	1.14	-0.52	0.58
Year * Forage	-	-	-	-

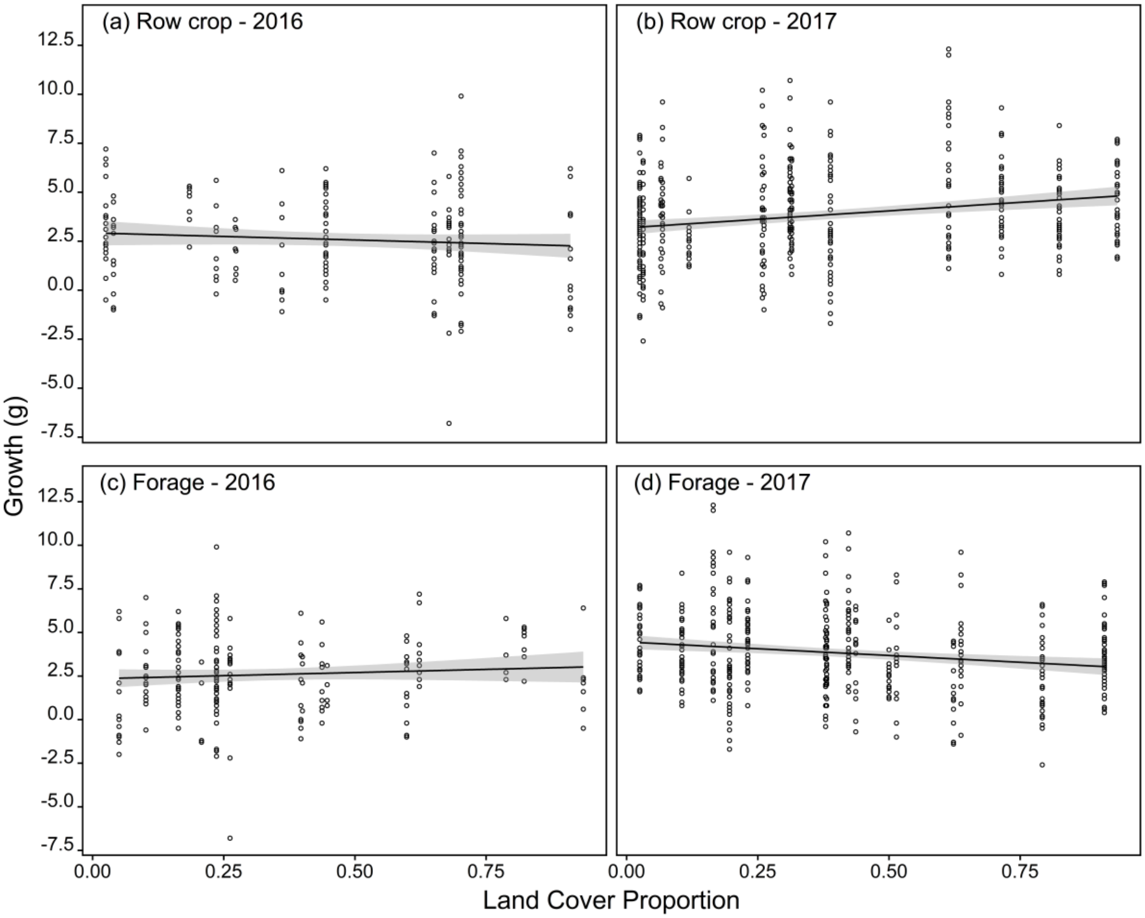


Figure 2.4. Scatterplot of Barn Swallow nestling growth (change in mass between day 8 to 15) (n = 603) measured at colonies near Guelph Ontario (nest = 134, sites = 19), in the breeding seasons of 2016 and 2017, plotted against row crop proportion (a-b) and proportion of forage (c-d) within 300 m of the site. Plots are separated by year (a,c – 2016, b,d – 2017). Line with shaded area indicates linear relationship and standard error.

Table 2.4. Generalized linear mixed effect model results for Barn Swallow fledging success (n = 552) measured at colonies near Guelph Ontario (sites = 22), in the breeding seasons of 2016 and 2017. The global model included fixed effects of proportion of row crop, proportion of forage, date, colony size, and year, and random effects of nest location, and site. Dropped terms are noted by dashes.

	Fledging Success			
	Coefficient	SE	z value	p-value
Intercept	1.24	0.18	6.80	< 0.001
Colony Size	-0.0087	0.023	-0.38	0.70
Date	-0.10	0.022	-4.52	< 0.001
Date^2	-	-	-	-
Year	-0.0026	0.044	-0.060	0.95
Row crop (2000 m)	0.28	0.23	1.23	0.22
Year * Row crop	-	-	-	-
Forage (2000 m)	0.18	0.36	0.49	0.62
Year * Forage	-	-	-	-

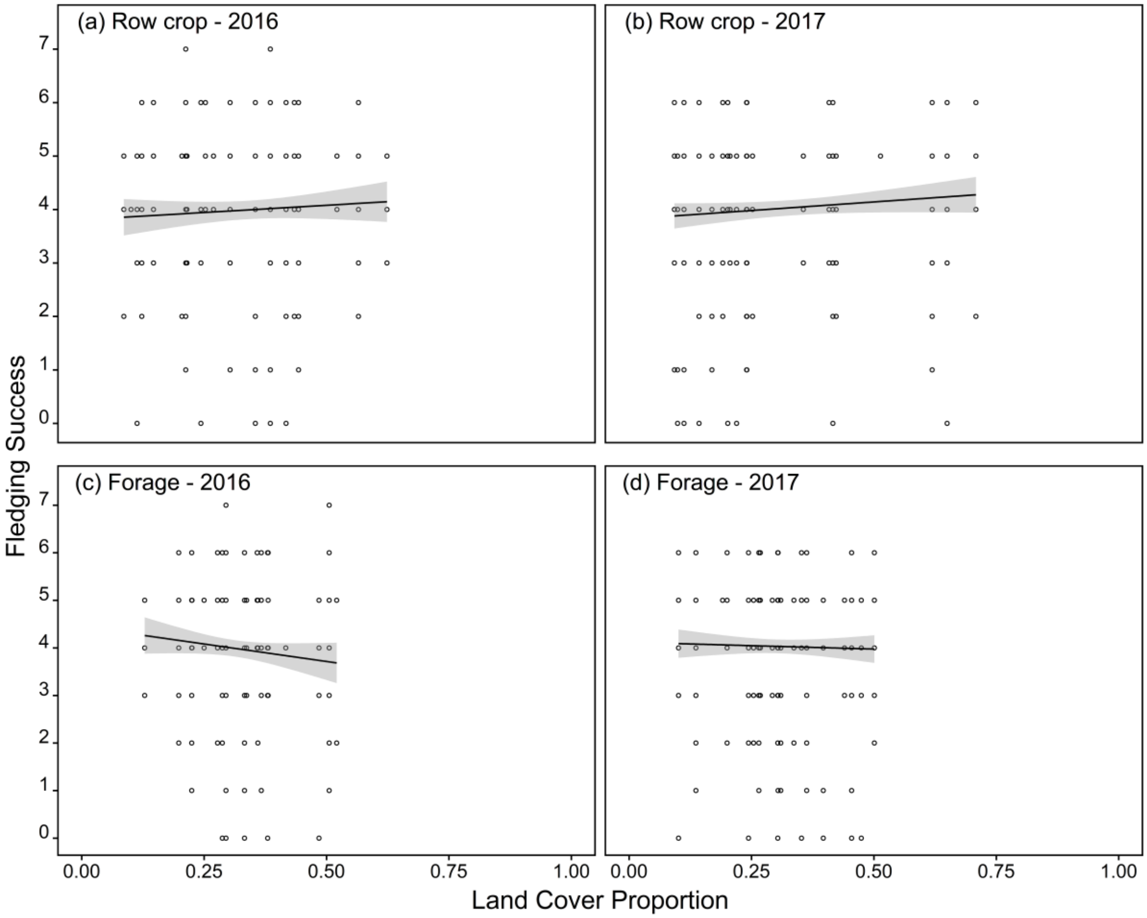


Figure 2.5. Scatterplot of Barn Swallow fledging success (n = 552) measured at colonies near Guelph Ontario (sites = 22), in the breeding seasons of 2016 and 2017, plotted against row crop proportion (a-b) and proportion of forage (c-d) within 2000 m of the site. Plots are separated by year (a,c – 2016, b,d – 2017). Line with shaded area indicates linear relationship and standard error.

2000; Morris et al. 2005; Hart et al. 2006), nestling condition was positively related to row crop proportion, after controlling for the effects of forage, year, date, and within brood competition. Despite an apparent positive relationship between row cropping and nestling condition, there was no effect of row crop proportion on pre-fledging condition, nestling growth rate, and fledging success. Overall, nestlings raised in landscapes with greater proportions of agriculturally intense land cover were in better condition earlier in the nestling stage but nestlings in worse condition compensated for any differences in condition by the pre-fledging stage and did not incur any negative effects on fledging success. This is the first study, to my knowledge, that found neutral to positive effects of agricultural intensification on an aerial insectivorous species, for which agricultural land-use changes, and pesticide usage, have been heavily implicated in population declines (Nebel et al. 2010; Nocera et al. 2012; Stanton et al. 2018).

I speculate that the positive relationship between increasing proportion of row crop and nestling condition is due to differences in nestling diet or provisioning rates in these environments, as the amount and quality of food can affect nestling condition (Konarzewski et al. 1996; Searcy et al. 2004; Twining et al. 2016). First, I propose that agriculturally intense land cover types may produce more abundant or larger insects, making them ideal foraging habitats for an aerial insectivore. Previous studies have focused on sampling insects within vegetation along field margins or more natural habitats, through sweep netting or similar methods, as researchers were largely focused on species that are not aerial insectivores, such as Corn Bunting, which primarily consumes Orthoptera and the larvae of Lepidoptera and Symphata (Brickle et al. 2000). Research on aerial insectivore diet has shown that swallows forage on arthropods from a wide range of orders, some of which could be sampled within the vegetation (e.g., Coleoptera, Hemiptera, and Orthoptera; Beal 1918; Johnston 1967), but many of which may not be adequately sampled (e.g., Diptera). Second, I hypothesize that aerial insects may be largely independent of habitat composition. In a metanalysis by Attwood et al. (2008), insect abundances in agricultural ecosystems were lower relative to less intensively managed ecosystems (e.g., native grasslands), but this analysis excluded highly mobile taxa, such as Diptera (e.g., Froerer et al. 2010), which are a large component of aerial insectivore diet (McCarty & Winkler 1999a).

Adult Barn Swallows may compensate for any negative aspects of reduced insect availability by increasing parental effort. Previous studies in aerial insectivores have shown that adults alter provisioning rates in response to foraging conditions, although these studies have shown the opposite effect, where adults increased provisioning under ideal conditions (Schifferli et al. 2014; Stanton et al. 2016). Alternatively, row crops may provide better foraging habitat, potentially increasing foraging efficiency by decreasing foraging time. The lack of effect for colony size suggests that competition for food is not limiting for this swallow population. High mobility in aerial insects combined with wind dispersal may facilitate a constantly mixing source of prey, providing a robust source of food within the aerial plankton. Future studies should investigate the relationships between nestling condition, parental quality, insect availability, and provisioning rates in these environments, as increased parental effort may supplement nestling diet at the expense of adult condition (e.g., Saino et al. 1999).

Surprisingly the was no row crop effect on pre-fledging condition, despite a row crop effect on nestling condition. Regardless of positive effects during the growth phase, nestlings were able to bridge the gap by the pre-fledging stage. Although pre-fledging condition has been directly related to survival in Barn Swallows (Evans et al. unpub ms.), nestlings may have an optimal fledging mass for wing loading which individuals reach via programmed anorexia (e.g., Wright et al. 2006). In swallows, nestling mass increases from birth until it peaks around day 13 and decreases slightly before levelling off (Zach & Mayoh 1982). While differences in effect of row crop on nestling and pre-fledging condition indicate some compensation in mass, without daily measurements it is impossible to say how much intermediate mass change occurred, as nestlings with lower mass may reach an ideal pre-fledging mass without programmed anorexia.

Previous studies have shown negative effects of agricultural intensification on nest productivity (Brickle et al. 2000; Hart et al. 2006; Ghilain and Bélisle 2008). If nestling survival is high, which seems to be the case with Barn Swallows in other populations (Ambrosini & Saino 2010), these condition effects may play a more important role in later life stages, such as the post-fledging period (Evans et al. unpub ms.), rather than directly affecting fledging success. As there was no effect of row crop proportion on pre-fledging condition, I do not expect reduced post-fledging survival through the mechanism of reduced body condition (Evans et al. unpub ms.), although other mechanisms may contribute to reduced post-fledging survival (e.g., predation risk; Suedkamp Wells et al. 2007).

Year-specific effects on nestling condition, pre-fledging condition, and growth could be due to environmental differences within each year of sampling. For example, 2017 had colder mean monthly temperature from May to August and greater precipitation from May to July, compared to 2016 (ECCC 2018; Figure 2.6). Warmer environmental

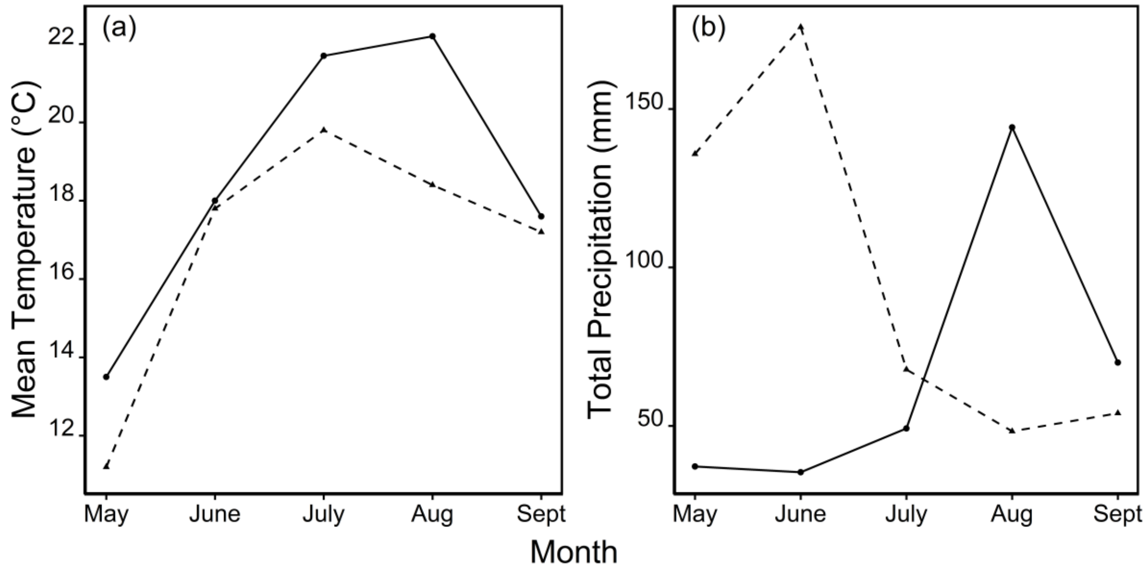


Figure 2.6. Line plot of mean monthly temperature (^{o}C) (a) and total monthly precipitation (mm) (b) in Guelph, southern Ontario, throughout the breeding seasons of 2016 (solid line) and 2017 (dashed line). Weather information was gathered from ECCC's historical data on monthly weather data (ECCC 2018), from the Fergus Shand Dam station in Fergus, Ontario.

temperatures in 2016 may have enabled parents to spend more time provisioning and less time brooding young, and young could dedicate more resources to growth and energy storage and less to thermoregulation (McCarty & Winkler 1999b; Pérez et al. 2008; Grüebler et al. 2010). Furthermore, flying insect availability is further reduced within agriculturally intense landscape during adverse weather conditions such as high wind and low temperatures, thus potentially proliferating the negative effects on foraging success and diet (Grüebler et al. 2008).

I used two measures of landscape structure (i.e., proportion of row crop and proportion of forage) to capture a gradient of agricultural intensification and a measure of semi-natural habitats. Other studies have used the number of pesticide applications as the measure of intensity (Brickle et al. 2000; Morris et al. 2005; Hart et al. 2006), or combined landscape inputs (e.g., crop type, pesticide amounts) with landscape structure into a single index of agricultural intensity at the landscape-level (Herzog et al. 2006; Hendrickx et al. 2007). There was a positive relationship between forage proportion and nestling body condition, but the effect was not as strong as the correlation between body condition and row cropping. I expected that the proportion of forage would positively benefit nestling condition, as Barn Swallows have been reported to spend the most time foraging above forages (pasture in this case) compared to cropped land (Evans et al. 2007), but the stronger positive effect of row cropping over forages suggests some added benefit of row crops to Barn Swallows.

Examining landscape from the scale of a patch is often inadequate to link spatial patterns with ecological phenomena (Ricketts et al. 2001; Steffan-Dewenter et al. 2002; Holland et al. 2004). These results suggest condition is best linked to landscape composition (row crops and forage) at a scale of 100 m (see Appendix B. Scale of effect figures for nestling condition; Figure B1-2). This scale is likely representative of typical adult Barn Swallow foraging distance during provisioning. This distance, while slightly shorter, is consistent with published data for provisioning Barn Swallows in Europe (188 m in the first brood and 138 m in the second brood; Turner 1980), and for other aerial insectivorous species in North America (100-200 m in Tree Swallows; McCarty & Winkler 1999).

2.5. Conclusion

It has been shown that agriculture is one of the greatest threats to birds (Green et al. 2005), and while this may be true in many cases, my work suggests that agricultural intensification may not affect all species equally. Currently, there is very little evidence that bird species benefit from agriculture, especially compared to the evidence implicating agriculture as having negative effects on breeding birds (e.g., Rands 1986; Herkert 1997; Brickle et al. 2000; Morris et al. 2005; Hart et al. 2006). My data suggests that Barn Swallows breeding in southern Ontario may be among the few who benefit from agriculture, at least in terms of nestling condition, but these benefits are likely lost by the pre-fledging stage. This finding highlights that careful consideration must be made when choosing age categories to sample, otherwise potential effects may be overestimated or hidden. Despite steep population declines in this region of the continent (Nebel et al. 2010; Michel et al. 2016), agriculture does not seem to be contributing to these declines. Furthermore, Barn Swallows utilize human-made structures, like barns, which constrains breeding site choice and demonstrates that agriculture provides nesting habitat. Although I found no negative effects on condition, growth rate, and fledging success, increased land-use intensity may negatively influence another aspect of reproductive biology, thus contributing to a reduction in reproductive fitness. This study demonstrates that further investigation is required to understand the complex mechanisms that are driving the decline of Barn Swallows in Southern Ontario, along with the rest of northeastern North America.

2.6. Literature cited

AAFC. 2017. Annual crop inventory. Agriculture and Agri-Food Canada, Science and Technology Branch. Contains information licensed under the Open Government License – Canada. [retrieved from: http://canada.ca/data/en/dataset/ba2645d5-4458-414d-b196-6303ac06c1c9].

Ambrosini R, Saino N. 2010. Environmental effects at two nested spatial scales on habitat choice and breeding performance of Barn Swallow. Evolutionary Ecology **24**:491–508.

Arcese P, Smith JNM. 1988. Effects of population density and supplemental food on reproduction in Song Sparrows. Journal of Animal Ecology **57**:119–136.

Attwood S, Maron M, House A, Zammit C. 2008. Do arthropod assemblages display globally consistent responses to intensified agricultural land use and management? Global Ecology and Biogeography **17**:585–599.

Bates D, Maechler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software **67**:1–48.

Beal FEL. 1918. Food habits of the swallows: a family of valuable native birds. US Department of Agriculture Bulletin **619**:1–28.

Benton TG, Bryant DM, Cole L, Crick HQP. 2002. Linking agricultural practice to insect and bird populations: a historical study over three decades. Journal of Applied Ecology **39**:673–687.

Brickle NW, Harper DGC, Aebischer NJ, Cockayne SH. 2000. Effects of agricultural intensification on the breeding success of Corn Buntings *Miliaria calandra*. Journal of Applied Ecology **37**:742–755.

Brown CR, Brown MB. 1999. Barn Swallow (*Hirundo rustica*). The Birds of North America Online. Available from http://birds.cornell.edu/BNA/account/ Barn_Swallow.html.

Burnham KP, Anderson DR. 2002. Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach. Springer Science and Business Media.

COSEWIC. 2011. COSEWIC assessment and status report on the Barn Swallows (*Hirundo rustica*) in Canada. Committee on the Status of Endangered Wildlife in Canada. Available from http://registrelep-sararegistry.gc.ca/document/ default_ e.cfm?documentID=2288.

Donald PF, Green R, Heath M. 2001. Agricultural intensification and the collapse of Europe’s farmland bird populations. Proceedings of the Royal Society of London B: Biological Sciences **268**:25–29.

Donald PF, Sanderson FJ, Burfield IJ, van Bommel FPJ. 2006. Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990–2000. Agriculture, Ecosystems and Environment **116**:189–196.

Dormann CF et al. 2012. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography **36**:27–46.

ECCC. 2018. Historical climate data. Environment and Climate Change Canada, Ottawa, Ontario. Available from Contains information licensed under the Open Government License – Canada. [retrieved from http://weather.gc.ca/index_e.html]

English PA, Green DJ, Nocera JJ. 2018. Stable isotopes from museum specimens may provide evidence of long-term change in the trophic ecology of a migratory aerial insectivore. Frontiers in Ecology and Evolution **6**:1–13.

ESRI. 2011. ArcGIS Desktop: release 10. Environmental Systems Research Institute, Redlands, CA: Environmental Systems Research Institute.

Evans KL, Wilson JD, Bradbury RB. 2007. Effects of crop type and aerial invertebrate abundance on foraging Barn Swallows *Hirundo rustica*. Agriculture, Ecosystems and Environment **122**:267–273.

Fernaz JM, Schifferli L, Grüebler MU. 2012. Ageing nestling Barn Swallows *Hirundo rustica*: an illustrated guide and cautionary comments. Ringing and Migration **27**:65–75.

Froerer KM, Peck SL, McQuate GT, Vargas RI, Jang EB, McInnis DO. 2010. Long-distance movement of *Bactrocera dorsalis* (Diptera: Tephritidae) in Puna, Hawaii: How far can they go? American Entomologist **56**:88–95.

Ghilain A, Bélisle M. 2008. Breeding success of Tree Swallows along a gradient of agricultural intensification. Ecological Applications **18**:1140–1154.

Green RE, Cornell SJ, Scharlemann JP, Balmford A. 2005. Farming and the fate of wild nature. Science **307**:550–555.

Grüebler MU, Korner-Nievergelt F, Von Hirschheydt J. 2010. The reproductive benefits of livestock farming in Barn Swallows *Hirundo rustica*: quality of nest site or foraging habitat? Journal of Applied Ecology **47**:1340–1347.

Grüebler MU, Morand M, Naef-Daenzer B. 2008. A predictive model of the density of airborne insects in agricultural environments. Agriculture, Ecosystems and Environment **123**:75–80.

Halekoh U, Højsgaard S. 2014. A Kenward-Roger approximation and parametric bootstrap methods for tests in linear mixed models – the R package pbkrtest. Journal of Statistical Software **59**:1–30.

Hart J, Milsom T, Fisher G, Wilkins V, Moreby S, Murray A, Robertson P. 2006. The relationship between Yellowhammer breeding performance, arthropod abundance and insecticide applications on arable farmland. Journal of Applied Ecology **43**:81–91.

Heagy A, Badzinski D, Bradley D, Falconer M, McCracken J, Reid RA, Richardson K. 2014. Recovery strategy for the Barn Swallow (*Hirundo rustica*) in Ontario. Ontario Recovery Strategy Series. Prepared for the Ontario Ministry of Natural Resources and Forestry, Peterborough, Ontario. Available from http://ontario.ca/ environment-and-energy/species-at-risk/mnr_sar_rs_brn_swl_en.pdf.

Hendrickx F, Maelfait J, Van Wingerden W, Schweiger O, Speelmans M, Aviron S, Augenstein I, Billeter R, Bailey D, Bukacek R. 2007. How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. Journal of Applied Ecology **44**:340–351.

Herkert JR. 1997. Bobolink *Dolichonyx oryzivorus* population decline in agricultural landscapes in the Midwestern USA. Biological Conservation **80**:107–112.

Herzog F et al. 2006. Assessing the intensity of temperate European agriculture at the landscape scale. European Journal of Agronomy **24**:165–181.

Holland JD, Bert DG, Fahrig L. 2004. Determining the spatial scale of species' response to habitat. Bioscience **54**:227–233.

Johnston RF. 1967. Seasonal variation in the food of the Purple Martin *Progne subis* in Kansas. Ibis **109**:8–13.

Jones TM, Ward MP, Benson TJ, Brawn JD. 2016. Variation in nestling body condition and wing development predict cause-specific mortality in fledgling Dickcissels. Journal of Avian Biology **48**:439–447.

Konarzewski M, Kowalczyk J, Swierubska T, Lewonczuk B. 1996. Effect of short-term feed restriction, realimentation and overfeeding on growth of Song Thrush (*Turdus philomelos*) nestlings. Functional Ecology **10**:97–105.

Labocha MK, Hayes JP. 2012. Morphometric indices of body condition in birds: a review. Journal of Ornithology **153**:1–22.

Lack D. 1966. Population Studies of Birds. Clarendon Press, Oxford.

Maness TJ, Anderson DJ. 2013. Predictors of juvenile survival in birds. Ornithological Monographs **78**:1–55.

Matson PA, Parton WJ, Power AG, Swift MJ. 1997. Agricultural intensification and ecosystem properties. Science **277**:504–509.

McCarty JP, Winkler DW. 1999a. Foraging ecology and diet selectivity of Tree Swallows feeding nestlings. The Condor **101**:246–254.

McCarty JP, Winkler DW. 1999b. Relative importance of environmental variables in determining the growth off nestling Tree Swallows *Tachycineta bicolor*. Ibis **141**:286–296.

Michel NL, Smith AC, Clark RG, Morrissey CA, Hobson KA. 2016. Differences in spatial synchrony and interspecific concordance inform guild-level population trends for aerial insectivorous birds. Ecography **39**:774–786.

Mitchell GW, Guglielmo CG, Wheelwright NT, Freeman-Gallant CR, Norris DR. 2011. Early life events carry over to influence pre-migratory condition in a free-living songbird. PLOS ONE **6**:e28838.

Morris AJ, Wilson JD, Whittingham MJ, Bradbury RB. 2005. Indirect effects of pesticides on breeding Yellowhammer (*Emberiza citrinella*). Agriculture, Ecosystems and Environment **106**:1–16.

Murphy MT. 2003. Avian population trends within the evolving agricultural landscape of eastern and central United States. The Auk **120**:20–34.

NABCI. 2016. The state of North America's birds 2016. Environment and Climate Change Canada, Ottawa, Ontario. Available from http://stateofthebirds.org/2016/.

Naef-Daenzer B, Widmer F, Nuber M. 2001. Differential post-fledging survival of Great and Coal Tits in relation to their condition and fledging date. Journal of Animal Ecology **70**:730–738.

Nebel S, Mills A, McCracken JD, Taylor PD. 2010. Declines of aerial insectivores in North America follow a geographic gradient. Avian Conservation and Ecology **5**:1.

Nocera JJ, Blais JM, Beresford DV, Finity LK, Grooms C, Kimpe LE, Kyser K, Michelutti N, Reudink MW, Smol JP. 2012. Historical pesticide applications coincided with an altered diet of aerially foraging insectivorous Chimney Swifts. Proceedings of the Royal Society B: Biological Sciences **279**:3114–3120.

Pérez JH, Ardia DR, Chad EK, Clotfelter ED. 2008. Experimental heating reveals nest temperature affects nestling condition in Tree Swallows (*Tachycineta bicolor*). Biology Letters **4**:468–471.

Pinhero J, Bates D. 2000. Mixed-effects Models in S and S-PLUS. Springer-Verlag, New York.

R Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing: Vienna, Austria.

Rands MRW. 1986. The survival of gamebird (Galliformes) chicks in relation to pesticide use on cereals. Ibis **128**:57–64.

Reynolds SJ, Schoech SJ, Bowman R. 2003. Diet quality during pre-laying and nestling periods influences growth and survival of Florida Scrub-jay (*Aphelocoma coerulescens*) chicks. Journal of Zoology **261**:217–226.

Ricketts TH, Daily GC, Ehrlich PR, Fay JP. 2001. Countryside biogeography of moths in a fragmented landscape: biodiversity in native and agricultural habitats. Conservation Biology **15**:378–388.

Rstudio Team. 2015. Rstudio: integrated development for R. Boston, MA: Rstudio, Inc.

Saino N, Ambrosini R, Caprioli M, Romano A, Romano M, Rubolini D, Scandolara C, Liechti F. 2017. Sex-dependent carry-over effects on timing of reproduction and fecundity of a migratory bird. Journal of Animal Ecology **86**:239–249.

Saino N, Calza S, Ninni P, Møller AP. 1999. Barn Swallows trade survival against offspring condition and immunocompetence. Journal of Animal Ecology **68**:999–1009.

Saino N, Romano M, Romano A, Rubolini D, Ambrosini R, Caprioli M, Parolini M, Scandolara C, Bazzi G, Costanzo A. 2015. White tail spots in breeding Barn Swallows *Hirundo rustica* signal body condition during winter moult. Ibis **157**:722–730.

Sauer JR, Niven DK, Hines JE, Ziolkowski J DJ, Pardieck KL, Fallon JE, Link WA. 2017. The North American breeding bird survey, results and analysis 1966 – 2015. Version 2.07.2017. USGS Patuxent Wildlife Research Center, Laurel, MD.

Schifferli L, Grüebler MU, Meijer HAJ, Visser GH, Naef-Daenzer B. 2014. Barn Swallow *Hirundo rustica* parents work harder when foraging conditions are good. Ibis **156**:777–787.

Searcy WA, Peters S, Nowicki S. 2004. Effects of early nutrition on growth rate and adult size in Song Sparrows *Melospiza melodia*. Journal of Avian Biology **35**:269–279.

Siikamäki P. 1998. Limitation of reproductive success by food availability and breeding time in Pied Flycatchers. Ecology **79**:1789–1796.

Stanton RL, Morrissey CA, Clark RG. 2016. Tree Swallow (*Tachycineta bicolor*) foraging responses to agricultural land use and abundance of insect prey. Canadian Journal of Zoology **94**:637–642.

Stanton RL, Morrissey CA, Clark RG. 2018. Analysis of trends and agricultural drivers of farmland bird declines in North America: a review. Agriculture, Ecosystems and Environment **254**:244–254.

Steffan-Dewenter I, Münzenberg U, Bürger C, Thies C, Tscharntke T. 2002. Scale-dependent effects of landscape context on three pollinator guilds. Ecology **83**:1421–1432.

Suedkamp Wells KM, Ryan MR, Millspaugh JJ, Thompson FR, Hubbard MW. 2007. Survival of postfledging grassland birds in Missouri. The Condor **109**:781–794.

Turner AK. 1980. The use of time and energy by aerial feeding birds. PhD Thesis. University of Stirling.

Twining CW, Brenna JT, Lawrence P, Shipley JR, Tollefson TN, Winkler DW. 2016. Omega-3 long-chain polyunsaturated fatty acids support aerial insectivore performance more than food quantity. Proceedings of the National Academy of Sciences **113**:10920–10925.

Visser ME, Holleman LJM, Gienapp P. 2006. Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. Oecologia **147**:164–172.

Vitz AC, Rodewald AD. 2011. Influence of condition and habitat use on survival of post-fledging songbirds. The Condor **113**:400–411.

Wilson S, Mitchell GW, Pasher J, McGovern M, Hudson M-AR, Fahrig L. 2017. Influence of crop type, heterogeneity and woody structure on avian biodiversity in agricultural landscapes. Ecological Indicators **83**:218–226.

Wright J, Markman S, Denney SM. 2006. Facultative adjustment of pre-fledging mass loss by nestling swifts preparing for flight. Proceedings of the Royal Society B: Biological Sciences **273**:1895–1900.

Zach R, Mayoh KR. 1982. Weight and feather growth of nestling Tree Swallows. Canadian Journal of Zoology **60**:1080–1090.

Chapter 3

Nestling diet of Barn Swallows (*Hirundo rustica*) in an agro-ecosystem: insights from fecal DNA barcoding and stable isotopes ($\delta^{13}C$, $\delta^{15}N$)

3.1. Introduction

Populations of grassland and farmland birds have experienced marked population declines as a result of habitat loss associated with increasing agricultural land-use intensity (Donald et al. 2001, 2006; Benton et al. 2002), including for example increases in field size and associated loss of field margins and hedgerows and reductions in fallow land (Robinson & Sutherland 2002; Tscharntke et al. 2005). For species breeding within agro-ecosystems, indirect effects of agricultural intensification such as reductions in prey insect availability due to habitat loss and pesticide and herbicide application have received comparatively little attention (reviewed in Stanton et al. 2018). Reduced insect availability in agriculturally intense landscapes is expected and has been documented (Hendrickx et al. 2007; Attwood et al. 2008; Grüebler et al. 2008). Higher pesticide usage and reduced prey availability can reduce nestling body condition (Brickle et al. 2000; Hart et al. 2006) with implications for survival (Naef-Daenzer et al. 2001; Mitchell et al. 2011; Jones et al. 2016; Evans et al. unpub ms.). This may be especially relevant for aerial insectivorous birds who rely entirely on flying insects as their sole source of food.

Across North America, aerial insectivorous birds have experienced the steepest population declines of any group of North American passerines (NABCI 2016; Sauer et al. 2017). A leading hypothesis for this guild-wide decline is a reduction in prey insect availability (Nebel et al. 2010; Nocera et al. 2012; Smith et al. 2015). Population declines

(Nebel et al. 2010; Michel et al. 2016) and migratory connectivity (Hobson et al. 2015) vary regionally within North America, suggesting local to regional environmental factors may be contributing to these declines. Several aerial insectivorous species, such as the Barn Swallow (*Hirundo rustica*), now primarily occupy human-associated structures, which highly restricts them to nest locations within modified landscapes, such as farms (Brown & Brown 1999). While long-term dietary shifts highlight the potential relationship between diets and agricultural land-use intensifications specifically pesticide usage (Nocera et al. 2012; English et al. 2018), and indirect evidence suggests a negative effect of row cropping on nestlings (e.g., Ghilain & Bélisle 2008), other studies suggest diet alone does not affect breeding success in aerial insectivores (Barn Swallows, Cliff Swallows *Petrochelidon pyrrhonota*, and Tree Swallows *Tachycineta bicolor*; Imlay et al. 2017). Therefore, there is an urgent need to investigate if there is a contemporary link between diet and agricultural land-use intensity for aerial insectivores to understand if reductions in food availability are contributing to observed declines.

Nestling diet of swallows is poorly documented in North America and is restricted to well-studied species such as Tree Swallows (see Quinney & Ankney 1985; McCarty & Winkler 1999a; Mengelkoch et al. 2004). DNA barcoding of fecal matter provides a potential tool allowing taxonomic identification of prey DNA remaining post-digestion (reviewed in Valentini et al. 2009). Fecal DNA barcoding has been applied to very few terrestrial avian studies (e.g., Joo & Park 2012; Jedlicka et al. 2013, 2016; Trevelline et al. 2016, 2018), but has been utilized in bats, which has allowed for identification of prey insects (e.g., Clare et al. 2009; Zeale et al. 2011; Long et al. 2013; Aizpurua et al. 2017). For an insectivorous species, DNA barcoding allows for identification of soft-bodied insects that are likely unidentifiable post-digestion, making visual fecal analysis difficult (but see Orłowski & Karg 2011). Despite the potential of DNA barcoding to add to current knowledge of nestling diet, to date there are other no published studies for aerial insectivorous species.

The measurement of naturally occurring stable isotopes in food webs has been used effectively to assess both sources of nutrients to consumers and their relative trophic position (Peterson & Fry 1987; Fry 2006; Boecklen et al. 2011) over various periods of temporal integration (Hobson & Clark 1992). Specifically, nitrogen stable-isotope ratios ($\delta^{15}N$) typically show a step-wise increase with trophic level, making them useful indicators of trophic position (Hobson & Welch 1992; Hobson et al. 1994; Boecklen et al. 2011). Stable-nitrogen isotope values in biota can be influenced by variation in nitrogen sources to plants, nitrogen fixation mechanisms, land-use practices and the use of chemical or organic fertilizer (Hobson 1999; Pardo & Nadelhoffer 2010). Furthermore, a growing body of evidence suggests that anthropogenic nitrogen inputs to terrestrial ecosystems everywhere are increasing and this is reflected in increased consumer $\delta^{15}N$ values in agricultural or anthropogenically influenced landscapes (Vitousek et al. 1997; Hobson 1999; Girard et al. 2012). Inorganic fertilizers have low initial $\delta^{15}N$ values (~0‰; Heaton 1986) but yearly tilling and ammonification of the soil leads to higher $\delta^{15}N$ values in agricultural land cover types (Kendal 1998). In terrestrial systems, carbon stable-isotope measurements ($\delta^{13}C$) have been used to differentiate photosynthetic pathway (i.e., C_3, C_4 or CAM; reviewed in Tieszen & Boutton 1989), aquatic vs. upland carbon inputs (France 1995) and plant water-use efficiency (Marshall et al. 2007). The strong utility in using $\delta^{13}C$ values in consumers to trace C_3 ($\delta^{13}C$ near -27‰) vs. C_4 ($\delta^{13}C$ near -12‰)

primary inputs makes this approach particularly useful for tracing corn-based carbon (a C_4 plant) in an otherwise C_3 landscape (e.g., hay, soybeans, winter wheat in southern Ontario; Mailvaganam 2018).

By integrating feather stable-isotope ($\delta^{13}C$ and $\delta^{15}N$) measurements along with DNA barcoding of nestling fecal matter, I investigated the effects of agricultural intensification on barn swallow nestling diet. I hypothesized that nestlings raised and fed from within agriculturally intense landscapes would have reduced diet richness due to reduced insect availability. First, I assessed the landscape-level effects of agricultural land use on stable-isotope values within nestling feathers, to determine where insects fed to nestlings originated. I predicted if nestlings were being provisioned insects from agriculturally intense landscapes than nestling feathers would have (1) more positive $\delta^{13}C$ values in landscapes with increased proportion of corn and (2) more positive $\delta^{15}N$ values in landscapes with higher agricultural intensity due to increased anthropogenic nitrogen inputs (i.e., fertilizer use, ammonification), resulting in differences in baseline $\delta^{15}N$ signature in these food webs. Second, I assessed the landscape-level effects of agricultural land use on nestling diet breadth and composition using fecal DNA barcoding. I predicted that if nestlings were being provisioned insects from landscapes comprised of high amounts of row crops that (3) diet breadth would be reduced due to reduced prey insect availability given reduced insect habitat diversity, and (4) prey items found within nestling diet would be representative of agricultural land use, such as the European Corn Borer *Ostrinia nubilalis*, and Fall Armyworm *Spodoptera frugiperda*.

3.2. Methods

3.2.1. Sample collection and sites

I conducted fieldwork at 22 Barn Swallow colonies in the breeding seasons of 2016 and 2017 (see Appendix A. Summary tables; Table A1) within Wellington County in southwestern Ontario, near Guelph, Ontario (43.55° N, 80.25° W). Timing of nest and clutch initiation was determined for all nests. Nestlings were banded with a unique United States Geological Survey aluminum leg band. Feathers for stable-isotope analysis were collected at day 15 after hatch, from all but one nestling within the nest (n = 192, nests = 55, site = 18 in 2016 and n = 96, nest = 27, site = 9 in 2017). Nests for feather sampling were chosen randomly within each site, attempting to sample evenly across sites and across the nesting season, but not all sites could be sampled in each year. Emphasis in 2017 was placed on sites at the extreme ends of the spectrum for agricultural composition, defined by the proportion of row cropping. Fecal samples were collected opportunistically whenever nestlings were handled, as defecation of a fecal sac often occurs during handling (n = 93, site = 17 in 2016 and n = 197, site = 21 in 2017). Fecal samples were combined for each nest collecting as many samples as possible, but samples could not be collected from every site. The number of fecal sacs collected per sample was recorded as a measure of how many nestlings contributed to the sample.

To compare prey stable-isotope values with nestling feathers, insects were collected from habitats (forage, row crops, wetland) in the surrounding landscape, as well as samples collected at the barn. Collection was performed non-quantitatively using a sweep net, sampling the upper portion of the vegetation and lower air column (~5-6ft above ground). Insects were sorted to taxonomic order, and insects within the order

Diptera were sorted to the level of family. Dipterans are hypothesized to be an important component of aerial insectivore diet (McCarty & Winkler 1999), thus isotopic analysis was limited to Diptera.

3.2.2. Stable-isotopic analyses

Feather samples (n = 192 from 18 sites in 2016, n = 91 from 9 sites 2017) were cleaned of surface oils using a 2:1 chloroform:methanol solvent and prepared for stable-isotopic ($\delta^{13}C$ and $\delta^{15}N$) analyses at the Stable-Isotope Laboratory (Environment Canada, Saskatoon, Canada). Insects (n = 91) were dried for 24 hours in the oven before weighing. For $\delta^{13}C$ and $\delta^{15}N$, 1 (± 0.03) mg of feather or insect was weighed into tin cups, crushed, and combusted using a Eurovector 3000 (Milan, Italy – www.eurovector.it) elemental analyzer. The resulting gases were separated by gas chromatography and introduced into a Nu Horizon (Nu Instruments, Wrexham, UK – www.nu-ins.com) triple-collector isotope-ratio mass-spectrometer via an open split. Stable-isotope values are expressed in delta (δ) notation, as parts per thousand (‰) deviation from the primary standards, atmospheric air ($\delta^{15}N$) and Vienna Pee Dee Belemnite (VPDB, $\delta^{13}C$). Internal laboratory standards were BWB III keratin ($\delta^{13}C$: -20‰, $\delta^{15}N$: 14.4‰) and PUGEL gelatin ($\delta^{13}C$: -13.6‰, $\delta^{15}N$: 4.73‰). Within-run (n = 7), measurement precision for $\delta^{13}C$ and $\delta^{15}N$ measurements were ± 0.15‰.

3.2.3. Fecal analyses

Fecal samples (n = 93 nests from 17 sites in 2016, n = 197 nests from 21 sites in 2017) were processed at the Canadian Center for DNA Barcoding (Guelph, Canada). For detailed methods, please refer to Appendix D, DNA barcoding protocol. Samples were amplified separately, using insect-specific primers targeting a 157 bp region of the COI gene (Zeale et al. 2011). Amplified samples were then pooled and sequenced using a 316 v.2 chip on an Ion Torrent PGM high-throughput sequencer (Thermo Fisher Scientific) in 2016 and a 530 chip on an Ion Torrent S5 high-throughput sequencer (Thermo Fisher Scientific) in 2017. Sequenced reads (i.e., number of individually sequenced PCR molecules) were grouped into operational taxonomic identifications (98% identity) and queried against the Barcode of Life Database (BOLD; www.boldsystems.org) reference library using a BLAST search to assign taxonomic identity. BLAST results were collapsed in unique taxonomic identifications per sample, filtered to remove low quality reads (minimum quality of QV20 and minimum length of 100 base pairs), and trimmed to remove primer and adapter sequences. Only identifications with 100 reads or more were accepted as genuine, as a conservative approach. DNA was successfully extracted and amplified from 290 fecal samples out of a total 336 samples across the years (93/95 samples in 2016, and 197/241 samples in 2017). I used two measures to describe nestling diet and detected prey items: (a) diet breadth, namely the total number of unique taxa (i.e., order, family, genus, or species level richness) that were detected within fecal samples via barcoding and (b) frequency of detection, or the number of times that a taxon is detected across all sampling units.

3.2.4. Landscape

Land cover proportions were measured using ESRI ArcMap 10 software (ESRI 2011). Landscape was classified and measured (i.e., proportions captured from 20 concentric buffers, 100 m to 2000 m) using annual crop inventory maps, from Agriculture and Agri-food Canada (AAFC 2017). I classified the landscape surrounding my sites as agricultural row crops (i.e., corn, soybeans, and wheat; hereafter ‘row crops’), natural grassland and pasture (hereafter ‘forage’), and open waterbodies and unwooded wetland (hereafter ‘water)’. I also classified corn separately from row crop. Row crop proportion was treated as a proxy for agricultural intensification, and the proportion of forage as a measure of semi-natural landscapes (e.g., Hendrickx et al. 2007).

3.2.5. Statistical analyses

All statistical analyses were performed using RStudio Version 1.0.136 and R version 3.3.1 statistical software (RStudio Team 2015; R Core Team 2016). To test whether $\delta^{13}C$ values within nestling feathers were higher in landscapes composed of greater amounts of corn, I used a linear mixed effect model (LMM) with $\delta^{13}C$ values as response variables (R package lme4; Bates et al. 2015). Mixed effects models were used due to the nested structure of sampling (random effects = nest location and site). The effect of landscape scale was first assessed separately for corn and water (for detailed methods on scale of effect analyses see Chapter 2). Proportion of corn and proportion of water were included as fixed effects at the most appropriate scale of effect, along with year interaction terms. Two-way interactions between year and land cover were included to account for the possibility of year-dependent effects of landscape on feather $\delta^{13}C$ values. Amount of surface water was included as a fixed effect to account for the possibility that $\delta^{13}C$ values may be affected by prey derived from aquatic vs. upland habitats (France 1995). Fixed effects for date (day of the year) and year were added to account for any seasonal changes in diet or agricultural practice that may affect stable-isotope ratios within nestling feathers. For example, water-use efficiency among C_3 plants would be expected to increase $\delta^{13}C$ values as temperatures increase later in summer (Marshall et al. 2007). To test whether feather δ^{15}N values were higher in more landscapes composed of a greater amount of row crops, I used a LMM with δ^{15}N values as the response and row crop amount as a fixed effect. Effect of landscape scale was first assessed for row crop, then row crop amount at the most appropriate scale of effect was included as a fixed effect, along with year as interaction terms. Presence of livestock was included as a binary fixed effect, as livestock manure could influence δ^{15}N values (Anderson & Cabana 2006). Again, date and year were added as fixed effects.

To test whether nestling diet breadth was reduced in more agriculturally intense environments, I used separate generalized linear mixed effect models (GLMM) with Poisson distributions. For each model, diet breadth was included as the response variable. I analyzed diet breadth at the level of family, as studies have shown that there is a strong correlation between generic richness and species richness, with diminishing but significant strength in correlation at higher taxonomic levels (Balmford et al. 1996a, 1996b). Furthermore, due to the short length of the molecular marker, I was less confident in lower taxonomic levels (i.e., species and genus) of prey identification. Because of the importance of dipterans to aerial insectivores, I analyzed diet breadth and composition within dipterans (hereafter 'Diptera diet breadth' and 'Diptera family composition') as well as across all other orders in the diet. The effect of landscape scale on diet breadth was first assessed, then row crop amount and forage amount were included as fixed effects at the most appropriate scale of effect, along with year interaction terms. Forage was included in this model, and no earlier models, as the purpose of this model was to assess the effect of agricultural intensification, which necessitates controlling for natural environments (e.g., Hendrickx et al. 2007). To account for the number of nestlings contributing to a fecal sample, the number of fecal sacs collected per sample were included as a fixed effect. Date and year were also included as fixed effects, for the same reasons outlined above.

Model selection for all LMMs and GLMMs was performed by assessing non-significant terms in order of decreasing p-value. Only interaction terms were removed from the model if non-significant, because their inclusion could affect the interpretation of lower-order terms, each of which was chosen for biological relevance. P-values for all linear mixed-effects models were estimated using parametric bootstrapping (R package pbkrtest; Halekoh & Højsgaard 2014). After assessment of interaction terms, effects from the best model were modelled using restricted maximum likelihood as this has been shown to produce less biased parameter estimates and standard errors (Pinhero & Bates 2000).

To assess diet composition, I used a permutational multivariate analysis of variance (PERMANOVA; package: vegan, function: adonis, permutations = 999; Oksanen et al. 2018). Distance measures for the presence-absence family matrix were calculated using the Jaccard method and adjusted for stepdistance (function = vegdist and stepdist, method = jaccard; Oksanen et al. 2018). To assess the effects of row crop on diet, amount of row crop was included as a fixed effect (4 levels: 0-25%, 25-50%, 50-75%, 75-100% row crop) measured using the most appropriate buffer distance found in the diet breadth scale of effect analysis. To account for variation in family composition due to site-specific or temporal effects, site id, date, and year were included as fixed effects in the model. Similarity between fecal samples, in terms of prey family composition, was visualized using non-metric multidimensional scaling (i.e., NMDS, function = metaMDS, method = jaccard; Oksanen et al. 2018).

3.3. Results

3.3.1 Landscape

Row crop (30.6% ± 22.7, mean ± SD; cover percentage within 1000 m) and forage (35.4% ± 16.2) were the predominant land cover types surrounding the sites. Corn covered a mean percentage of 11.3% ± 11.3 in 2016 and 5.7% ± 5.5 in 2017. Water was present in the landscapes surrounding sites but was not a major component overall (0.6% ± 2.1 within 1000 m, and only present within 100 m of one site). Examining all sites, the amount of row crop did not change between years (Paired t-test; $t = -0.16$, $p = 0.88$), but the amount of corn decreased in 2017 (Paired t-test; mean difference = 0.056, $t = 2.31$, $p = 0.03$), likely from crop rotations.

3.3.2. Stable isotopes

Nestling Barn Swallows had feather $\delta^{13}C$ and $\delta^{15}N$ values ranging from -25.7 to -19.8‰, and 9.2 to 13.1 ‰ respectively. There were significant differences among mean $\delta^{13}C$ values (ANOVA; $F_{20,267} = 19.65$, $p < 0.001$; Table 3.1) and mean $\delta^{15}N$ values (ANOVA; $F_{20,267} = 71.07$, $p < 0.001$; Table 3.1) among sites. After applying trophic discrimination factors (+2.7‰ $\delta^{13}C$, +4‰ $\delta^{15}N$; Hobson & Bairlein 2003) to present them as feather equivalent values, insect stable-isotope values ranged from -26.3 to -7.3‰ for $\delta^{13}C$ and 4.6 to 26.2‰ for $\delta^{15}N$. No differences in Diptera isotope values were found for $\delta^{13}C$ (ANOVA; $F_{3,92} = 1.35$, $p = 0.26$) and $\delta^{15}N$ (ANOVA; $F_{3,92} = 0.24$, $p = 0.87$) among habitat (barn, forage, row crop, and water). The isotopic range of adjusted insect tissues

Table 3.1. Site-specific summary for stable isotopes within nestling Barn Swallow feathers and relevant landscape predictors. Sample sizes provided are the number feather samples (n = 288). Stable-isotope values are provided as mean isotope values ± standard deviation. Land cover percentages for row crop and corn were captured using the most appropriate buffer radius, determined via scale of effect analysis, for each respective feather isotope (2000 m and 1700 m). Dashes signify that a site was not sampled in that year.

			2016			2017		
Site	Mean δ^{13}C‰ ± SD	Mean δ^{15}N‰ ± SD	n	Row crop (%)	Corn (%)	n	Row crop (%)	Corn (%)
BH	-22.50 ± 0.16	10.96 ± 0.19	11	21.5	8.2	-	-	-
CK	-22.79 ± 0.68	11.52 ± 0.48	11	11.3	5.9	12	11.2	0.9
CT	-23.61 ± 0.46	10.66 ± 0.43	13	14.7	8.6	-	-	-
FF	-22.65 ± 0.02	11.08 ± 0.15	3	43.4	28.4	-	-	-
FL	-22.97 ± 0.32	11.44 ± 0.31	17	38.5	17.1	-	-	-
FS	-23.44 ± 0.55	10.81 ± 0.38	7	35.5	13.1	-	-	-
GL	-23.13 ± 0.08	11.36 ± 0.16	4	26.9	6.9	-	-	-
HI	-22.79 ± 0.10	11.46 ± 0.13	9	41.7	13.3	-	-	-
HM	-23.30 ± 0.10	10.19 ± 0.43	15	21.2	6.8	-	-	-
MF	-22.27 ± 0.66	12.25 ± 0.41	28	56.5	21.1	-	-	-
MS	-23.39 ± 0.21	11.27 ± 0.30	10	24.3	14.3	-	-	-
NE	-22.66 ± 0.18	10.76 ± 0.24	10	30.3	15.2	-	-	-
OL	-22.89 ± 0.19	11.66 ± 0.23	-	-	-	8	19.1	10.0
OS	-22.77 ± 0.53	12.53 ± 0.30	5	62.4	13.1	21	65.0	22.7
PE	-21.94 ± 0.64	11.90 ± 0.46	26	44.2	22.5	4	41.6	12.6
RW	-24.29 ± 1.16	11.36 ± 0.51	4	25.3	11.6	8	25.2	8.0
SH	-23.36 ± 0.13	9.45 ± 0.19	3	10.1	2.7	8	9.9	1.0
SU	-22.78 ± 0.10	12.45 ± 0.13	4	52.1	20.0	-	-	-
SZ	-23.11 ± 1.42	10.54 ± 0.24	-	-	-	7	9.2	2.6
VV	-21.70 ± 0.18	12.61 ± 0.33	-	-	-	20	70.8	13.4
WE	-23.52 ± 0.40	10.45 ± 0.44	12	12.3	3.7	8	14.3	5.1

for both δ^{13}C and δ^{15}N values overlapped all recorded nestling feather values, showing considerable spread in isotopic space (Figure 3.1).

There was an effect of scale on the relationship between feather δ^{13}C values and both the amount of corn and the amount water in the surrounding landscape (see Appendix F. Scale of effect figures for nestling diet; Figure F1). The best-fitting model indicated that feather δ^{13}C values were best predicted using a buffer radius of 1700 m or 400 m to capture the amount of corn and water, respectively. There was a strong positive linear relationship between the amount of corn in the surrounding landscape and feather δ^{13}C values, but no relationship with water (Table 3.2 and Figure 3.2). There were date and year effects, indicating that values were more positive later in the season and in 2017 (Table 3.2).

Scale affected the relationship between feather δ^{15}N values and the amount of cropped land in the surrounding landscape (see Appendix F. Scale of effect figures for nestling diet; Figure F2). The best-fitting model indicated that feather δ^{15}N values vary most strongly with row crop amount at a radius of 2000 m. There was a strong positive linear relationship between the amount of row crop in the surrounding landscape and feather δ^{15}N values, but no relationship with date or livestock presence (Table 3.3 and Figure 3.3). Feather δ^{15}N values were more positive in 2017 (Table 3.3).

3.3.3. Fecal DNA barcoding

Fecal DNA barcoding detected 1644 prey items from 12 orders, 99 families, and 252 genera (for the complete taxonomic list see Appendix E. Diet summary; Table E1). Only prey items within the phylum Arthropoda were considered viable prey items. Species-

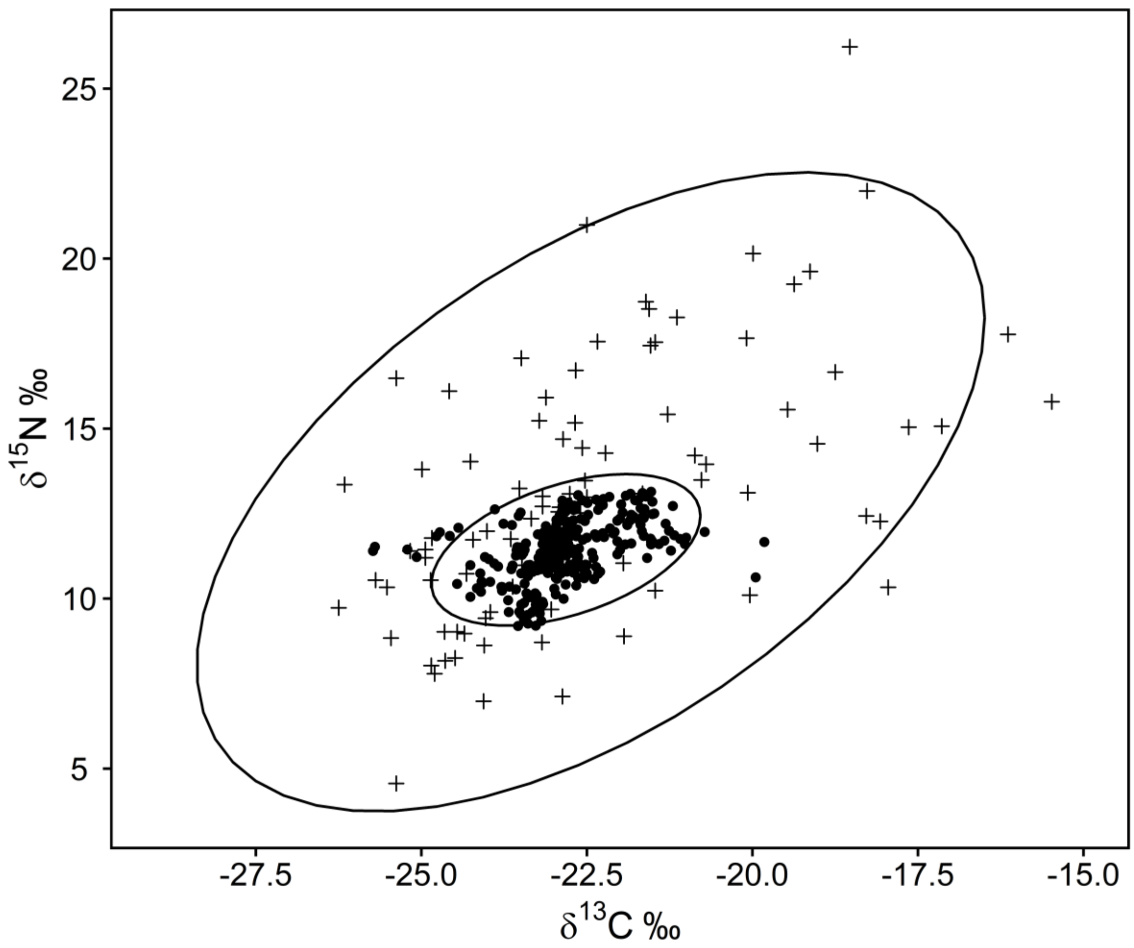


Figure 3.1. Scatterplot of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable-isotope values from nesting Barn Swallow feathers (black points, n = 192), collected near Guelph Ontario (nests = 79, sites = 21), in the breeding seasons of 2016 and 2017, and dipterans (plus symbols, n = 91) collected near Guelph Ontario (sites = 8) in 2017. Discrimination factors have been applied to insect isotope values to compare them to nestling feather values. Ellipses show normal distributions for feather isotope values and insect isotope values.

Table 3.2. Linear mixed effect model results for δ^{13}C‰ values from Barn Swallow nestling feathers (n = 288) collected near Guelph Ontario (nests = 79, sites = 21), in the breeding seasons of 2016 and 2017. The global model included fixed effects of proportion of corn, proportion of water, date, and year, and random effects of nest location and site. Dropped terms are noted by dashes (-).

	Carbon (δ^{13}C‰)			
	Coefficient	SE	t value	p-value
Intercept	-26.80	0.55	-48.42	-
Date	0.016	0.0024	6.18	< 0.001
Year	0.57	0.12	4.60	< 0.001
Corn (1700 m)	5.48	1.30	4.23	< 0.01
Year * Corn	-	-	-	-
Water (400 m)	-9.14	10.06	-0.91	0.38
Year * Water	-	-	-	-

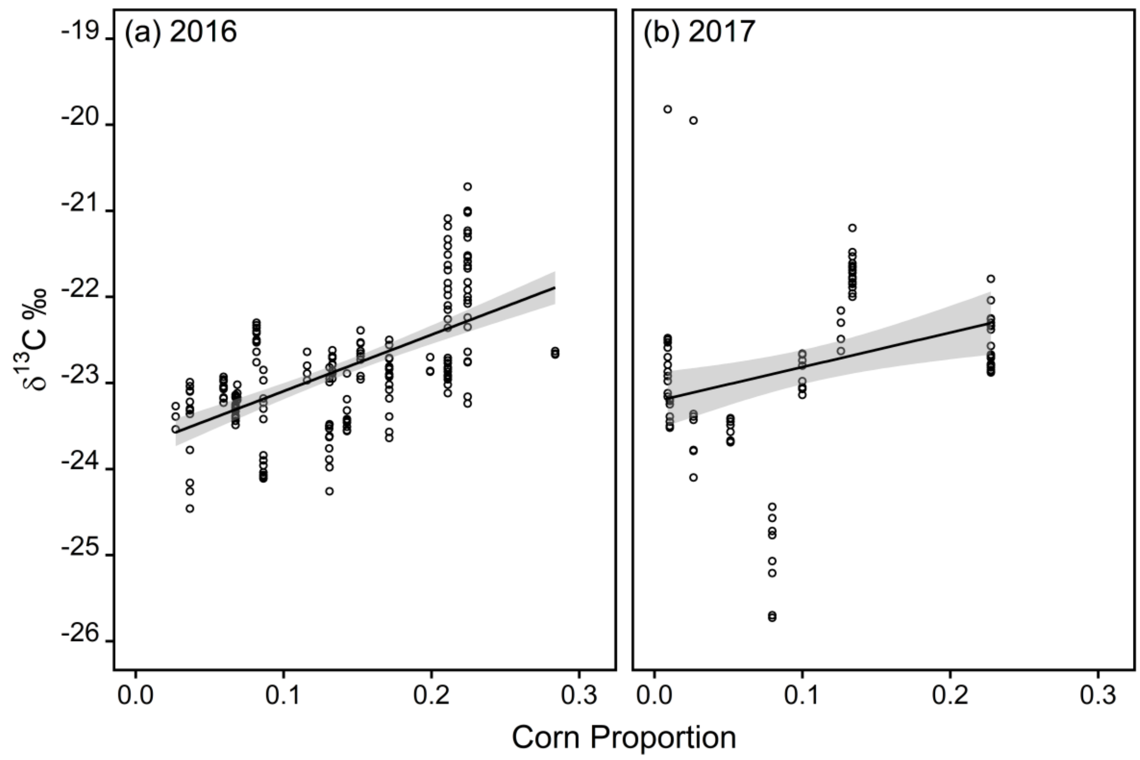


Figure 3.2. Scatterplot of nestling Barn Swallow feather $\delta^{13}C$ values plotted against the proportion of corn within 1700 m of the breeding colony. Feather samples (n = 288) were collected near Guelph Ontario (nests = 79, sites = 21), in the breeding seasons of 2016 and 2017. Plots are separated by year (a – 2016, b - 2017). Line with shaded area indicates linear trend with standard error.

Table 3.3. Linear mixed effect model results for δ^{15}N‰ values from Barn Swallow nestling feathers (n = 288) collected near Guelph Ontario (nests = 79, sites = 21), in the breeding seasons of 2016 and 2017. The global model included fixed effects of proportion of row crop, date, and year, and random effects of nest location and site. Dropped terms are noted by dashes (-).

	Nitrogen (δ^{15}N‰)			
	Coefficient	SE	t value	p-value
Intercept	10.83	0.46	23.61	-
Livestock	-0.31	0.23	-1.37	0.20
Date	-0.0022	0.0019	-1.18	0.25
Year	0.22	0.065	3.45	< 0.01
Row crop (2000 m)	3.13	0.61	5.10	< 0.001
Year * Row crop	-	-	-	-

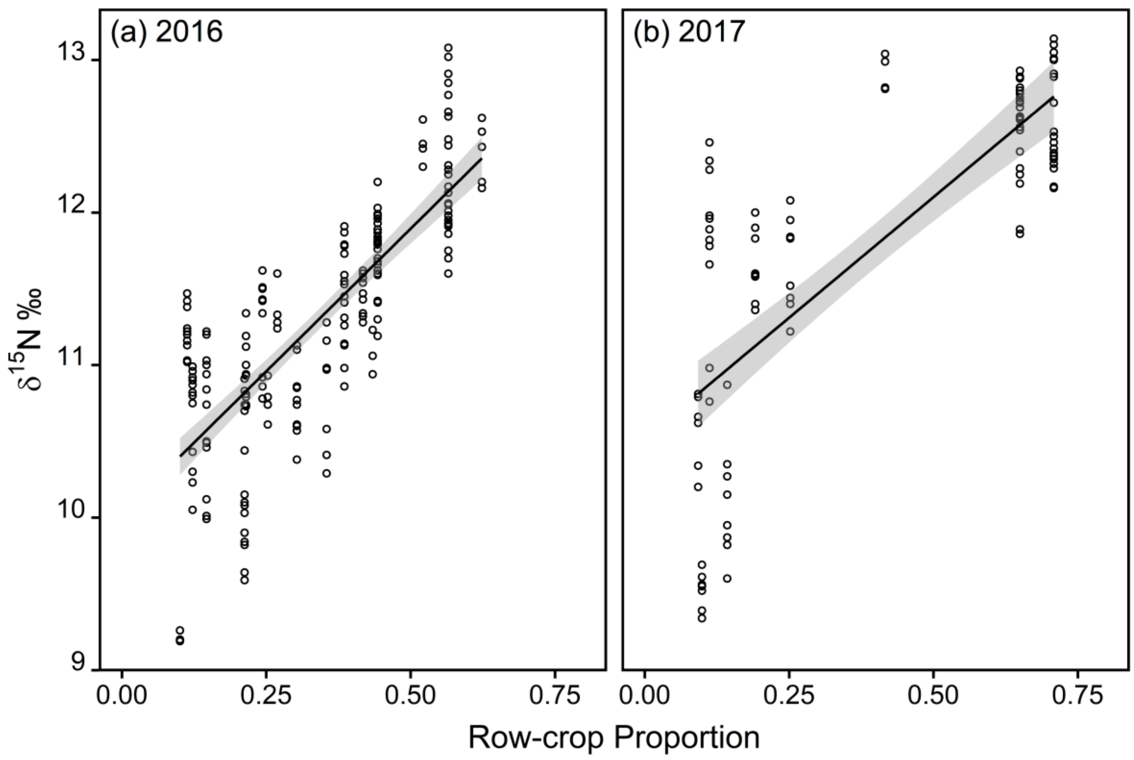


Figure 3.3. Scatterplot of nestling Barn Swallow feather δ ^{15}N values plotted against the proportion of row crop within 2000 m of the breeding colony. Feather samples (n = 288) were collected near Guelph Ontario (nests = 79, sites = 21), in the breeding seasons of 2016 and 2017. Plot are separated by year (a – 2016, b - 2017). Line with shaded area indicates linear trend with standard error.

level identification could not always be reached, but a minimum of 389 unique taxonomic identifications were found. Diptera represented 80% of identified prey, followed by Coleoptera, Lepidoptera, Hymenoptera, and Hemiptera, which together made up only 17% of the total prey items (Figure 3.4). Lastly, the other seven orders made up only 1% of prey items (Figure 3.4). Frequency of detection for the majority of families was low, as 67 of 99 families were only detected in 5 or fewer samples (Figure 3.5), but some families were detected in up to 150 samples (families with the highest frequency of detection summarized in Table 3.4). Family richness showed high correlation with richness at lower taxonomic levels (species, r = 0.89; genus, r = 0.93), and to a lesser extent order richness (r = 0.65), supporting my choice to examine family.

The relationship between diet breadth and the proportion of row crop in the surrounding landscape was affected by scale, but no detectable effect was found for forage (see Appendix F. Scale of effect figures for nestling diet; Figure F3). The best-fitting model indicated that diet breadth was best predicted using a buffer radius of 200 m and 800 m to capture the effect of row crop and forage proportion, respectively. Row crop amount was negatively correlated with diet breadth in 2016 but less so in 2017 (GLMM; sites = 21, n = 290; Table 3.5 and Figure 3.6). The proportion of forage and the number of fecal sacs collected had no effect on diet breadth, but there was a negative effect of both date and year on diet breadth (Table 3.5). No effect of scale on the relationship between Diptera diet breadth and the proportion of row crop or proportion forage in the surrounding landscape was found (see Appendix F. Scale of effect figures for nestling diet; Figure F4), so I used 100 m to capture the proportion of row crop and proportion of forage as it was the best model. There was no relationship between the

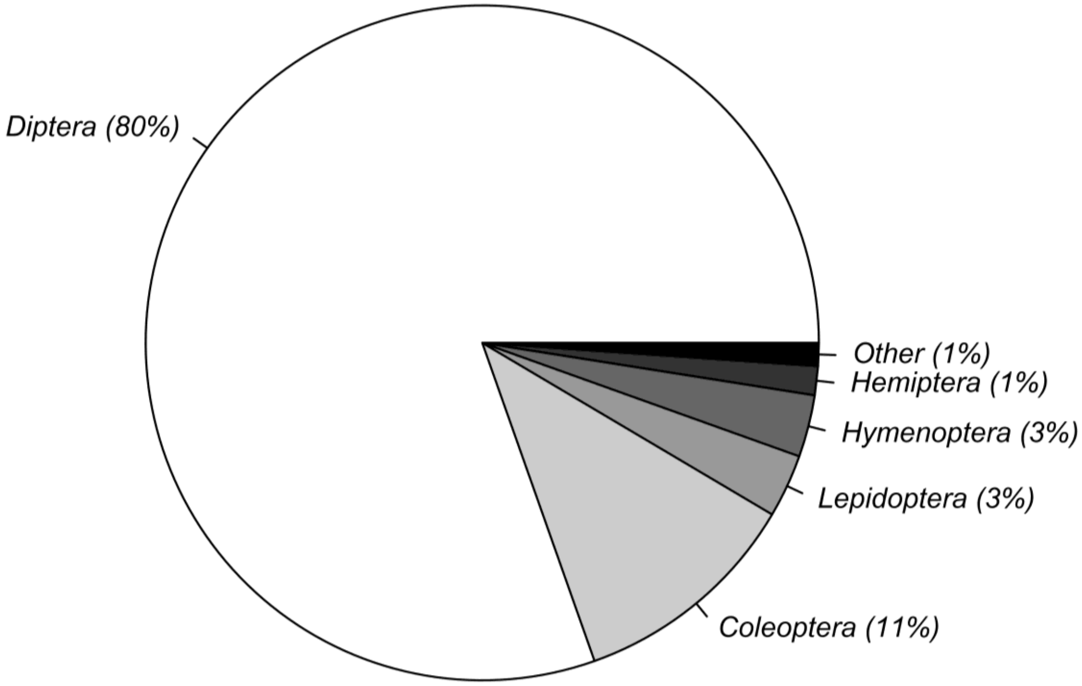


Figure 3.4. Pie chart showing nestling Barn Swallow diet, by prey order, detected using DNA barcoding of nestling feces (n = 290) collected near Guelph Ontario (sites = 21), in the breeding seasons of 2016 and 2017. Percentages show the number of prey items detected divided by the total number of unique detections (1644 prey items), across all samples (n = 290).

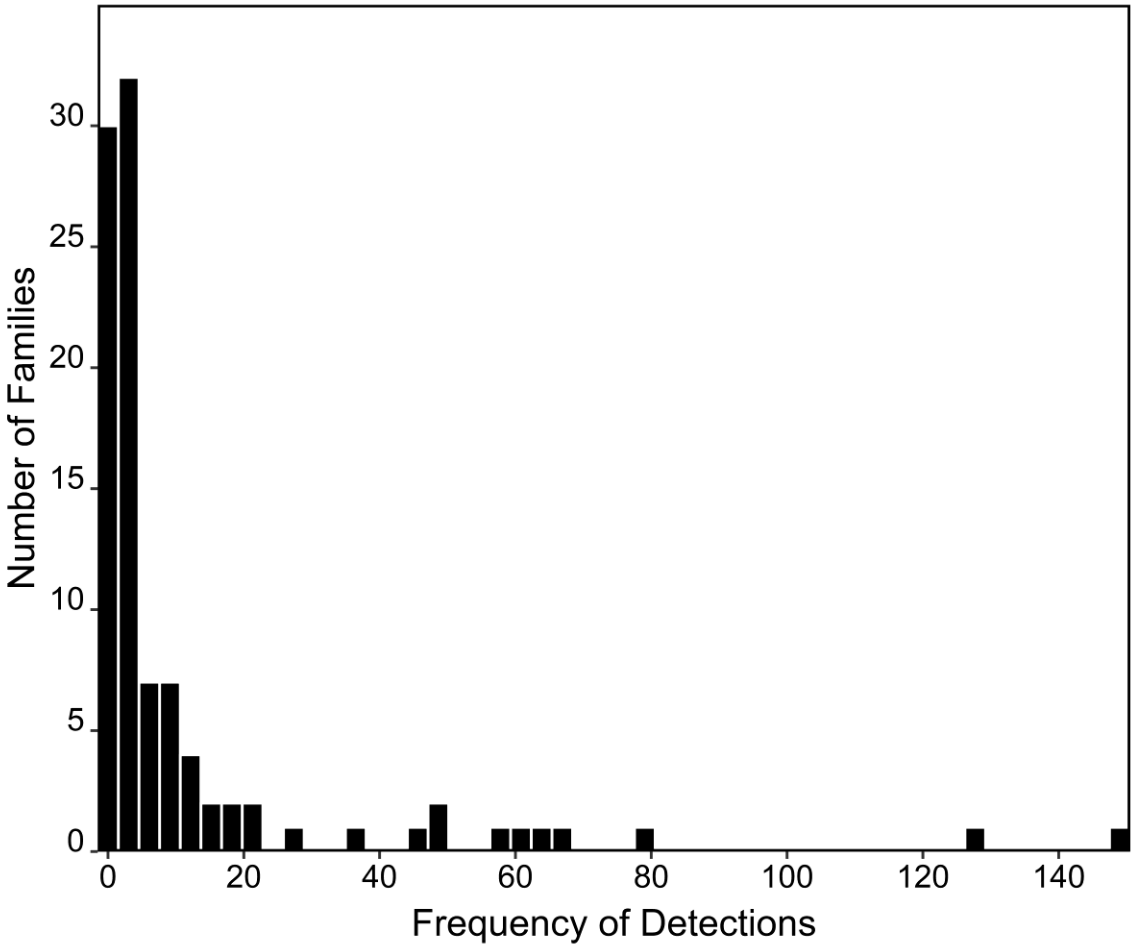


Figure 3.5. Frequency histogram showing frequency of detection for all families detected with DNA barcoding of nestling Barn Swallow feces (n = 290) collected near Guelph Ontario (sites = 21), in the breeding seasons of 2016 and 2017. Bars show the number of families at each frequency of detection.

Table 3.4. Summary table of the most common families (frequency of detections, *Freq* ≥ 10) detected with DNA barcoding of nestling Barn Swallow feces (n = 290) collected near Guelph Ontario (sites = 21), in the breeding seasons of 2016 and 2017.

Family	Common Name	*Freq*
Tachinidae	Tachinids flies	150
Calliphoridae	Blow flies	128
Limoniidae	Limoniid crane flies	79
Sarcophagidae	Flesh flies	66
Tipulidae	Large crane flies	63
Curculionidae	Weevils	60
Tabanidae	Deer flies	57
Anthomyiidae	Root-maggot flies	49
Muscidae	House flies	48
Syrphidae	Hover flies	47
Asilidae	Robber flies	36
Hydrophilidae	Water scavenger beetles	26
Culicidae	Mosquitoes	22
Ichneumonidae	Parasitoid wasps	22
Sepsidae	Black scavenger flies	18
Carabidae	Ground beetles	17
Chrysomelidae	Leaf beetles	16
Miridae	Plant bugs	14
Dolichopodidae	Long-legged flies	13
Hesperiidae	Skippers	13
Scathophagidae	Dung flies	12
Stratiomyidae	Soldier flies	12
Geometridae	Geometrid moths	10
Pipunculidae	Big-headed flies	10
Staphylinidae	Rove beetles	10

Table 3.5. Generalized linear mixed effect model results for nestling Barn Swallow diet breadth, as detected by DNA barcoding of nestling feces (n = 290) collected near Guelph Ontario (sites = 21), in the breeding seasons of 2016 and 2017. The global model included fixed effects of proportion of row crop, proportion of forage, date, year, and the number of fecal samples, and random effect of site. Dropped terms are noted by dashes (-).

	Diet Breadth			
	Coefficient	SE	z value	p-value
Intercept	2.13	0.14	14.72	< 0.001
Samples	-0.047	0.028	-1.68	0.092
Date	-0.065	0.032	-2.028	< 0.05
Year	-0.79	0.093	-8.41	< 0.001
Row crop (200 m)	-0.56	0.20	-2.75	< 0.01
Year * Row crop	0.48	0.22	2.13	< 0.05
Forage (800 m)	-0.070	0.21	-0.34	0.73
Year * Forage	-	-	-	-

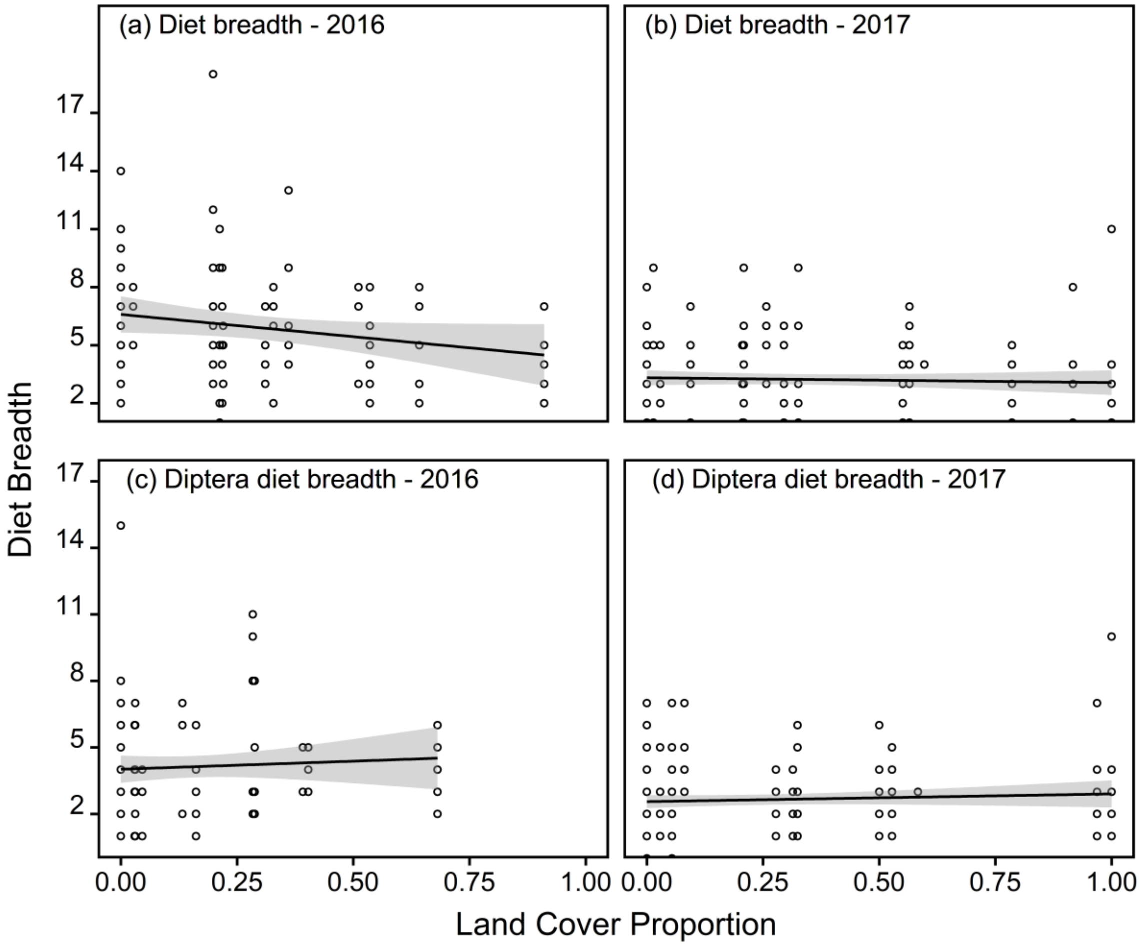


Figure 3.6. Scatterplot of nestling Barn Swallow diet breadth (a-b) and Diptera diet breadth (c-d), at the family level, plotted against the proportion of row crop within 200 m and 100 m of the breeding colony respectively. Diet breadth was detected with DNA barcoding of nestling feces (n = 290) collected near Guelph Ontario (sites = 21), in the breeding seasons of 2016 and 2017. Plots are separated by year (a,c – 2016, b,d – 2017). Line with shaded area indicates linear trend with standard error.

proportion of row crop or proportion of forages and Diptera diet breadth (GLMM; sites = 21, n = 290; Table 3.6 and Figure 3.6). Again, there were negative effects of both date and year on Diptera diet breadth (Table 3.6).

There were marginal differences in diet composition with the proportion of row crop (PERMANOVA; $F_{3,287} = 1.63$, $R^2 = 0.016$, $p = 0.052$), but no differences in Diptera composition with the proportion of row crop (PERMANOVA; $F_{3,283} = 0.71$, $R^2 = 0.0071$, $p = 0.77$). When visualized via ordination, no differences were seen for diet composition (NMDS; model stress was 0.17 in 2016, 0.12 in 2017; Figure 3.7a-b) or Diptera diet composition (NMDS; model stress, 0.14 in 2016, 0.10 in 2017; Figure 3.7c-d). There were significant site, date, and year effects on diet composition (site, $F_{19,287} = 1.37$, $R^2 = 0.085$, $p = 0.009$; date, $F_{1,287} = 7.36$, $R^2 = 0.024$, $p = 0.001$; year, $F_{1,287} = 1.84$, $R^2 = 0.012$, $p = 0.002$) and Diptera diet composition (site, $F_{19,283} = 1.46$, $R^2 = 0.093$, $p = 0.003$; date, $F_{1,283} = 6.22$, $R^2 = 0.021$, $p = 0.001$; year, $F_{3,283} = 3.11$, $R^2 = 0.010$, $p = 0.01$).

3.4. Discussion

Using both fecal DNA and feather stable-isotope analysis, I identified landscape-level effects of agricultural intensification on diet of nestling swallows. I predicted that Barn Swallow nestlings raised in more agriculturally intense environments would be provisioned insects from within agro-ecosystems resulting in reduced diet breadth. Nestling feather isotope values were related to agricultural land use, indicating differences in diet, or diet source, along a gradient of agricultural intensification. Specifically, stable-nitrogen values varied with the proportion of row crop while stable-carbon values varied with the proportion of corn in the surrounding landscape. These results suggest that nestling diet is derived, at least in part, from agricultural food webs.

Table 3.6. Generalized linear mixed effect model results for nestling Barn Swallow Diptera diet breadth, as detected by DNA barcoding of nestling feces (n = 290), collected near Guelph Ontario (sites = 21), in the breeding seasons of 2016 and 2017. The global model included fixed effects of proportion of row crop, proportion of forage, date, year, and the number of fecal samples, and random effect of site. Dropped terms are noted by dashes (-).

	Diptera Diet Breadth			
	Coefficient	SE	z value	p-value
Intercept	1.66	0.19	8.58	< 0.001
Samples	-0.044	0.030	-1.44	0.15
Date	-0.096	0.037	-2.60	< 0.01
Year	-0.53	0.072	-7.32	< 0.001
Row crop (100 m)	0.041	0.19	0.22	0.83
Year * Row crop	-	-	-	-
Forage (100 m)	-0.10	0.20	-0.51	0.61
Year * Forage	-	-	-	-

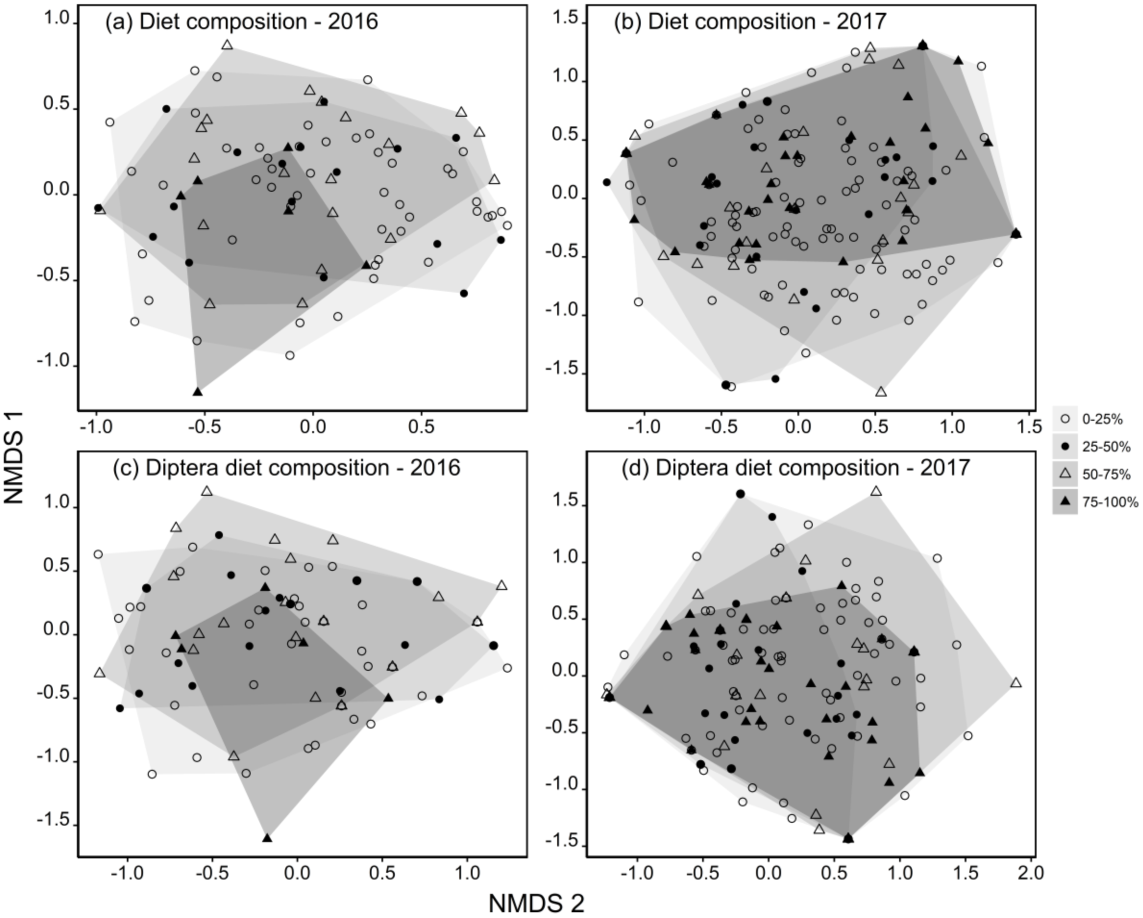


Figure 3.7. NMDS plot of nestling Barn Swallow diet composition (a-b) and Diptera diet composition (c-d) detected with DNA barcoding of nestling feces (n = 290) collected near Guelph Ontario (sites = 21), in the breeding seasons of 2016 and 2017. Plot are separated by year (a,c – 2016, b,d – 2017). Symbols represent the proportion of row crop surrounding each site, grouped into discrete factors (0-25%, 25-50%, 50-75%, 75-100%). Groups are also represented by shaded minimum convex polygons.

In contrast, DNA barcoding of fecal matter identified few crop pest species. As predicted, nestling diet breath was negatively associated with the proportion of row crop in both years, indicating negative effects of diet derived from these landscapes. Despite negative effects on overall diet, dipteran prey items, which were the most detected prey items, were unaffected by agricultural intensity, suggesting a robust diet base. Overall, I found that nestling Barn Swallows raised within agro-ecosystems are being provisioned insects from agricultural food webs for at least part of their diet, but there is little evidence to suggest negative effects of intensification on nestling diet.

Both $\delta^{13}C$ and $\delta^{15}N$ values in nestling feathers were more strongly related to landscape at large-scales. Stable-carbon isotope values correlated most strongly to the proportion of corn within 1700 m, a result expected from the strong C_4 isotopic signal of corn within an otherwise C_3 landscape. Contrary to predictions, there was no evidence of a relationship between $\delta^{13}C$ values and the proportion of surface water in the surrounding landscape, likely due to a general lack of water in the landscape. This large-scale relationship between corn and $\delta^{13}C$ suggests movement in either provisioning Barn Swallows or prey insects, but this scale is much greater than previously reported foraging distances in swallows (Turner 1980; McCarty & Winkler 1999). To compensate for reduced insect availability, adult swallows may be making long-distance movements, spending more time away from the nest foraging (Stanton et al. 2016). Alternatively, aerial insects are making these movements or being dispersed via wind, as aerial insects are highly mobile (Froerer et al. 2010).

Stable-nitrogen isotope values correlated most strongly to the proportion of row crop at a buffer radius of 2000 m. I interpreted this large-scale positive effect between

δ^{15}N and row cropping as field-specific enrichment via nitrogenous fertilizers (Girard et al. 2012), but also agricultural run-off of fertilizer into surrounding non-agricultural habitats (e.g., Hebert & Wassenaar 2001; Anderson & Cabana 2005, 2006; Møller et al. 2018). There were significant year effects on both δ^{13}C and δ^{15}N values, suggesting differences in land use between years, but there was no difference in row crop proportion and little difference in corn proportion between years. Ultimately teasing apart these effects into exact mechanisms of enrichment is impossible (Anderson & Cabana 2006) and I was unable to measure agro-chemical inputs such as fertilizer, but the strong correlation between row crop proportion and the lack of a relationship between livestock presence indicates that fertilizer inputs are a likely contributor.

Consistent with previous reports on swallow nestlings (McCarty & Winkler 1999; Bellavance et al. 2018), dipteran prey items were the most detected order of insects within nestling diets (80% of detections). Very few families (67/99) were found in more than five samples, indicating little consistency in nestling diet, outside of select families. Furthermore, similarity in diet composition between samples showed no relationship with agricultural intensification, suggesting opportunistic prey selection. The only non-dipteran families that were seen in more than 20 diet samples were weevils (Curculionidae, 21% of samples), water-scavenger beetles (Hydrophilidae, 9%) and parasitoid wasps (Ichneumonidae, 8%). Despite this, prevalence large-bodied prey (e.g., *Winthemia rufopicta*, +10 mm size, frequency of detection = 55), may support parental selectivity for larger prey (McCarty & Winkler 1999), but without information on dietary proportions, disentangling this effect is impossible.

Crop pest species were notably absent from nestling fecal samples, with Seed Corn Maggots *Delia platura* being the only exception, showing up in 19 of 290 of analyzed samples. As nestling $\delta^{13}C$ values were higher in areas of more corn land cover, I expected higher prevalence of insect prey that forage directly on corn for at least one stage of their life cycle, such as lepidopterans (e.g., European Corn Borer *Ostrinia nubilalis,* and Fall Armyworm *Spodoptera frugiperda*; Pest Management Centre 2015). This disconnect is likely because Barn Swallows are diurnal foragers and these lepidopterans are predominantly nocturnal fliers. The most detected dipteran family in nestling diet was Tachinidae, which was seen in 150 of 290 samples. Tachinid flies are parasitoids of lepidopteran and symphatan larvae, several of which are pests of crops. As the larvae develop within their host's body, relying on their tissues as a nutrient source, it is likely that this exchange of nutrients causes tachinid flies to be enriched in ^{13}C. Rather than foraging directly on corn pests, the prevalence of tachinid flies provides a potential carbon pathway to nestling feathers. Unfortunately, few tachinid flies were captured during insect sampling, and I was unable to measure prey $\delta^{13}C$ values.

Nestling diet breadth was inversely related to agricultural intensity, which is consistent with previous studies on aerial insectivorous bats within agro-ecosystems (e.g., Aizpurua et al. 2017). The effect of landscape was most strong within 100 m, highlighting the importance of the landscape directly surrounding breeding colonies in determining diet. Reductions in diet breadth could indicate either higher selectivity for beneficial prey or reduced richness of insects surrounding the site. Previous studies reporting negative effects of intensification on insect availability and reproductive success have been focused on ground-dwelling foragers who primary prey items are found within vegetation (e.g., Corn Bunting *Miliaria calandra*, Brickle et al. 2000; and Yellowhammer *Emberiza citronella*, Morris et al. 2005). Moreover, when only dipteran prey items were included in my models, nestling diet breadth and composition did not correlate with the proportion of row crop or forage at any scale. Therefore, smaller scale negative effects of agricultural intensity influencing less mobile insects may be driving this reduction in diet breadth. Although they have low overall detection, these less mobile and generally larger bodied prey items (e.g., Coleoptera) may supplement nestling diet.

There were negative effects of date and year on diet breadth. Negative effects of date are consistent with previous reports on Diptera availability throughout the season (Rioux Paquette et al. 2013; Bellavance et al. 2018). Seasonal changes, such as pesticide use, influencing prey insect availability may be driving this difference. Both corn and soybeans are reliant on pesticide applications (Gallivan et al. 2001), and pesticides have been detected in insects provisioned to nestling swallows (Haroune et al. 2015). Further investigation is required, necessitating detailed aerial insect sampling to determine the effects of agricultural intensification on prey availability and nestling diet. Observed negative effects of year may be driven by climate, as 2016 was hotter overall and less precipitation than 2017 (see Chapter 2). But significant year effects may be due to methodological differences in DNA barcoding between years (i.e., Ion Torrent PGM high-throughput sequencer in 2016 and S5 high-throughput sequencer in 2017). Although this year effect may be real, I cannot confidently conclude that methods did not contribute.

High proportions of hard-bodied insects, like coleopterans, in aerial insectivore diet have been attributed to selectivity for larger prey items (Orłowski & Karg 2011), but this may be an overestimation of the true dietary proportion of hard-bodied diet items as they have a higher probability of remaining visually identifiable after digestion. Using DNA barcoding, soft-bodied flies were the most detected prey items (80% of detections). I was unable to quantify diet beyond presence/absence, possibly obscuring identification of preference for prey types. This was unavoidable, as DNA barcoding is limited to presence-absence detection rather than quantitative measures of dietary proportions because of biases in prey-specific DNA survival during digestion (Deagle & Tollit 2007) along with differential amplification among DNA species during PCR (Wintzingerode et al. 1997), both of which add uncertainty between the number of barcoding reads and the proportions of ingested diet. Despite this, there is continued effort towards the development of a method to quantify DNA reads as dietary proportions, but these studies require experimentation with empirically known diet (Deagle et al. 2018), which is not possible for a free-living aerial insectivore.

3.5. Conclusion

Here I report a comprehensive summary of Barn Swallow nestling diet that included at least 99 families and 389 species, more than any other published study on any nestling's diet. Furthermore, I highlight potential predictors of agricultural land use using stable-isotope values within nestling feathers. In line with previous reports, I found evidence of negative impacts of agricultural intensification on nestling diet composition. However, further work is needed to assess the effects of agricultural intensification on insect availability in the broader landscape. Future research efforts should also be made to investigate the direct effects of agricultural intensification, through pesticide exposure, as these results suggests that land-use types such as corn contribute to the food webs in which Barn Swallows provision nestlings. Increased agricultural intensity may be contributing to a decline of Barn Swallows in southern Ontario through reductions in diet, but these results are not conclusive as they also suggest that a robust, highly mobile, source of aerial prey items may be buffering aerial insectivore diet to local land-use effects.

3.6. Literature cited

AAFC. 2017. Annual crop inventory. Agriculture and Agri-Food Canada, Science and Technology Branch. Contains information licensed under the Open Government License – Canada. [retrieved from: https://www.open.canada.ca/data/en/dataset/ba2645d5-4458-414d-b196-6303ac06c1c9].

Aizpurua, O et al. 2017. Agriculture shapes the trophic niche of a bat preying on multiple pest arthropods across Europe: evidence from DNA metabarcoding. Molecular Ecology **27**:815–825.

Anderson C, Cabana G. 2005. $\delta^{15}N$ in riverine food webs: effects of N inputs from agricultural watersheds. Canadian Journal of Fisheries and Aquatic Sciences **62**:333–340.

Anderson C, Cabana G. 2006. Does $\delta^{15}N$ in river food webs reflect the intensity and origin of N loads from the watershed? Science of The Total Environment **367**:968–978.

Attwood S, Maron M, House A, Zammit C. 2008. Do arthropod assemblages display globally consistent responses to intensified agricultural land use and management? Global Ecology and Biogeography **17**:585–599.

Balmford A, Green M, Murray M. 1996a. Using higher-taxon richness as a surrogate for species richness: I. Regional tests. Proceedings of the Royal Society of London B: Biological Sciences **263**:1267–1274.

Balmford A, Jayasuriya AH, Green M. 1996b. Using higher-taxon richness as a surrogate for species richness: II. Local applications. Proceedings of the Royal Society of London B: Biological Sciences **263**:1571–1575.

Bates D, Maechler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software **67**:1–48.

Bellavance V, Bélisle M, Savage J, Pelletier F, Garant D. 2018. Influence of agricultural intensification on prey availability and nestling diet in Tree Swallows (*Tachycineta bicolor*). Canadian Journal of Zoology **96**:1053–1065.

Benton TG, Bryant DM, Cole L, Crick HQP. 2002. Linking agricultural practice to insect and bird populations: a historical study over three decades. Journal of Applied Ecology **39**:673–687.

Boecklen WJ, Yarnes CT, Cook BA, James AC. 2011. On the use of stable isotopes in trophic ecology. Annual Review of Ecology, Evolution, and Systematics **42**:411–440.

Brickle NW, Harper DGC, Aebischer NJ, Cockayne SH. 2000. Effects of agricultural intensification on the breeding success of Corn Buntings *Miliaria calandra*. Journal of Applied Ecology **37**:742–755.

Brown CR, Brown MB. 1999. Barn Swallow (*Hirundo rustica*). The Birds of North America Online. Available from https://www.bna.birds.cornell.edu/BNA/account/Barn_Swallow.html.

Clare EL, Fraser EE, Braid HE, Fenton MB, Hebert PD. 2009. Species on the menu of a generalist predator, the eastern red bat (*Lasiurus borealis*): using a molecular approach to detect arthropod prey. Molecular Ecology **18**:2532–2542.

Deagle BE, Thomas AC, McInnes JC, Clarke LJ, Vesterinen EJ, Clare EL, Kartzinel TR, Eveson JP. 2018. Counting with DNA in metabarcoding studies: how should we convert sequence reads to dietary data? Molecular Ecology **2018**:1–16

Deagle BE, Tollit DJ. 2007. Quantitative analysis of prey DNA in pinniped faeces: potential to estimate diet composition? Conservation Genetics **8**:743–747.

Donald PF, Green R, Heath M. 2001. Agricultural intensification and the collapse of Europe’s farmland bird populations. Proceedings of the Royal Society of London B: Biological Sciences **268**:25–29.

Donald PF, Sanderson FJ, Burfield IJ, van Bommel FPJ. 2006. Further evidence of continent-wide impacts of agricultural intensification on European farmland birds, 1990–2000. Agriculture, Ecosystems & Environment **116**:189–196.

English PA, Green DJ, Nocera JJ. 2018. Stable isotopes from museum specimens may provide evidence of long-term change in the trophic ecology of a migratory aerial insectivore. Frontiers in Ecology and Evolution **6**:1-13.

ESRI. 2011. ArcGIS Desktop: release 10. Environmental Systems Research Institute, Redlands, CA: Environmental Systems Research Institute.

France R. 1995. Critical examination of stable isotope analysis as a means for tracing carbon pathways in stream ecosystems. Canadian Journal of Fisheries and Aquatic Sciences **52**:651–656.

Froerer KM, Peck SL, McQuate GT, Vargas RI, Jang EB, McInnis DO. 2010. Long-distance movement of *Bactrocera dorsalis* (Diptera: Tephritidae) in Puna, Hawaii: how far can they go? American Entomologist **56**:88–95.

Fry B. 2006. Stable Isotope Ecology. Springer.

Gallivan GJ, Surgeoner GA, Kovach J. 2001. Pesticide risk reduction on crops in the province of Ontario. Journal of Environmental Quality **30**:798–813.

Ghilain A, Bélisle M. 2008. Breeding success of Tree Swallows along a gradient of agricultural intensification. Ecological Applications **18**:1140–1154.

Girard J, Baril A, Mineau P, Fahrig L. 2012. Foraging habitat and diet of Song Sparrows (*Melospiza melodia*) nesting in farmland: a stable isotope approach. Canadian Journal of Zoology **90**:1339–1350.

Grüebler MU, Morand M, Naef-Daenzer B. 2008. A predictive model of the density of airborne insects in agricultural environments. Agriculture, Ecosystems and Environment **123**:75–80.

Halekoh U, Højsgaard S. 2014. A Kenward-Roger approximation and parametric bootstrap methods for tests in linear mixed models - the R package pbkrtest. Journal of Statistical Software **59**:1–30.

Haroune L, Cassoulet R, Lafontaine M-P, Bélisle M, Garant D, Pelletier F, Cabana H, Bellenger J-P. 2015. Liquid chromatography-tandem mass spectrometry determination for multiclass pesticides from insect samples by microwave-assisted solvent extraction followed by a salt-out effect and micro-dispersion purification. Analytica Chimica Acta **891**:160–170.

Hart J, Milsom T, Fisher G, Wilkins V, Moreby S, Murray A, Robertson P. 2006. The relationship between Yellowhammer breeding performance, arthropod abundance and insecticide applications on arable farmland. Journal of Applied Ecology **43**:81–91.

Heaton TH. 1986. Isotopic studies of nitrogen pollution in the hydrosphere and atmosphere: a review. Calibration of the Phanerozoic Time Scale **59**:87–102.

Hebert CE, Wassenaar LI. 2001. Stable nitrogen isotopes in waterfowl feathers reflect agricultural land use in western Canada. Environmental Science and Technology **35**:3482–3487.

Hendrickx F, Maelfait J, Van Wingerden W, Schweiger O, Speelmans M, Aviron S, Augenstein I, Billeter R, Bailey D, Bukacek R. 2007. How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. Journal of Applied Ecology **44**:340–351.

Hobson KA. 1999. Stable-carbon and nitrogen isotope ratios of songbird feathers grown in two terrestrial biomes: implications for evaluating trophic relationships and breeding origins. The Condor **101**:799–805.

Hobson KA, Bairlein F. 2003. Isotopic fractionation and turnover in captive Garden Warblers (*Sylvia borin*): implications for delineating dietary and migratory associations in wild passerines. Canadian Journal of Zoology **81**:1630–1635.

Hobson KA, Clark RG. 1992. Assessing avian diets using stable isotopes I: turnover of ^{13}C in tissues. The Condor **94**:181–188.

Hobson KA, Kardynal KJ, Van Wilgenburg SL, Albrecht G, Salvadori A, Cadman MD, Liechti F, Fox JW. 2015. A continent-wide migratory divide in North American breeding Barn Swallows (*Hirundo rustica*). PLOS ONE **10**:e0129340.

Hobson KA, Piatt JF, Pitocchelli J. 1994. Using stable isotopes to determine seabird trophic relationships. Journal of Animal Ecology **63**:786–798.

Hobson KA, Welch HE. 1992. Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}C$ and $\delta^{15}N$ analysis. Marine Ecology Progress Series **84**:9–18.

Imlay TL, Mann HAR, Leonard ML. 2017. No effect of insect abundance on nestling survival or mass for three aerial insectivores. Avian Conservation and Ecology **12:**19.

Jedlicka JA, Sharma AM, Almeida RP. 2013. Molecular tools reveal diets of insectivorous birds from predator fecal matter. Conservation Genetics Resources **5**:879–885.

Jedlicka JA, Vo A-TE, Almeida RPP. 2016. Molecular scatology and high-throughput sequencing reveal predominately herbivorous insects in the diets of adult and nestling Western Bluebirds (*Sialia mexicana*) in California vineyards. The Auk **134**:116–127.

Johnston RF. 1967. Seasonal variation in the food of the Purple Martin *Progne subis* in Kansas. Ibis **109**:8–13.

Jones TM, Ward MP, Benson TJ, Brawn JD. 2016. Variation in nestling body condition and wing development predict cause-specific mortality in fledgling Dickcissels. Journal of Avian Biology **48**:439–447.

Joo S, Park S. 2012. Identification of bird species and their prey using DNA barcode on feces from Korean traditional village groves and forests (maeulsoop). Animal Cells and Systems **16**:488–497.

Kendall C. 1998. Tracing nitrogen sources and cycling in catchments. Pages 519–576 in J. McDonnell, editor. Isotope Tracers in Catchment Hydrology. Elsevier, Amsterdam.

Long BL, Kurta A, Clemans DL. 2013. Analysis of DNA from feces to identify prey of Big Brown Bats (*Eptesicus fuscus*) caught in apple orchards. The American Midland Naturalist **170**:287–297.

Mailvaganam S. 2018. Area, yield, production and farm value of specified field crops, Ontario, 2012 - 2017 (imperial and metric units). Ontario Ministry of Agriculture, Food, and Rural Affairs.

Marshall JD, Brooks JR, Lajtha K. 2007. Sources of variation in the stable isotopic composition of plants. Stable Isotopes in Ecology and Environmental Science **2**:22–60.

McCarty JP, Winkler DW. 1999. Foraging ecology and diet selectivity of Tree Swallows feeding nestlings. The Condor **101**:246–254.

Mengelkoch JM, Niemi GJ, Regal RR. 2004. Diet of the nestling Tree Swallow. The Condor **106**:423–429.

Michel NL, Smith AC, Clark RG, Morrissey CA, Hobson KA. 2016. Differences in spatial synchrony and interspecific concordance inform guild-level population trends for aerial insectivorous birds. Ecography **39**:774–786.

Mitchell GW, Guglielmo CG, Wheelwright NT, Freeman-Gallant CR, Norris DR. 2011. Early life events carry over to influence pre-migratory condition in a free-living songbird. PLOS ONE **6**:e28838.

Møller AP, Laursen K, Hobson KA. 2018. Retrospectively analysing condition in historical samples of birds. Journal of Zoology **305**:188–195.

Morris AJ, Wilson JD, Whittingham MJ, Bradbury RB. 2005. Indirect effects of pesticides on breeding Yellowhammer (*Emberiza citrinella*). Agriculture, Ecosystems and Environment **106**:1–16.

NABCI. 2016. The state of North America's birds 2016. Environment and Climate Change Canada, Ottawa, Ontario. Available from http://stateofthebirds.org/2016/.

Naef-Daenzer B, Widmer F, Nuber M. 2001. Differential post-fledging survival of Great and Coal Tits in relation to their condition and fledging date. Journal of Animal Ecology **70**:730–738.

Nebel S, Mills A, McCracken JD, Taylor PD. 2010. Declines of aerial insectivores in North America follow a geographic gradient. Avian Conservation and Ecology **5**:1.

Nocera JJ, Blais JM, Beresford DV, Finity LK, Grooms C, Kimpe LE, Kyser K, Michelutti N, Reudink MW, Smol JP. 2012. Historical pesticide applications coincided with an altered diet of aerially foraging insectivorous Chimney Swifts. Proceedings of the Royal Society B: Biological Sciences **279**:3114–3120.

Oksanen J et al. 2018. vegan: community ecology package. Community ecology package, version 2.4-6.

Orłowski G, Karg J. 2011. Diet of nestling Barn Swallows *Hirundo rustica* in rural areas of Poland. Open Life Sciences **6**:1023–1035.

Pardo LH, Nadelhoffer KJ. 2010. Using nitrogen isotope ratios to assess terrestrial ecosystems at regional and global scales. Pages 221–249 in J. B. West, G. J. Bowen, T. E. Dawson, and K. P. Tu, editors. Isoscapes: Understanding Movement, Pattern, and Process on Earth Through Isotope Mapping. Springer Netherlands, Dordrecht.

Pest Management Centre. 2015. Crop profile for sweet corn in Canada. Agriculture and Agri-Food Canada. Ottawa, Ontario.

Peterson BJ, Fry B. 1987. Stable isotopes in ecosystem studies. Annual Review of Ecology and Systematics **18**:293–320.

Pinhero J, Bates D. 2000. Mixed-effects Models in S and S-PLUS. Springer-Verlag, New York.

Quinney TE, Ankney CD. 1985. Prey size selection by Tree Swallows. The Auk **102**:245–250.

R Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing: Vienna, Austria.

Rioux Paquette S, Garant D, Pelletier F, Bélisle M. 2013. Seasonal patterns in Tree Swallow prey (Diptera) abundance are affected by agricultural intensification. Ecological Applications **23**:122–133.

Robinson RA, Sutherland WJ. 2002. Post-war changes in arable farming and biodiversity in Great Britain. Journal of Applied Ecology **39**:157–176.

RStudio Team. 2015. RStudio: integrated development for R. Boston, MA: RStudio, Inc.

Sauer JR, Niven DK, Hines JE, Ziolkowski J DJ, Pardieck KL, Fallon JE, Link WA. 2017. The North American breeding bird survey, results and analysis 1966 - 2015. Version 2.07.2017. USGS Patuxent Wildlife Research Center, Laurel, MD.

Smith AC, Hudson M-AR, Downes CM, Francis CM. 2015. Change points in the population trends of aerial-insectivorous birds in North America: synchronized in time across species and regions. PLOS ONE **10**:e0130768.

Stanton RL, Morrissey CA, Clark RG. 2016. Tree Swallow (*Tachycineta bicolor*) foraging responses to agricultural land use and abundance of insect prey. Canadian Journal of Zoology **94**:637–642.

Stanton RL, Morrissey CA, Clark RG. 2018. Analysis of trends and agricultural drivers of farmland bird declines in North America: a review. Agriculture, Ecosystems and Environment **254**:244–254.

Tieszen LL, Boutton TW. 1989. Stable carbon isotopes in terrestrial ecosystem research. Pages 167–195 in P. W. Rundel, J. R. Ehleringer, and K. A. Nagy, editors. Stable Isotopes in Ecological Research. Springer New York.

Trevelline BK, Latta SC, Marshall LC, Nuttle T, Porter BA. 2016. Molecular analysis of nestling diet in a long-distance Neotropical migrant, the Louisiana Waterthrush (*Parkesia motacilla*). The Auk **133**:415–428.

Trevelline BK, Nuttle T, Hoenig BD, Brouwer NL, Porter BA, Latta SC. 2018. DNA metabarcoding of nestling feces reveals provisioning of aquatic prey and resource partitioning among Neotropical migratory songbirds in a riparian habitat. Oecologia **187**:85–98.

Tscharntke T, Klein AM, Kruess A, Steffan-Dewenter I, Thies C. 2005. Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. Ecology Letters **8**:857–874.

Turner AK. 1980. The use of time and energy by aerial feeding birds. PhD Thesis. University of Stirling.

Valentini A, Pompanon F, Taberlet P. 2009. DNA barcoding for ecologists. Trends in Ecology and Evolution **24**:110–117.

Vitousek PM, Aber JD, Howarth RW, Likens GE, Matson PA, Schindler DW, Schlesinger WH, Tilman DG. 1997. Human alteration of the global nitrogen cycle: sources and consequences. Ecological Applications **7**:737–750.

Wintzingerode FV, Göbel UB, Stackebrandt E. 1997. Determination of microbial diversity in environmental samples: pitfalls of PCR-based rRNA analysis. FEMS Microbiology Reviews **21**:213–229.

Zeale MR, Butlin RK, Barker GL, Lees DC, Jones G. 2011. Taxon-specific PCR for DNA barcoding arthropod prey in bat faeces. Molecular Ecology Resources **11**:236–244.

Chapter 4

General Discussion

Expansion and intensification of agriculture is one of the greatest threats to bird populations globally (Green et al. 2005) but, clearly, such processes affect different species differently. Although reduced food availability in agro-ecosystems is hypothesized to have driven the decline of farmland birds in general, for aerial insectivores, few studies have examined the effects of agricultural intensification on reproductive success (e.g., Ghilain & Bélisle 2008), nestling diet, and body condition (e.g., Michelson et al. 2018). Understanding the factors affecting nestling condition is important because condition at fledging is an important predictor of subsequent survival (Mitchell et al. 2011; Evans et al. unpub ms.). Here, I provide a preliminary investigation into landscape-level effects of agricultural intensification on a semi-colonial aerial insectivorous bird breeding in farmlands, focusing on how landscape composition affects nestling condition and diet.

4.1. Key findings

4.1.1. Effects of agricultural intensification

My initial prediction was that negative effects of agricultural intensification on nestling diet would affect nestling condition and growth (e.g., Konarzewski et al. 1996; Searcy et al. 2004; Twining et al. 2016), but I found mixed evidence. Proportion of row crop was positively related to nestling condition, but was unrelated to nestling growth and pre-fledgling condition. This relationship with nestling condition may reflect a benefit of row crops as open habitat beneficial for foraging for Barn Swallows or that row crops support higher densities of prey species such as tachinid flies. Despite finding a positive relationship between row crop and nestling condition, I found a negative relationship between row crop and diet breadth. I speculate that reduced diet breadth may indicate a preference for beneficial prey types rather than reduced diet amount in these environments, given the relationship found with nestling body condition. Alternatively, increased richness of prey in diets of Barn Swallows occupying more natural landscapes may simply reflect opportunistic foraging by parents. Regardless, being born within landscapes composed of greater proportion of row crop did not translate to higher or lower pre-fledging condition or fledging success in this system. Although I found contrasting effects of agricultural intensification on nestling condition and diet, there were no differences in productivity with proportion of row crop. Taken together, these results provide evidence that agricultural intensification is not detrimental to the breeding success of Barn Swallows in this area.

4.1.2. Nestling diet source

I found strong relationships between agricultural land use and nestling feather isotope values ($\delta^{13}C$ and $\delta^{15}N$), indicating that nestling diet is at least partially derived from agricultural land cover types. Interestingly, this effect was strongest at large scales likely indicating large movements (~2km) of either consumer, prey, or both. Conversely, nestling condition and diet breadth both were affected by landscape at much smaller scales (100-200 m). These results support a realized foraging distance of ~200 m (Turner 1980; McCarty & Winkler 1999; Ambrosini et al. 2002). As discussed above, I speculate that reduced dietary richness in high row crop landscapes may reflect preferential or opportunistic foraging patterns in barn swallows. Differences in scale of effect between isotopes and diet composition suggest a possible filtering of invertebrate prey in landscapes with high amounts of row crop, where less mobile insects are negatively affected by agricultural intensification near the colony. For example, when only richness of dipteran prey was examined, all scale of effect was lost, and there were no detectable effects of agricultural intensification on diet breadth or composition. I interpret this evidence as supporting the idea that prey insects are making major movements, as Diptera are highly mobile (e.g., Froerer et al. 2010) and were the predominant component of nestling diet. I hypothesize that dipteran prey exists as a robust source of highly mobile aerial prey allowing aerial insectivores to mitigate any negative effects of local land use on diet.

4.2. Conservation implications

Populations of Barn Swallows in Canada are declining regionally (Nebel et al. 2010; Michel et al. 2016) and are recognized as being threatened federally in Canada. This research provides evidence that agricultural intensification has little effect on nestling Barn Swallows, from the standpoint of condition and productivity, but may negatively affect nestling diet and, ultimately, adult fitness if adults work harder to provision young in more intensively farmed landscapes. As there was no effect of agricultural intensification on pre-fledging condition, I do not expect any consequences for survival in agriculturally intense areas (Naef-Daenzer et al. 2001; Mitchell et al. 2011; Jones et al. 2016). Consequently, variation in agricultural intensity is not likely contributing to reduced productivity of Barn Swallows breeding in Southern Ontario at contemporary population densities and levels of agricultural intensity (Michel et al. 2016). Despite this, there is still potential risk for agriculturally intense landscapes to be detrimental to breeding aerial insectivores. Intensification of agricultural land use can be accompanied by a loss of open barns and subsequently the loss of entire colonies, which represents a huge loss of productivity to the population (e.g., 4-6 young per brood, 2 broods per breeding pair, and 3-20+ breeding pairs per colony). As Barn Swallows and other aerial insectivorous species provide insect control as an important ecosystem service (Kelly et al. 2013), conserving aerial insectivores within agricultural environments is in the best interest of private landowners and environmental sustainability. Contrary to initial predictions, my recommendation based on these results would be to prevent the loss of breeding sites regardless of agricultural intensity, as my results suggest that productivity is not affected by agricultural intensification, at least to the levels I observed. However, I caution that additional monitoring should take place, especially if population densities of breeding Barn Swallows increase given the possibility of negative density-dependent effects.

4.3. Study assumptions

Rather than comparing a subset of sites at either extreme on the agricultural intensity gradient, I attempted to assess the effect of row crop proportion on diet, condition, and productivity. This allowed us to use a scale of effect analyses to tease out exactly at what scale nestling Barn Swallow traits were predicted by agricultural land use. I assume that this context presents a more realistic landscape composition with a mix of agriculture, semi-natural forages, and small forest patches, although this limits comparison with more extremes of intensity, such as the Canadian prairies where regional trends in Barn Swallow populations are also negative (Michel et al. 2016). One aspect of my study sites in Ontario that might differ from other regions is a lack of wetlands. Wetlands and waterbodies are hypothesized to be important to foraging swallows, especially in times of bad weather (M. Cadman pers. obs.), which may have buffered effects of agricultural intensification in those areas. In Tree Swallows, diet was composed of aquatic emergent prey items regardless of agricultural intensity (Michelson et al. 2018). Although this is peripheral to my hypotheses, it is an important component of swallow foraging ecology and would have been interesting to see how wetlands affected nestling diet in these agro-ecosystems.

Agricultural intensification represents several modern agricultural practices designed to maximize food productivity, including optimizing pesticide and fertilizer inputs as well as homogenizing cropped landscapes to maximize field size (Robinson & Sutherland 2002). For this thesis, I assumed that row crop amount, accounting for the proportion of forage (e.g., Hendrickx et al. 2007), was a suitable index of agricultural intensification. Other indexes have integrated fertilizer inputs, livestock densities, and pesticide amounts into a single index (Herzog et al. 2006). While simple to measure in practice, this approach has limitations, as it cannot account for processes such as pesticide and fertilizer amounts, crop type, connectivity, or field size. Surveying each landowner within 2km of each site (22 sites across two years) to gain information on a field by field basis was logistically not possible for this study system and landowners in this area varied in their willingness to provide such information. Another missing aspect of agricultural intensification from my analyses is extent of livestock. Although livestock presence at the focal barn was included as a predictor in the isotope models, I did not include livestock density in any other landscape model due to logistical difficulties of measuring livestock density at a landscape level. This may have influenced my results, as studies show that livestock presence influences the site selection and reproductive success of breeding Barn Swallows (Ambrosini et al. 2002; Grüebler et al. 2010). Furthermore, livestock farming in Europe is correlated with reduced population declines (Ambrosini et al. 2012). Although, there are components of agricultural intensification that were not accounted for in my index, I am confident that that measure captures landscape-level changes in agricultural intensity.

4.4. Future direction

Future studies should attempt to approach the question of the effects of agricultural intensity on aerial insectivores on smaller, more focused, scales. First, studies should directly quantify aerial insect prey availability while simultaneously focusing on the effects on diet and nestling condition. Few studies have directly assessed agricultural effects on insect prey availability as a mechanism contributing to reduced condition in nestlings of birds (Brickle et al. 2000; Morris et al. 2005; Hart et al. 2006) and none have been conducted on aerial insectivores and aerial prey. A previous study showed no effects of insect availability on fledging success or mass in nestling swallows, but their sites were limited to semi-natural landscapes with little influence of agricultural intensification (Imlay et al. 2017). While my results support no effect of agricultural intensification on nestling condition and success, I did not consider other measures of agricultural intensity in my analyses. Pesticides have been shown to have indirect effects on nestling condition, growth, foraging behaviour, and prey insect availability in other farmland breeding species (Boatman et al. 2004). Furthermore, there is recent concern that neonicotinoid pesticides show strong correlations with aerial insectivore declines (Hallmann et al. 2014). Therefore, pesticide type and amount, should be incorporated in an index of agricultural intensification (see Herzog et al. 2006), as they likely differ among crop type/strain and farming practice.

If nestling condition, success, and dipteran diet are truly independent of agricultural intensification, the relationship between agricultural intensification, parental effort, and condition of adults should be investigated. Unfortunately, I was unable to assign adult Barn Swallows to nests, preventing any measure of parental quality, or effort. Although I found very little evidence for an effect of agricultural intensification influencing nestling condition or fledging success, the cost of reduced prey availability may be to adult condition and survival. Previous studies have shown that adults can increase effort to feed young in habitats with lower prey availability (Schifferli et al. 2014; Stanton et al. 2016), but this comes at a cost to themselves (Saino et al. 1999). In Tree Swallows, studies have shown an overall increase in provisioning rates in agricultural areas (Stanton et al. 2016), in addition to reduced adult body mass and condition (Michelson et al. 2018). In Barn Swallows, no studies have compared foraging and provisioning rates between areas of high and low agricultural intensity. Future studies should assign adults to nests to investigate the effects of agricultural intensification on parental provisioning (foraging distance, time spent foraging, or number of trips) and the consequences for parent condition and survival.

4.5. Conclusions

Ultimately the aim of this research was to inform conservation planning to mitigate agricultural effects on a species at risk living in a human-modified landscape. While continued concern for the long-term effects of agricultural intensification is relevant for many species (Stanton et al. 2018), I provide little evidence of long-term negative repercussions to breeding within agriculturally intense landscapes for the Barn Swallow. Furthermore, I present the first study to find positive effects of agricultural intensification on an aerial insectivorous species. Although I found negative effects of agricultural intensification on nestling diet breadth and evidence that nestlings were provisioned from within agriculturally intense land cover types, it is unclear whether this directly ties to nestling condition or fledging success. Altogether, this research represents an important step towards understanding the complex relationship between agricultural intensification and breeding farmland birds.

4.6. Literature cited

Ambrosini R, Bolzern AM, Canova L, Arieni S, Møller AP, Saino N. 2002. The distribution and colony size of barn swallows in relation to agricultural land use. Journal of Applied Ecology **39**:524–534.

Ambrosini R, Rubolini D, Trovo P, Liberini G, Bandini M, Romano A, Sicurella B, Scandolara C, Romano M, Saino N. 2012. Maintenance of livestock farming may buffer population decline of the Barn Swallow *Hirundo rustica*. Bird Conservation International **22**:411–428.

Boatman ND, Brickle NW, Hart JD, Milsom TP, Morris AJ, Murray AWA, Murray KA, Robertson PA. 2004. Evidence for the indirect effects of pesticides on farmland birds. Ibis **146**:131–143.

Brickle NW, Harper DGC, Aebischer NJ, Cockayne SH. 2000. Effects of agricultural intensification on the breeding success of Corn Buntings *Miliaria calandra*. Journal of Applied Ecology **37**:742–755.

Froerer KM, Peck SL, McQuate GT, Vargas RI, Jang EB, McInnis DO. 2010. Long-distance movement of *Bactrocera dorsalis* (Diptera: Tephritidae) in Puna, Hawaii: how far can they go? American Entomologist **56**:88–95.

Ghilain A, Bélisle M. 2008. Breeding success of Tree Swallows along a gradient of agricultural intensification. Ecological Applications **18**:1140–1154.

Green RE, Cornell SJ, Scharlemann JP, Balmford A. 2005. Farming and the fate of wild nature. Science **307**:550–555.

Grüebler MU, Korner-Nievergelt F, Von Hirschheydt J. 2010. The reproductive benefits of livestock farming in Barn Swallows *Hirundo rustica*: quality of nest site or foraging habitat? Journal of Applied Ecology **47**:1340–1347.

Hallmann CA, Foppen RP, van Turnhout CA, de Kroon H, Jongejans E. 2014. Declines in insectivorous birds are associated with high neonicotinoid concentrations. Nature **511**:341–343.

Hart J, Milsom T, Fisher G, Wilkins V, Moreby S, Murray A, Robertson P. 2006. The relationship between Yellowhammer breeding performance, arthropod abundance and insecticide applications on arable farmland. Journal of Applied Ecology **43**:81–91.

Hendrickx F, Maelfait J, Van Wingerden W, Schweiger O, Speelmans M, Aviron S, Augenstein I, Billeter R, Bailey D, Bukacek R. 2007. How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. Journal of Applied Ecology **44**:340–351.

Herzog F et al. 2006. Assessing the intensity of temperate European agriculture at the landscape scale. European Journal of Agronomy **24**:165–181.

Imlay TL, Mann HAR, Leonard ML. 2017. No effect of insect abundance on nestling survival or mass for three aerial insectivores. Avian Conservation and Ecology **12**:19.

Jones TM, Ward MP, Benson TJ, Brawn JD. 2016. Variation in nestling body condition and wing development predict cause-specific mortality in fledgling Dickcissels. Journal of Avian Biology **48**:439–447.

Kelly JF, Bridge ES, Frick WF, Chilson PB. 2013. Ecological energetics of an abundant aerial insectivore, the Purple Martin. PLOS ONE **8**:e76616.

Konarzewski M, Kowalczyk J, Swierubska T, Lewonczuk B. 1996. Effect of short-term feed restriction, realimentation and overfeeding on growth of Song Thrush (*Turdus philomelos*) nestlings. Functional Ecology **10**:97–105.

McCarty JP, Winkler DW. 1999. Foraging ecology and diet selectivity of Tree Swallows feeding nestlings. The Condor **101**:246–254.

Michel NL, Smith AC, Clark RG, Morrissey CA, Hobson KA. 2016. Differences in spatial synchrony and interspecific concordance inform guild-level population trends for aerial insectivorous birds. Ecography **39**:774–786.

Michelson CI, Clark RG, Morrissey CA. 2018. Agricultural land cover does not affect the diet of Tree Swallows in wetland-dominated habitats. The Condor **120**:751–764.

Mitchell GW, Guglielmo CG, Wheelwright NT, Freeman-Gallant CR, Norris DR. 2011. Early life events carry over to influence pre-migratory condition in a free-living songbird. PLOS ONE **6**:e28838.

Morris AJ, Wilson JD, Whittingham MJ, Bradbury RB. 2005. Indirect effects of pesticides on breeding Yellowhammer (*Emberiza citrinella*). Agriculture, Ecosystems and Environment **106**:1–16.

Naef-Daenzer B, Widmer F, Nuber M. 2001. Differential post-fledging survival of Great and Coal Tits in relation to their condition and fledging date. Journal of Animal Ecology **70**:730–738.

Nebel S, Mills A, McCracken JD, Taylor PD. 2010. Declines of aerial insectivores in North America follow a geographic gradient. Avian Conservation and Ecology **5**:1.

Robinson RA, Sutherland WJ. 2002. Post-war changes in arable farming and biodiversity in Great Britain. Journal of Applied Ecology **39**:157–176.

Saino N, Calza S, Ninni P, Møller AP. 1999. Barn Swallows trade survival against offspring condition and immunocompetence. Journal of Animal Ecology **68**:999–1009.

Schifferli L, Grüebler MU, Meijer HAJ, Visser GH, Naef-Daenzer B. 2014. Barn Swallow *Hirundo rustica* parents work harder when foraging conditions are good. Ibis **156**:777–787.

Searcy WA, Peters S, Nowicki S. 2004. Effects of early nutrition on growth rate and adult size in Song Sparrows *Melospiza melodia*. Journal of Avian Biology **35**:269–279.

Stanton RL, Morrissey CA, Clark RG. 2016. Tree Swallow (*Tachycineta bicolor*) foraging responses to agricultural land use and abundance of insect prey. Canadian Journal of Zoology **94**:637–642.

Stanton RL, Morrissey CA, Clark RG. 2018. Analysis of trends and agricultural drivers of farmland bird declines in North America: a review. Agriculture, Ecosystems and Environment **254**:244–254.

Turner AK. 1980. The use of time and energy by aerial feeding birds. PhD Thesis. University of Stirling.

Twining CW, Brenna JT, Lawrence P, Shipley JR, Tollefson TN, Winkler DW. 2016. Omega-3 long-chain polyunsaturated fatty acids support aerial insectivore performance more than food quantity. Proceedings of the National Academy of Sciences **113**:10920–10925.

Appendix A. Summary tables

Table A1. Location of sites, with year-specific information on landscape composition (within 100 m) and colony size. A buffer radius of 100 m was the strongest radius for two of four response variables (nestling condition, pre-fledging condition). Asterisks (*) indicate sites that were sampled in the marked year but dropped from all condition and success models. Site information (colony size and landscape variables) for dropped sites was not included, as they were not included in any analyses.

				2016			2017		
Site	Latitude	Longitude	Year	Colony Size	Row crop (%)	Forage (%)	Colony Size	Row crop (%)	Forage (%)
BH	43.55628	-80.1838	2016/2017	6	28.79	45.46	13	27.78	50.00
CK	43.76947	-80.2154	2016/2017	18	39.13	60.87	20	50.00	44.12
CT	43.55891	-80.1118	2016/2017	12	3.08	96.92	10	8.11	91.89
FF	43.70984	-80.2893	2016/2017	3	4.62	58.46	5	2.86	54.29
FL	43.56922	-80.1788	2016/2017*	30	0	98.43	-	-	-
FS	43.69639	-80.2828	2016/2017	15	13.24	66.18	14	0	70.59
GL	43.60413	-80.2649	2016	9	13.64	74.24	-	-	-
HI	43.69939	-80.2795	2016/2017	16	2.94	88.24	14	5.41	89.19
HM	43.75192	-80.1494	2016/2017	17	0	94.12	24	0	97.22
MF	43.58908	-80.1975	2016/2017	22	16.18	75.00	25	52.78	33.33
MO	43.73864	-80.1959	2016/2017	3	0	100.00	3	0	100.00
MS	43.79508	-80.228	2016/2017	7	0	94.01	11	0	91.43
NE	43.79886	-80.2338	2016/2017	19	28.36	71.64	20	32.43	67.57
OL	43.7437	-80.1497	2016*/2017	-	-	-	14	0	88.57
OS	43.60244	-80.1985	2016/2017	13	68.12	31.88	13	100.00	0
PE	43.66417	-80.2851	2016/2017	47	0	43.94	37	0	47.06
RW	43.60669	-80.1246	2016/2017	5	0	98.48	7	0	97.22
SH	43.5197	-80.1258	2016/2017	2	0	76.12	4	0	77.78
SU	43.71665	-80.3388	2016/2017	2	48.48	51.52	3	58.33	41.67
SZ	43.5444	-80.1351	2016/2017	9	40.30	58.21	11	31.43	68.57
VV	43.81656	-80.4326	2017	-	-	-	12	96.88	0
WE	43.52476	-80.11	2016/2017	16	0	70.15	16	0	66.67

Table A2. Summary statistics for mass, wing length, and breeding statistics, separated by age and brood number, for Barn Swallows breeding near Guelph Ontario in the 2016 and 2017. Hatch dates (ordinal dates), clutch sizes, and fledged numbers are only reported for nests that survived until hatch.

		2016		2017		Both	
		n	Mean (SD)	n	Mean (SD)	n	Mean (SD)
Day eight	Mass (g)	547	17.22 (2.45)	1286	16.52 (2.21)	1833	16.73 (2.31)
	Wing (mm)		37.74 (6.36)		43.53 (4.89)		35.49 (5.57)
Day 15	Mass (g)	364	19.85 (1.62)	420	20.34 (1.95)	784	20.11 (1.82)
	Wing (mm)		74.62 (4.94)		72.59 (5.00)		73.53 (5.07)
Brood one	Hatch date (ordinal)	140	167 (6)	217	166 (7)	357	166 (7)
	Clutch size		5.06 (0.83)		5.00 (0.77)		5.03 (0.79)
	Fledging number		4.31 (1.41)		4.28 (1.27)		4.29 (1.33)
Brood two	Hatch date (ordinal)	96	206 (9)	95	211 (6)	191	209 (8)
	Clutch size		4.33 (0.83)		4.15 (0.64)		4.24 (0.74)
	Fledging number		3.53 (1.09)		3.47 (1.18)		3.50 (1.13)

Appendix B. Scale of effect figures for nestling condition

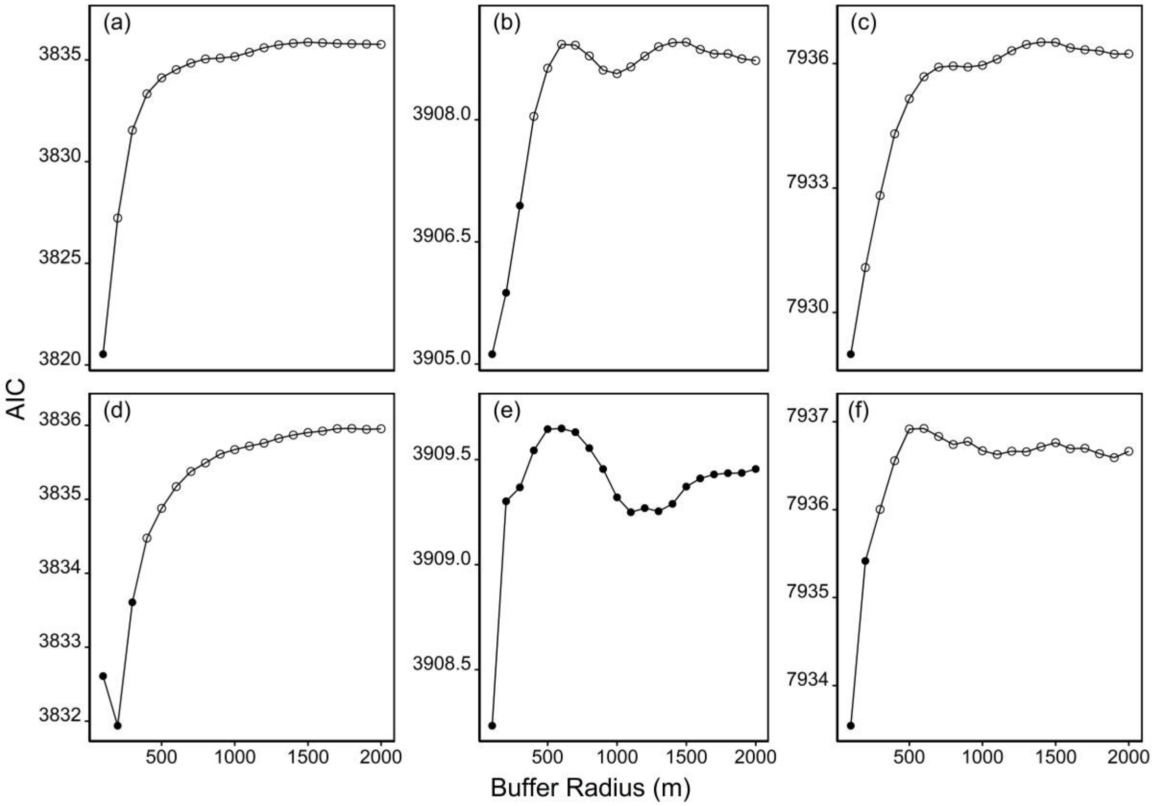


Figure B1. The effect of scale on the relationship between Barn Swallow nesting (day 6 - 10) mass and (a-c) row crop proportion or (d-f) forage amount, showing AIC values resulting from LMMs using landscape data captured using a specified buffer radius (x-axis). Plots are separated by year (a,d – 2016, b,e – 2017, c,f – 2016/2017. Filled points indicate models that are competitive with the best model (i.e., AIC values within 2.0 AIC of the lowest AIC model).

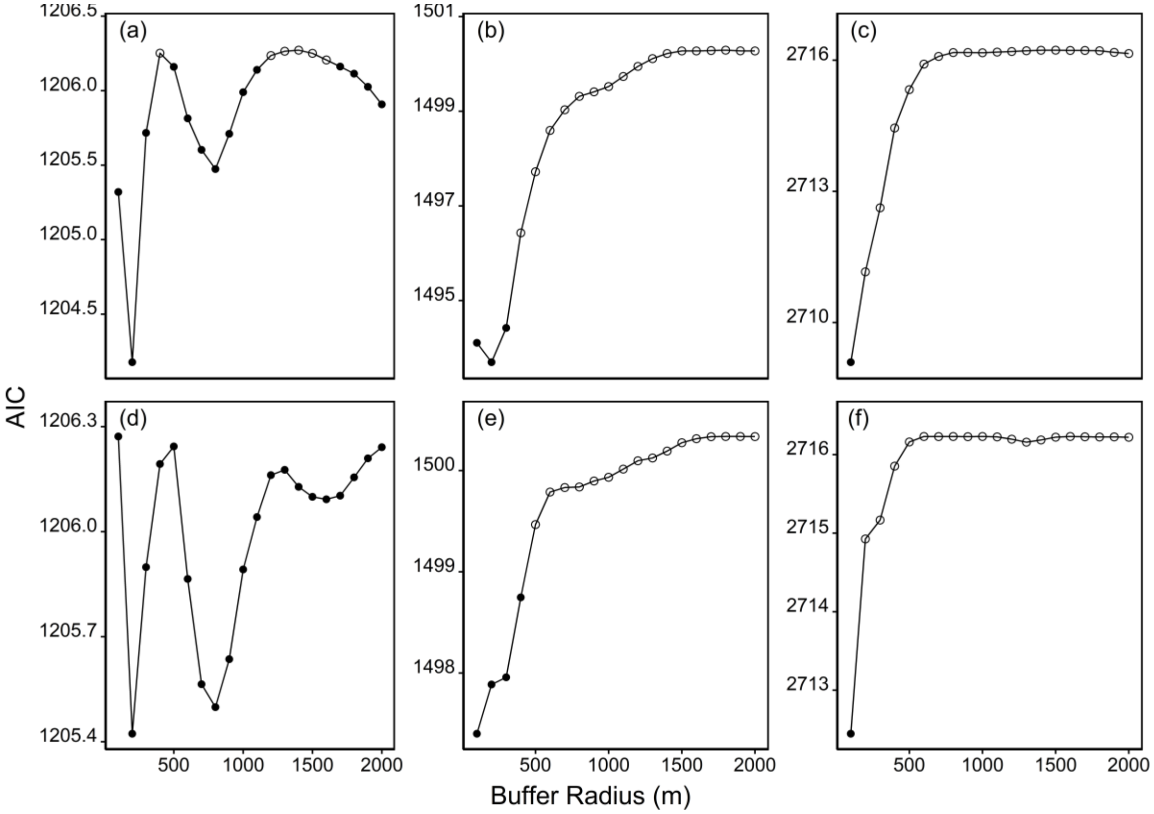


Figure B2. The effect of scale on the relationship between Barn Swallow pre-fledging (day 15) mass and (a-c) row crop proportion or (d-f) forage amount, showing AIC values resulting from LMMs using landscape data captured using a specified buffer radius (x-axis). Plots are separated by year (a,d – 2016, b,e – 2017, c,f – 2016/2017). Filled points indicate models that are competitive with the best model (i.e., AIC values within 2.0 AIC of the lowest AIC model).

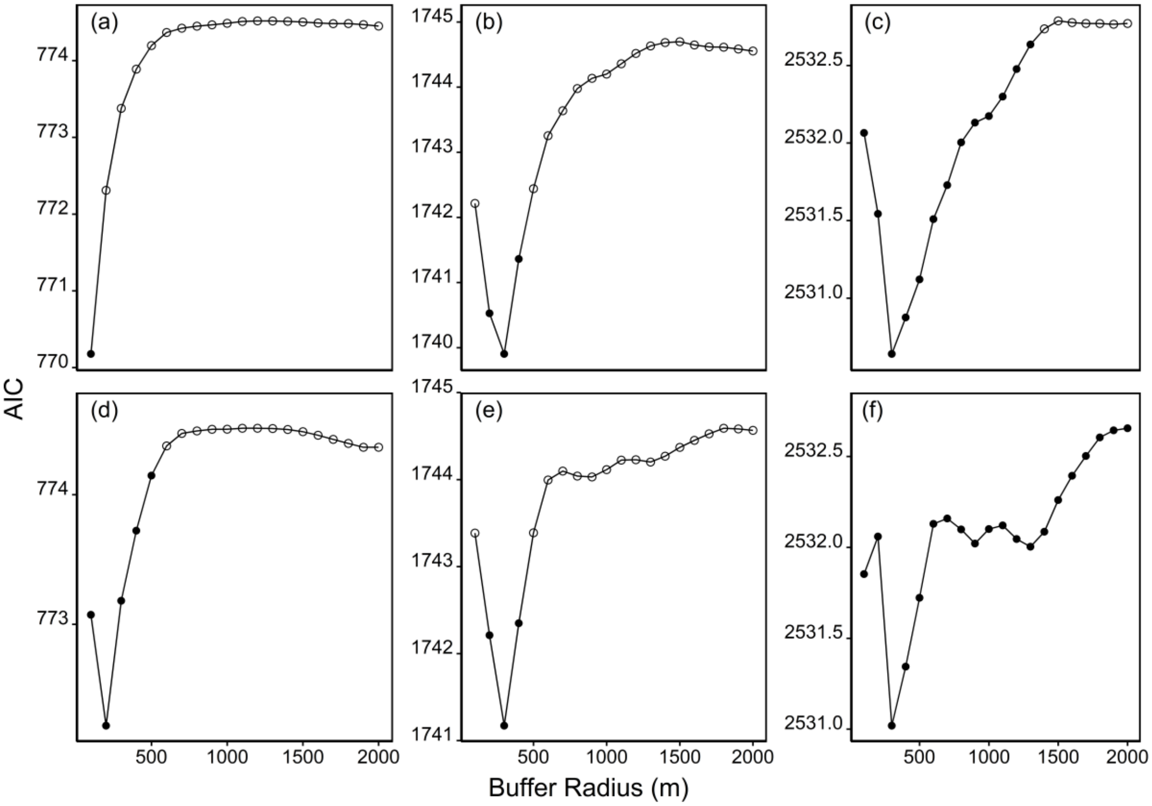


Figure B3. The effect of scale on the relationship between Barn Swallow nestling growth (change in mass between day 8 and 15) and (a-c) row crop proportion or (d-f) forage amount, showing AIC values resulting from LMMs using landscape data captured using a specified buffer radius (x-axis). Plots are separated by year (a,d – 2016, b,e – 2017, c,f – 2016/2017). Filled points indicate models that are competitive with the best model (i.e., AIC values within 2.0 AIC of the lowest AIC model).

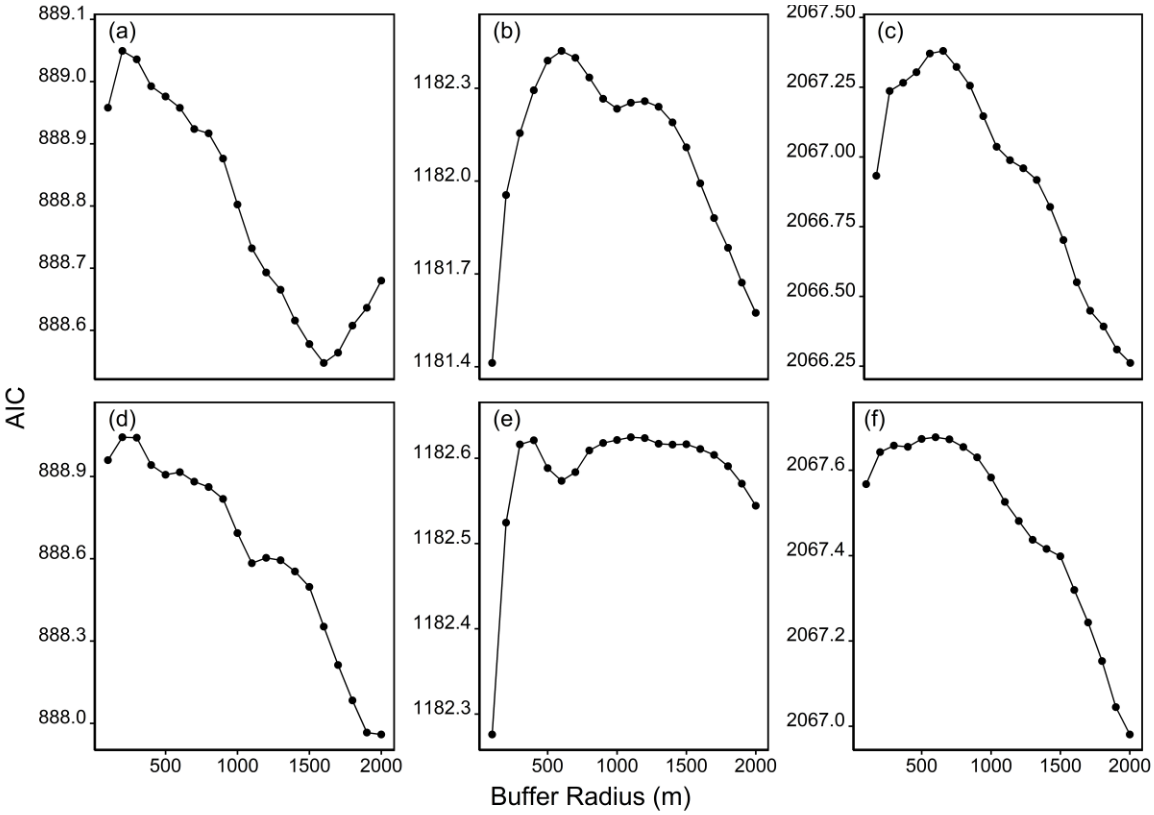


Figure B4. The effect of scale on the relationship between Barn Swallow fledging success and (a-c) row crop proportion or (d-f) forage amount, showing AIC values resulting from GMLMs using landscape data captured using a specified buffer radius (x-axis). Plots are separated by year (a,d – 2016, b,e – 2017, c,f – 2016/2017). Filled points indicate models that are competitive with the best model (i.e., AIC values within 2.0 AIC of the lowest AIC model).

Appendix C. Relationship between nestling mass and structural size

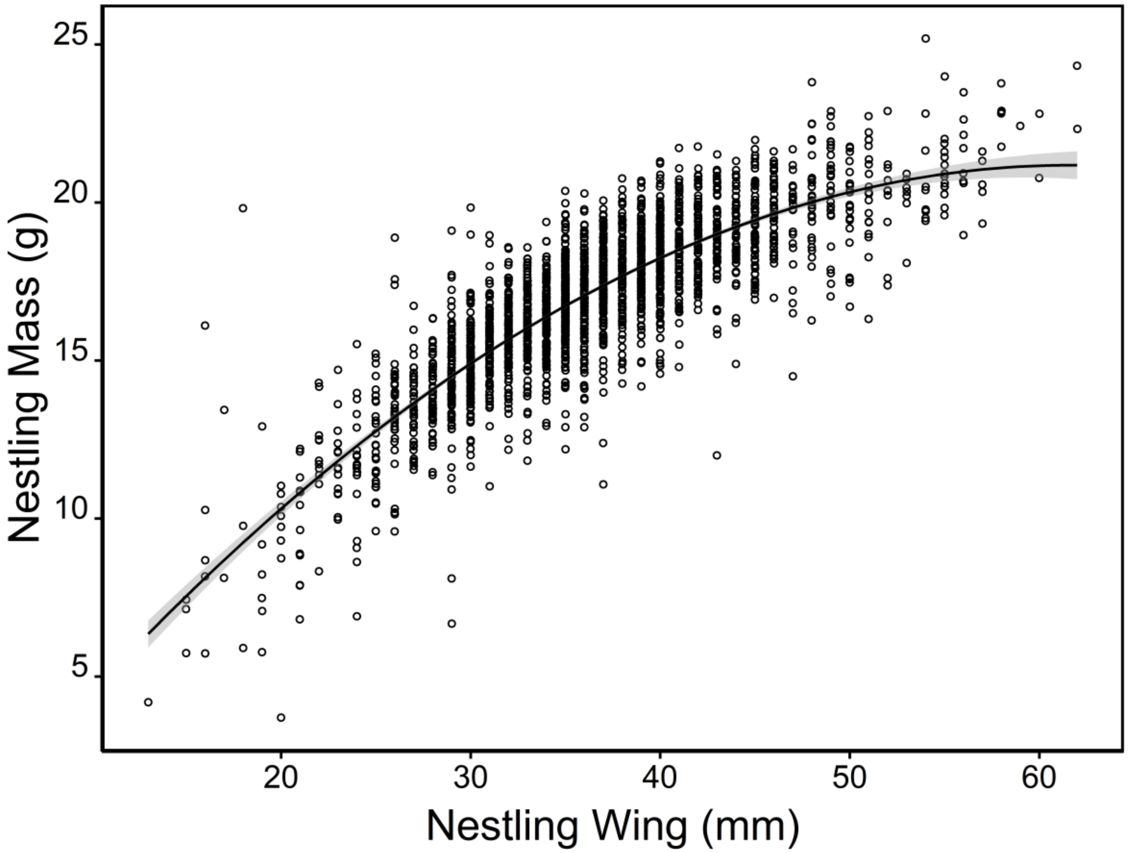


Figure C1. Scatterplot of nestling mass (g) plotted against nestling wing (mm). Line with shaded area indicates curvilinear equation ($y = x + x^2$) with standard error.

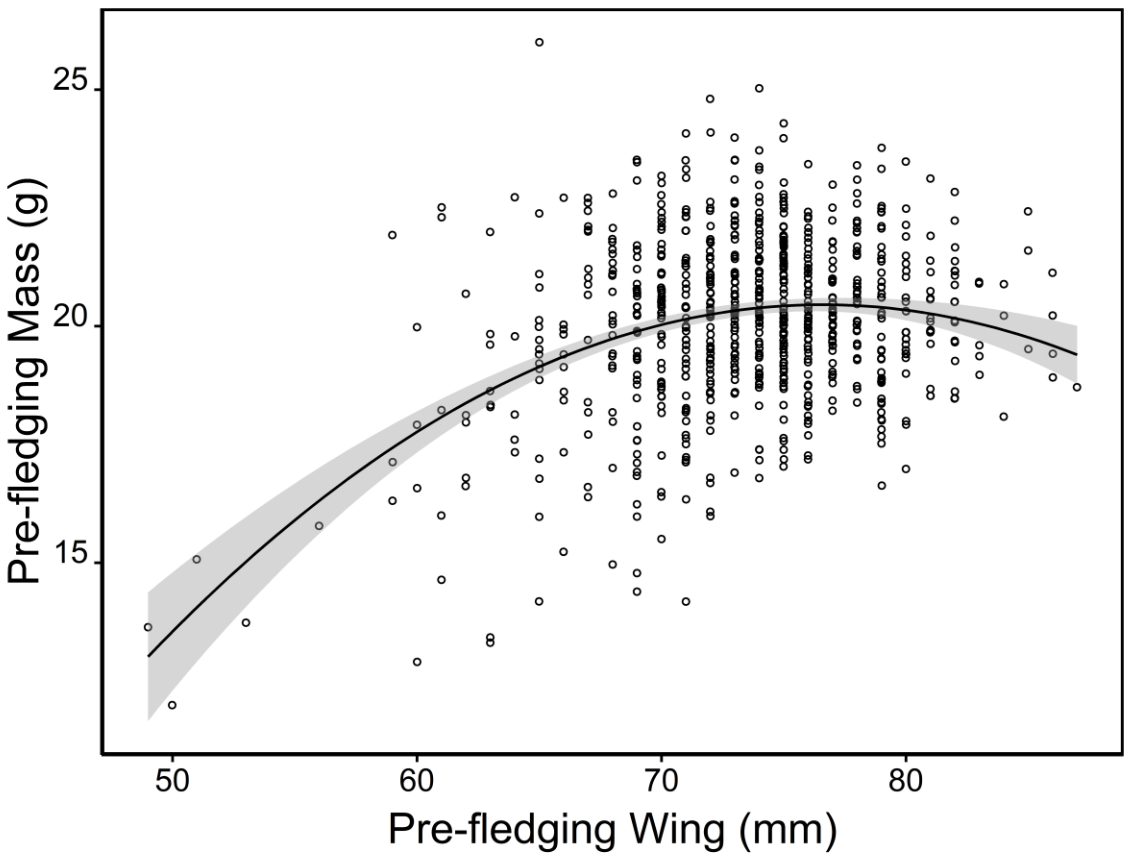


Figure C2. Scatterplot of pre-fledging mass (g) plotted against pre-fledging wing (mm). Line with shaded area indicates curvilinear equation ($y = x + x^2$) with standard error.

Appendix D. DNA barcoding protocol

Detailed methods were provided by the Canadian Center for DNA Barcoding. Samples were vortexed in a 15 mL tube containing 2 ceramic beads, and DNA was extracted using 5 mL ProK mixture and insect lysis buffer. The resulting mixture was incubated at 56°C overnight. A 50 µL subsample was mixed with 100 µL of binding mix and transferred to a glass fibre plate, washed with 180 µL of protein wash buffer followed by 750 µL of wash buffer and then eluted in 40 µL of elution buffer. Samples were amplified separately, using insect-specific primers targeting a 157 basepair region of the mitochondrial gene cytochrome c oxidase I (COI; Zeale et al. 2011). For each plate (96-wells), the processed samples were tagged using 12 forward multiplex identifier (MID) tags and 8 reverse MID tags. Once tagged, the samples were amplified using PCR. The PCR mixture consisted of 2 µL of DNA, 2 µL of dH 2 O, 0.625 µL 50 nM MgCl 2, 6.25 µL of 10% trehalose, 1.25 µL of 10X buffer, 0.125 µL of 10µM of each the forward and reverse primer, 0.0625 µL of 10 µM dNTP, and 0.06 µL of Platinum Taq (5U/µL). PCR was conducted at 94°C for 2 mins, followed by 60 cycles of 30s at 94°C, 30s at 53°C and 30s at 72°C, followed by a final extension of 5 min at 72°C and then held at 10°C. Amplicons were visualized using 4 µL on an E-Gel (Thermo Fisher Scientific). PCR products for each plate were pooled and amplicons were purified using magnetic bead protocol outlined in (Prosser & Hebert 2017) using double-size selection to purify for the target amplicon length (~284 bp). After cleaning, the amplified product was quantified using a Qubit 2.0 fluorometer (Thermo Fisher Scientific) and adjusted to 1 ng µL -1. In 2016, the sequencing library was prepared by templating and enriching with the Ion OneTouch 2 System (Thermo Fisher Scientific). In 2017, the sequencing library was automatically prepared by templating using an Ion Chef platform (Thermo Fisher Scientific). The library was sequenced using a 316 v.2 chip on an Ion Torrent PGM (Thermo Fisher Scientific) in 2016, and a 530 chip on an Ion Torrent S5 high-throughput sequencer (Thermo Fisher Scientific) in 2017.

Literature Cited

Prosser SWJ, Hebert PDN. 2017. Rapid identification of the botanical and entomological sources of honey using DNA metabarcoding. Food Chemistry **214**:183–191.

Zeale MR, Butlin RK, Barker GL, Lees DC, Jones G. 2011. Taxon-specific PCR for DNA barcoding arthropod prey in bat faeces. Molecular Ecology Resources **11**:236–244.

Appendix E. Diet summary

Table E1. Comprehensive summary of all detected arthropod prey items, across all samples. Low-quality reads were removed along with identifications less than 100 reads per sample, as a conservative approach. Species names are reported precisely as output from the BLAST results. *Freq* is the frequency of detection and *Reads* is the total number of reads during sequencing, across all samples and years, that were grouped into the reported taxonomic identification. This table summarizes 389 species, 252 genera, 99 families, and 12 orders.

Class	Order	Family	Species	*Freq*	*Reads*
Arachnida	Araneae	Araneidae	*Eustala anastera*	1	354
			Neoscona arabesca	1	267
		Salticidae	*Phidippus clarus*	1	607
		Theridiidae	*Parasteatoda tabulata*	1	619
Diplopoda	Julida	Julidae	*Julus scandinavius*	2	593
Insecta	Coleoptera	Anthribidae	*Anthribus nebulosus*	1	1109
		Carabidae	*Agonum bicolor*	1	193
			Amara eurynota	4	47923
			Amara littoralis	2	1994
			Amara sinuosa	9	82134
			Bembidion versicolor	1	375
			Bembidion mimus	1	283
			Bembidion obtusum	1	1012
			Bembidion quadrimaculatum	1	895
			Dromius piceus	1	29301
			Dyschirius erythrocerus	1	841
			Dyschirius larochellei	2	360
		Cerambycidae	*Callimoxys sanguinicollis*	1	277
			Lepturges confluens	1	178
			Tetrops praeusta	1	9714
		Chrysomelidae	*Dibolia borealis*	2	1610
			Oulema melanopus	14	72392
			Systena frontalis	1	2146
			Galerucinae sp.	1	116
		Curculionidae	*Hylesinus aculeatus*	1	227
			Hypera postica	8	5718
			Hypera meles	3	1569
			Phyllobius oblongus	9	20906
			Polydrusus formosus	7	41176
			Rhinoncus bruchoides	1	257
			Scolytus multistriatus	3	66033
			Sitona hispidulus	34	408828
			Tychius picirostris	2	16677
			Curculionidae sp.	6	7204
		Dermestidae	*Anthrenus scrophulariae*	1	2675
			Dermestes frischii	1	491
		Dytiscidae	*Hydrocolus rubyae*	1	1496

	Elateridae	*Dalopius pallidus*	1	220
	Histeridae	*Euspilotus assimilis*	1	5151
	Hydrophilidae	*Cercyon haemorrhoidalis*	20	36869
		Helophorus nitiduloides	1	209
		Sphaeridium scarabaeoides	7	5117
		Hydrophilidae sp.	1	106
	Nitidulidae	*Fabogethes nigrescens*	2	374
	Ptinidae	*Hemicoelus carinatus*	4	14340
		Ptinidae sp.	2	542
	Ripiphoridae	*Ripiphorus fasciatus*	4	26361
	Scarabaeidae	*Onthophagus nuchicornis*	2	23714
	Scirtidae	*Cyphon variabilis*	2	3463
	Staphylinidae	*Aleochara verna*	2	18543
		Carpelimus sp.	1	206
		Lithocharodes longicollis	1	6972
		Tachinus jacuticus jacuticus	1	239
		Tachyporus sp.	4	16653
		Xantholinus linearis	1	199
		Staphylinidae sp.	1	116
	Tetratomidae	*Tetratomidae sp.*	2	308
Diptera	Acroceridae	*Acroceridae sp.*	1	130
	Anthomyiidae	*Alliopsis fractiseta*	1	631
		Delia florilega	36	69581
		Delia pilifemur	1	124
		Delia platura	19	38652
		Delia sp.	8	2131
		Eustalomyia festiva	1	2243
		Fucellia sp.	1	123
		Hylemyza partita	1	204
		Lasiomma sp.	2	1826
		Lasiomma cuneicorne	1	144
		Pegoplata infirma	1	263
		Zaphne implicata	1	110
		Anthomyiinae sp.	1	367
		Anthomyiidae sp.	1	631
	Asilidae	*Dioctria sp.*	34	368138
		Asilidae sp.	3	27993
	Bibionidae	*Dilophus femoratus*	1	3271
	Bolitophilidae	*Bolitophila austriaca*	1	101
	Bombyliidae	*Systropus macer*	1	135
		Villa lateralis	1	251
	Calliphoridae	*Calliphora coloradensis*	1	608
		Calliphora livida	1	897
		Calliphora loewi	1	251
		Calliphora vomitoria	5	1444
		Calliphora montana	2	799
		Lucilia illustris	9	2529
		Lucilia sp.	2	470
		Melanomya bicolor	2	1626
		Phormia regina	17	14805
		Pollenia griseotomentosa	16	47640
		Pollenia pediculata	97	332948
		Pollenia rudis	3	518
		Pollenia labialis	1	4694
	Cecidomyiidae	*Cecidomyiinae sp.*	1	189
		Cecidomyiidae sp.	9	3585

Ceratopogonidae	*Forcipomyia sp.*	1	1298
	Ceratopogonidae sp.	1	127
Chironomidae	*Chironomus acidophilus*	1	303
	Chironomus sp.	1	234
	Cryptochironomus sp.	1	334
	Limnophyes minimus	1	143
	Orthocladius sp.	1	293
	Procladius sp.	2	651
	Chironominae sp.	2	426
	Tanypodinae sp.	1	285
	Chironomidae sp.	1	272
Chloropidae	*Oscinella sp.*	1	220
	Thaumatomyia trifasciata	2	448
	Trachysiphonella sp.	1	151
	Chloropidae sp.	2	25303
Culicidae	*Aedes cinereus*	2	2228
	Aedes fitchii	3	7859
	Aedes japonicus	1	118
	Aedes provocans	7	5496
	Aedes vexans	3	2938
	Aedes tahoensis	1	230
	Aedes sp.	4	1376
	Anopheles quadrimaculatus	1	139
	Coquillettidia perturbans	2	2457
	Culex sp.	2	1303
	Culicinae sp.	5	1284
	Culicidae sp.	2	1296
Cylindrotomidae	*Cylindrotomidae sp.*	2	14504
Dolichopodidae	*Chrysotus sp.*	1	210
	Dolichopus plumipes	2	903
	Hydrophorus chrysologus	1	133
	Sympycnus lineatus	8	9636
	Dolichopodidae sp.	2	1196
	Diaphorinae sp.	1	109
Drosophilidae	*Drosophila affinis*	3	10441
	Drosophila funebris	1	160
	Drosophila suzukii	1	1977
	Drosophila subquinaria	1	141
	Scaptomyza pallida	3	14775
Empididae	*Anthepiscopus sp.*	1	132
	Rhamphomyia longicauda	2	2035
Ephydridae	*Psilopa leucostoma*	3	963
	Ephydridae sp.	1	316
Fanniidae	*Fannia atra*	1	193
	Fannia americana	1	3430
	Fannia sp.	3	2082
Hybotidae	*Ocydromia sp.*	1	1278
	Platypalpus sp.	1	208
	Hybotidae sp.	1	113
Limoniidae	*Antocha saxicola*	2	21938
	Dicranomyia frontalis	1	1085
	Dicranomyia sp.	29	35523
	Dicranophragma sp.	1	162
	Euphylidorea platyphallus	5	21955
	Geranomyia sp.	2	8423
	Helius flavipes	1	135

	Limnophila sp.	1	113
	Metalimnobia solitaria	1	186
	Ormosia affinis	2	2652
	Pilaria tenuipes	1	47921
	Pseudolimnophila inornata	2	64749
	Pseudolimnophila luteipennis	4	16187
	Limoniidae sp.	59	352945
Milichiidae	*Leptometopa latipes*	2	1553
Muscidae	*Coenosia tigrina*	1	282
	Gymnodia humilis	2	446
	Hebecnema nigra	1	580
	Hebecnema umbratica	2	5593
	Helina depuncta	11	6603
	Helina troene	1	1022
	Helina sp.	3	1143
	Hydrotaea aenescens	3	3369
	Hydrotaea pilitibia	2	460
	Macrorchis ausoba	1	2032
	Morellia podagrica	1	109
	Musca autumnalis	4	837
	Muscina flukei	2	598
	Muscina levida	6	3727
	Muscina pascuorum	2	321
	Muscina sp. 1 AKR	1	840
	Mydaea detrita	2	412
	Myospila meditabunda	7	2811
	Neodexiopsis rufitibia	1	389
	Pentacricia aldrichii	1	196
	Stomoxys calcitrans	15	19011
Mycetophilidae	*Mycetophila sp.*	1	116
Mycetophilidae	*Mycetophilidae sp.*	4	1000
Pediciidae	*Tricyphona sp.*	1	433
Phoridae	*Diplonevra nitidula*	1	191
Pipunculidae	*Elmohardyia sp. AZ3*	1	800
	Pipunculus sp. ON15	10	35071
Platystomatidae	*Rivellia steyskali*	2	1916
Psychodidae	*PschodididGC sp. 1*	1	1503
Psychodidae	*Psychoda sp.*	1	157
Psychodidae	*Psychodidae sp.*	1	318
Rhagionidae	*Rhagio tringarius*	6	6072
Sarcophagidae	*Amobia sp.*	1	163
	Boettcheria latisterna	2	3434
	Helicobia rapax	1	11434
	Macronychia sp.	2	2832
	Metopia sp.	1	207
	Ravinia acerba	4	20091
	Ravinia querula	10	82779
	Ravinia stimulans	7	29973
	Ravinia sp.	16	42692
	Sarcophaga aldrichi	2	470
	Sarcophaga caerulescens	12	39145
	Sarcophaga crassipalpis	1	6373
	Sarcophaga polistensis	2	2517
	Sarcophaga subvicina	25	125225
	Sarcotachinella sinuata	2	9531
	Sarcophaginae sp.	1	4174

	Sarcophagidae sp.	6	3050
Scathophagidae	*Scathophaga stercoraria*	12	15137
Sciaridae	*Bradysia pallipes*	1	156
	Mouffetina pulchricornis	1	368
Sepsidae	*Sepsis neocynipsea*	1	1021
	Sepsis punctum	15	12055
	Themira minor	2	12652
Simuliidae	*Simulium decorum*	2	1507
	Simulium verecundum complex	3	5475
Sphaeroceridae	*Copromyza equina*	2	421
	Lotophila atra	3	6662
	Minilimosina parva	1	540
	Sphaerocera curvipes	4	2065
	Sphaeroceridae sp.	1	143
Stratiomyidae	*Allognosta fuscitarsis*	5	6948
	Beris fuscipes	1	204
	Odontomyia cincta	1	278
	Odontomyia virgo	2	1264
	Stratiomys obesa	2	393
	Stratiomyidae sp.	1	1722
Syrphidae	*Chrysogaster antitheus*	1	19635
	Eristalis transversa	1	3941
	Eristalis sp.	1	2295
	Eupeodes sp.	3	786
	Melanostoma sp.	1	675
	Orthonevra nitida	1	825
	Parhelophilus laetus	1	202
	Platycheirus unknown sp. 1	1	287
	Platycheirus sp.	6	7648
	Sericomyia chrysotoxoides	1	411
	Sphaerophoria sp.	2	1445
	Syritta pipiens	4	9452
	Syrphus knabi	4	2015
	Syrphus ribesii	5	3399
	Syrphus torvus	3	2209
	Syrphus sp.	13	10694
	Temnostoma barberi	1	300
	Toxomerus geminatus	5	4157
	Xylota quadrimaculata	2	522
Tabanidae	*Hybomitra epistates*	25	77691
	Hybomitra illota	1	1694
	Hybomitra lasiophthalma	27	29625
	Hybomitra lurida	3	1267
	Hybomitra minuscula	2	284
	Hybomitra frosti	2	1203
	Hybomitra sodalis	2	4632
	Hybomitra sp.	6	5548
	Tabanus similis	15	9607
	Tabanus novaescotiae	2	4410
	Tabanus sp.	3	497
	Tabaninae sp.	3	386
	Tabanidae sp.	2	211
Tachinidae	*Admontia sp.*	1	4538
	Archytas californiae	3	41429
	Archytas apicifer	1	117

	Archytas instabilis	1	111
	Archytas metallicus	1	2564
	Belvosia Woodley17	59	963130
	Blondelia hyphantriae	2	584
	Chaetogaedia townsendi	1	222
	Chaetogaedia sp.	7	1636
	Cryptomeigenia sp.	1	349
	Dinera grisescens	3	20022
	Epalpus signifer	2	2759
	Euexorista rebaptizata	2	738
	Eumea sp.	4	3027
	Exorista larvarum	1	1893
	Exorista dydas	1	198
	Gymnoclytia occidua	1	118
	Houghia coccidella	1	555
	Hubneria sp.	1	854
	Leschenaultia nr. sp. Z	3	861
	Leschenaultia fulvipes	8	7718
	Lespesia datanarum	2	1595
	Lespesia sp.	1	1786
	Linnaemya sp.	6	1713
	Loewia foeda	1	667
	Myxexoristops bonsdorffi	10	3542
	Oswaldia assimilis	1	1990
	Oswaldia minor	1	115
	Patelloa sp.	1	66006
	Phorocera exigua	1	281
	Platymya sp.	4	10671
	Prooppia crassiseta	1	145
	Pseudopachystylum debile	1	1154
	Ptilodexia conjuncta	1	466
	Strongygaster sp.	1	250
	Tachinomyia nigricans	3	5148
	Uramya pristis	1	2266
	Winthemia illinoiensis	3	2465
	Winthemia rufopicta	55	259206
	Winthemia sinuata	12	12350
	Winthemia sminthurae	4	33801
	Winthemia sp.	26	12927
	Exoristinae sp.	6	1478
	Tachinidae sp.	71	886907
Tephritidae	*Rhagoletis suavis*	1	107
	Urophora quadrifasciata	2	299
	Urophora cardui	1	4382
Therevidae	*Therevidae sp.*	2	12143
Tipulidae	*Angarotipula illustris*	23	213472
	Ctenophora sp.	2	5665
	Nephrotoma alterna	3	10056
	Nephrotoma eucera	3	3537
	Nephrotoma ferruginea	35	169998
	Tipula bicolor	3	819
	Tipula duplex	1	554
	Tipula johnsoniana	2	6979
	Tipula penobscot	1	5695
	Tipula sayi	1	138
	Tipula hermannia	3	10349

		Tipulinae sp.	1	706
		Tipulidae sp.	4	7681
	Ulidiidae	*Physiphora demandata*	3	7525
		Diptera sp.	26	24115
Ephemeroptera	Ephemeridae	*Hexagenia atrocaudata*	1	6115
Hemiptera	Aphrophoridae	*Philaenus spumarius*	5	6419
	Clastopteridae	*Clastoptera obtusa*	1	358
	Corixidae	*Callicorixa audeni*	1	708
	Miridae	*Lygus lineolaris*	13	29385
	Miridae	*Neolygus tinctus*	1	105
	Pentatomidae	*Neottiglossa undata*	1	209
	Rhyparochromidae	*Megalonotus sabulicola*	1	1325
Hymenoptera	Braconidae	*Macrocentrus sp.*	1	137
	Braconidae	*Meteorus sp.*	2	779
	Cynipidae	*Cynipidae sp.*	1	199
	Diprionidae	*Diprion similis*	2	851
		Gilpinia hercyniae	1	697
	Figitidae	*Figitinae sp.*	1	185
		Figitidae sp.	9	25685
Hymenoptera	Ichneumonidae	*Bathyplectes curculionis*	5	6045
		Campoletis flavicincta	1	538
		Diplazon laetatorius	2	4182
		Enizemum cf. ornatum	1	161
		Mesochorus americanus	1	5950
		Mesochorus sp.	2	944
		Ophion keala	1	582
		Triclistus sp.	1	6573
		Tromatobia ovivora	1	230
		Tromatobia sp.	1	297
		Tryphon seminiger	7	33973
		Campopleginae sp.	1	180
		Cryptinae sp.	1	209
		Ctenopelmatinae sp.	1	17143
		Ichneumoninae sp.	1	208
	Perilampidae	*Perilampus chrysopae*	1	483
	Sierolomorphidae	*Sierolomorpha sp.*	2	5753
	Tenthredinidae	*Dolerus elderi elderi*	2	489
Lepidoptera	Argyresthiidae	*Argyresthia canadensis*	1	382
	Crambidae	*Chrysoteuchia topiarius*	1	170
		Neodactria luteolellus	1	18405
		Parapediasia teterrellus	1	797
		Sitochroa palealis	1	747
	Erebidae	*Lymantria dispar dispar*	1	153
		Orgyia leucostigma	1	1169
		Palthis angulalis	1	1142
	Geometridae	*Chlorochlamys chloroleucaria*	1	1160
		Eupithecia miserulata	2	842
		Pasiphila rectangulata	7	29784
	Hepialidae	*Pharmacis lupulina*	1	106
	Hesperiidae	*Anatrytone logan*	2	656
		Ancyloxypha numitor	1	1631
		Polites mystic	4	27113
		Polites peckius	5	9237
		Polites themistocles	1	651
		Thymelicus lineola	2	8546
	Lasiocampidae	*Tolype dayi*	1	169

	Noctuidae	*Apamea sordens*	1	106
		Apamea devastator	2	3824
		Neoligia exhausta	1	859
		Tricholita signata	1	150
	Nymphalidae	*Coenonympha tullia*	2	440
	Sesiidae	*Synanthedon pini*	1	24244
	Tineidae	*Tinea columbariella*	1	12711
	Tortricidae	*Cnephasia asseclana*	2	746
		Cochylis hoffmanana	1	110
		Platynota semiustana PS2	1	107
	Ypsolophidae	*Ochsenheimeria sp.*	2	1089
Odonata	Aeshnidae	*Rhionaeschna multicolor*	1	3127
	Coenagrionidae	*Enallagma sp.*	1	2476
Siphonaptera	Ceratophyllidae	*Ceratophyllidae sp.*	1	431
Trichoptera	Hydroptilidae	*Hydroptilidae sp.*	1	557
	Leptoceridae	*Triaenodes nox*	1	255
	Polycentropodidae	*Polycentropus confusus*	1	140

Appendix F. Scale of effect figures for nestling diet

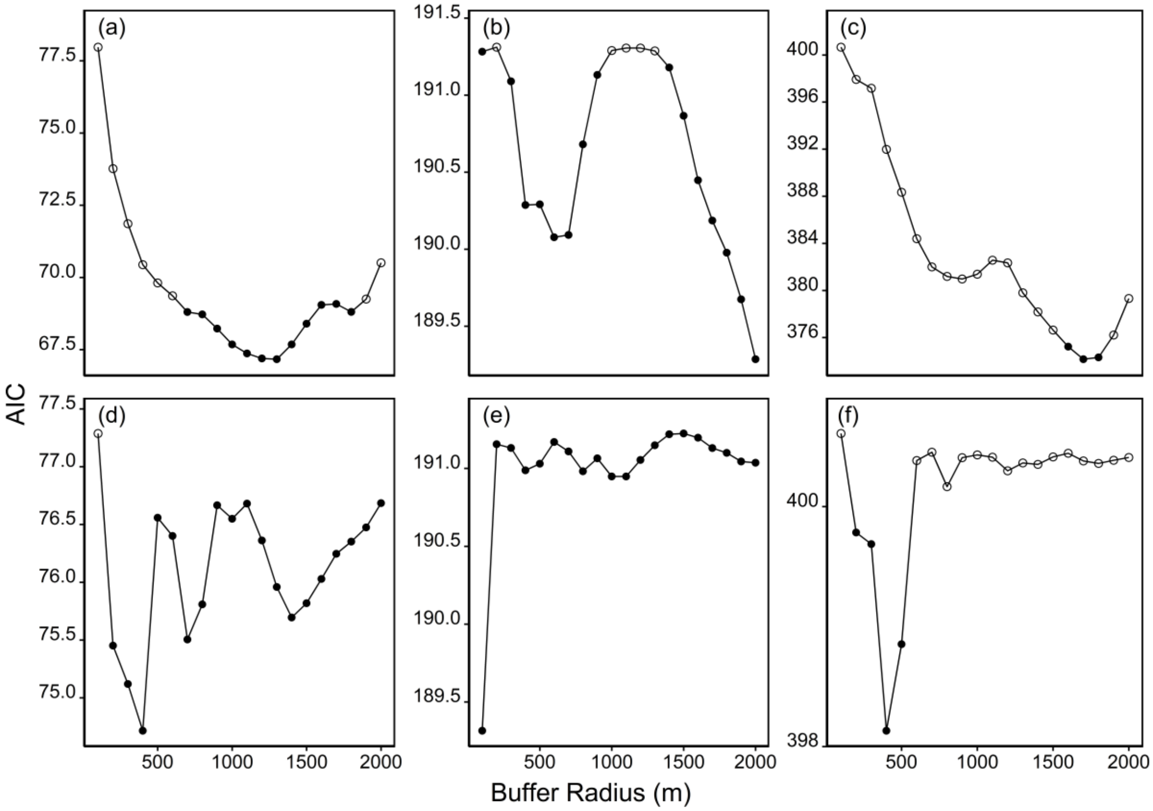


Figure F1. The effect of scale on the relationship between δ^{13}C values in Barn Swallow nestling feathers and the proportion of corn (a-c) and the proportion of water (d-f). Plots show AIC values resulting from linear mixed effects models using landscape data from different buffer radii (x-axis). Plots are separated by year (a and d – 2016, b and e – 2017, c and f – 2016/2017). Filled points indicate models that are competitive with the best model (i.e., AIC values within 2.0 AIC of the lowest AIC model).

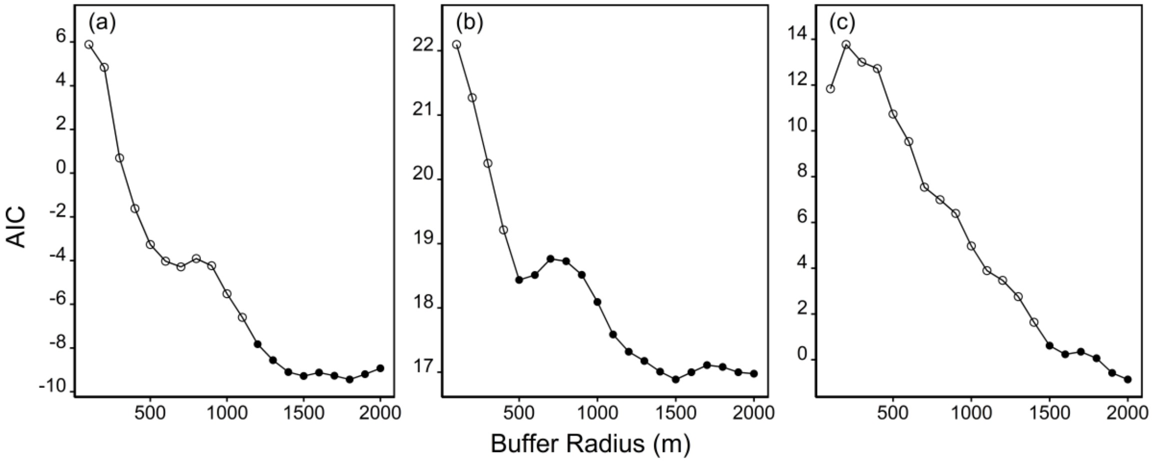


Figure F2. The effect of scale on the relationship between δ^{15}N values in Barn Swallow nestling feathers and the proportion of row crop (a-c). Plots show AIC values resulting from linear mixed effects models using landscape data from different buffer radii (x-axis). Plots are separated by year (a – 2016, b – 2017, c – 2016/2017). Filled points indicate models that are competitive with the best model (i.e., AIC values within 2.0 AIC of the lowest AIC model).

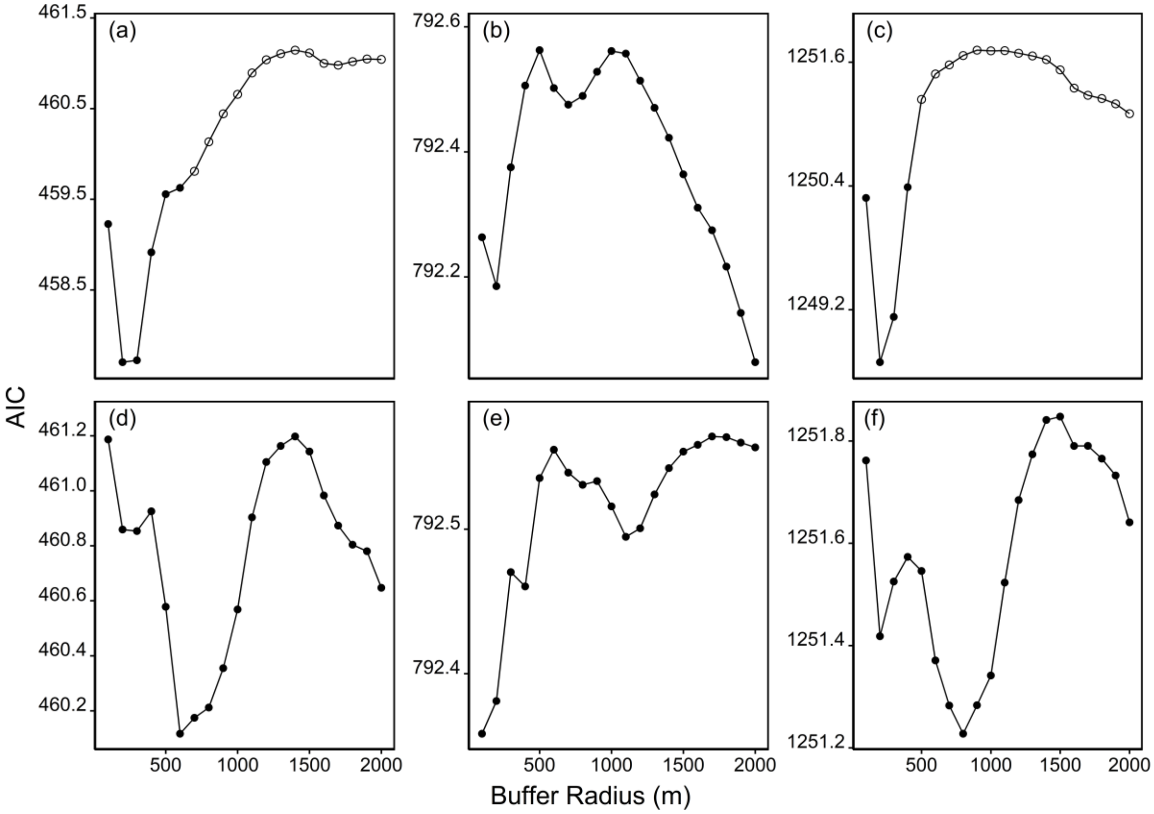


Figure F3. The effect of scale on the relationship between Barn Swallow nestling diet breadth, as detected by DNA barcoding of nestling feces, and the proportion of row crop (a-c) and forage (d-f). Plots show AIC values resulting from linear mixed effects models using landscape data from different buffer radii (x-axis). Plots are separated by year (a,d – 2016, b,e – 2017, c,f – 2016/2017). Filled points indicate models that are competitive with the best model (i.e., AIC values within 2.0 AIC of the lowest AIC model).

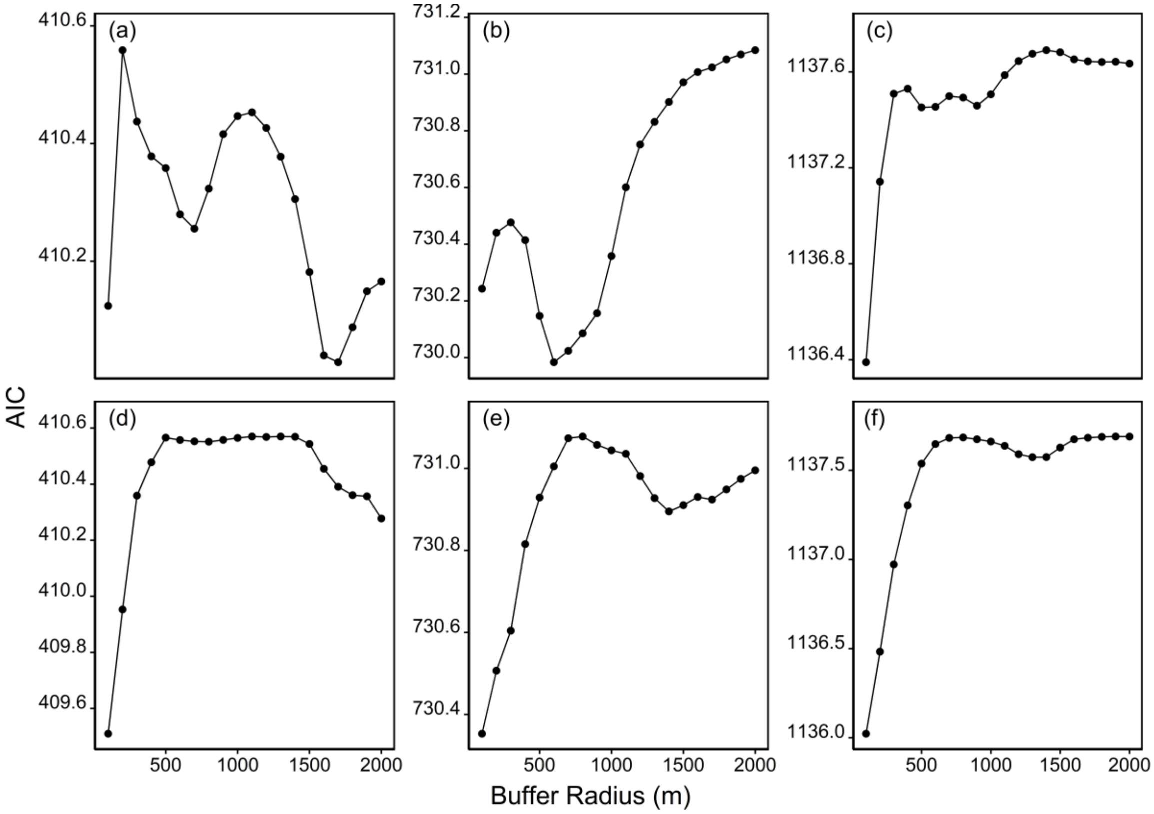
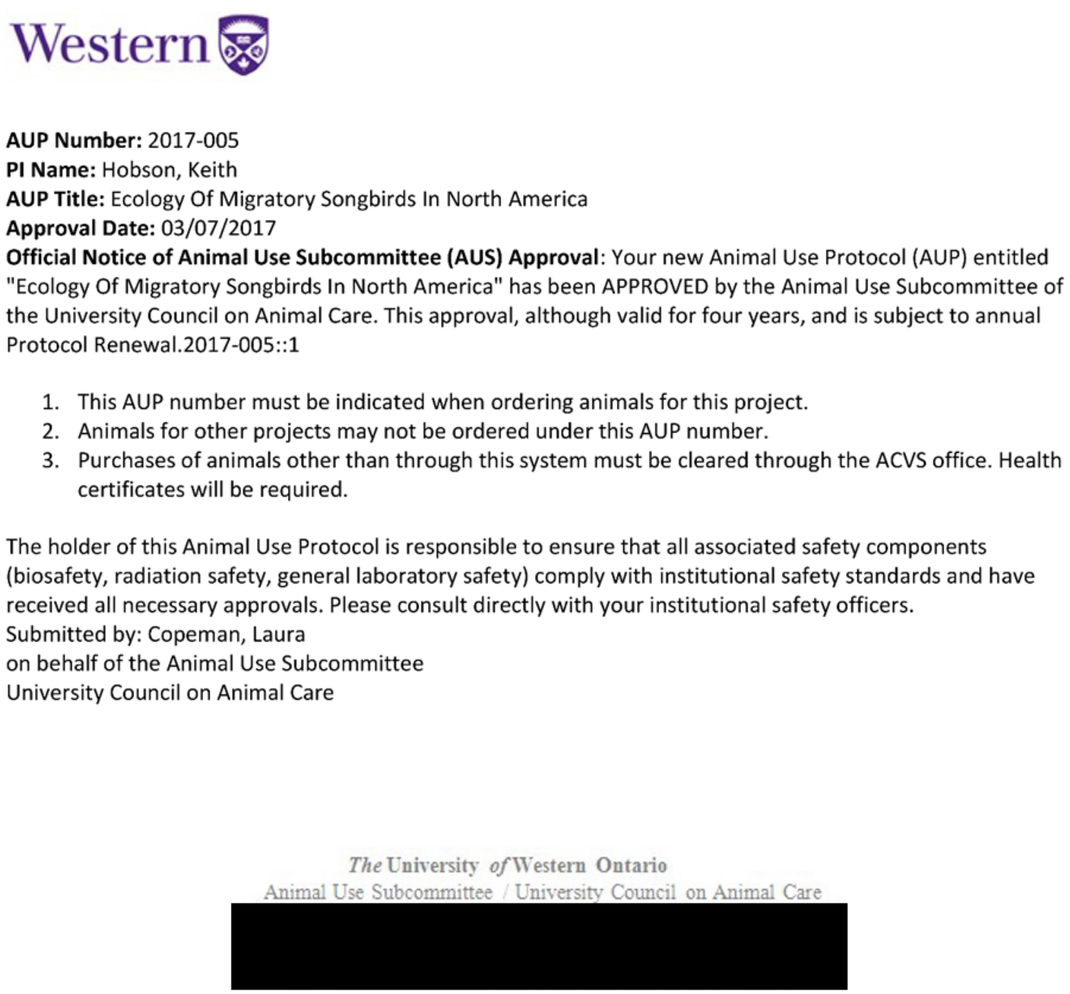


Figure F4. The effect of scale on the relationship between Barn Swallow nestling Diptera diet breadth, as detected by DNA barcoding of nestling feces, and the proportion of row crop (a-c) and forage (d-f). Plots show AIC values resulting from linear mixed effect models using landscape data from different buffer radii (x-axis). Plots are separated by year (a,d – 2016, b,e – 2017, c,f – 2016/2017). Filled points indicate models that are competitive with the best model (i.e., AIC values within 2.0 AIC of the lowest AIC model).

Appendix G. Animal use protocol approval



Western

AUP Number: 2017-005
PI Name: Hobson, Keith
AUP Title: Ecology Of Migratory Songbirds In North America
Approval Date: 03/07/2017
Official Notice of Animal Use Subcommittee (AUS) Approval: Your new Animal Use Protocol (AUP) entitled "Ecology Of Migratory Songbirds In North America" has been APPROVED by the Animal Use Subcommittee of the University Council on Animal Care. This approval, although valid for four years, and is subject to annual Protocol Renewal.2017-005::1

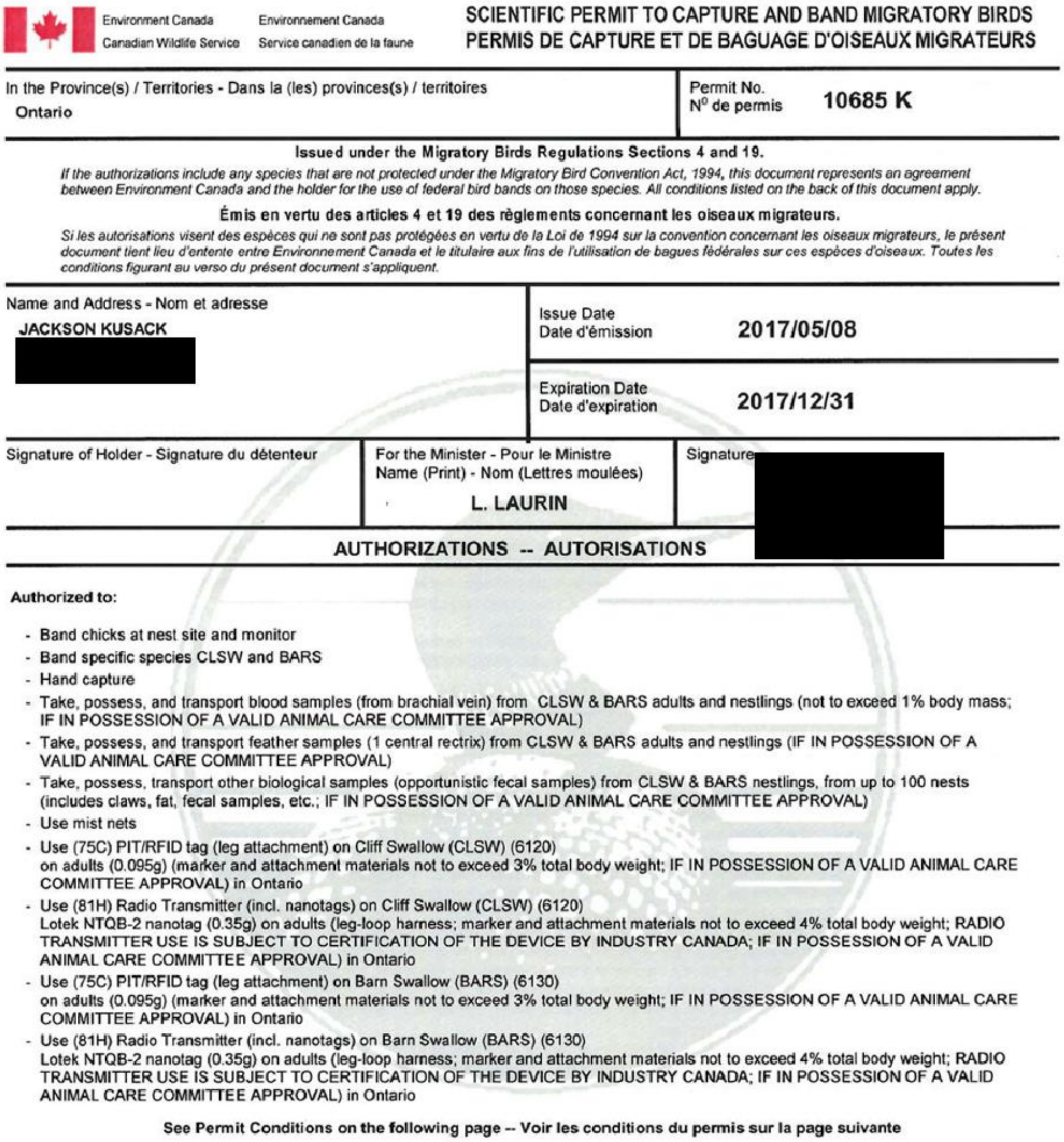
1. This AUP number must be indicated when ordering animals for this project.
2. Animals for other projects may not be ordered under this AUP number.
3. Purchases of animals other than through this system must be cleared through the ACVS office. Health certificates will be required.

The holder of this Animal Use Protocol is responsible to ensure that all associated safety components (biosafety, radiation safety, general laboratory safety) comply with institutional safety standards and have received all necessary approvals. Please consult directly with your institutional safety officers.
Submitted by: Copeman, Laura
on behalf of the Animal Use Subcommittee
University Council on Animal Care

The University *of* Western Ontario
Animal Use Subcommittee / University Council on Animal Care

[redacted]

Appendix H. Sub-banding permit



Environment Canada / Environnement Canada
Canadian Wildlife Service / Service canadien de la faune

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

In the Province(s) / Territories - Dans la (les) provinces(s) / territoires
Ontario

Permit No. / Nº de permis **10685 K**

Issued under the Migratory Birds Regulations Sections 4 and 19.

If the authorizations include any species that are not protected under the Migratory Bird Convention Act, 1994, this document represents an agreement between Environment Canada and the holder for the use of federal bird bands on those species. All conditions listed on the back of this document apply.

Émis en vertu des articles 4 et 19 des règlements concernant les oiseaux migrateurs.

Si les autorisations visent des espèces qui ne sont pas protégées en vertu de la Loi de 1994 sur la convention concernant les oiseaux migrateurs, le présent document tient lieu d'entente entre Environnement Canada et le titulaire aux fins de l'utilisation de bagues fédérales sur ces espèces d'oiseaux. Toutes les conditions figurant au verso du présent document s'appliquent.

Name and Address - Nom et adresse
JACKSON KUSACK
[redacted]

Issue Date / Date d'émission 2017/05/08

Expiration Date / Date d'expiration 2017/12/31

Signature of Holder - Signature du détenteur

For the Minister - Pour le Ministre
Name (Print) - Nom (Lettres moulées)
L. LAURIN

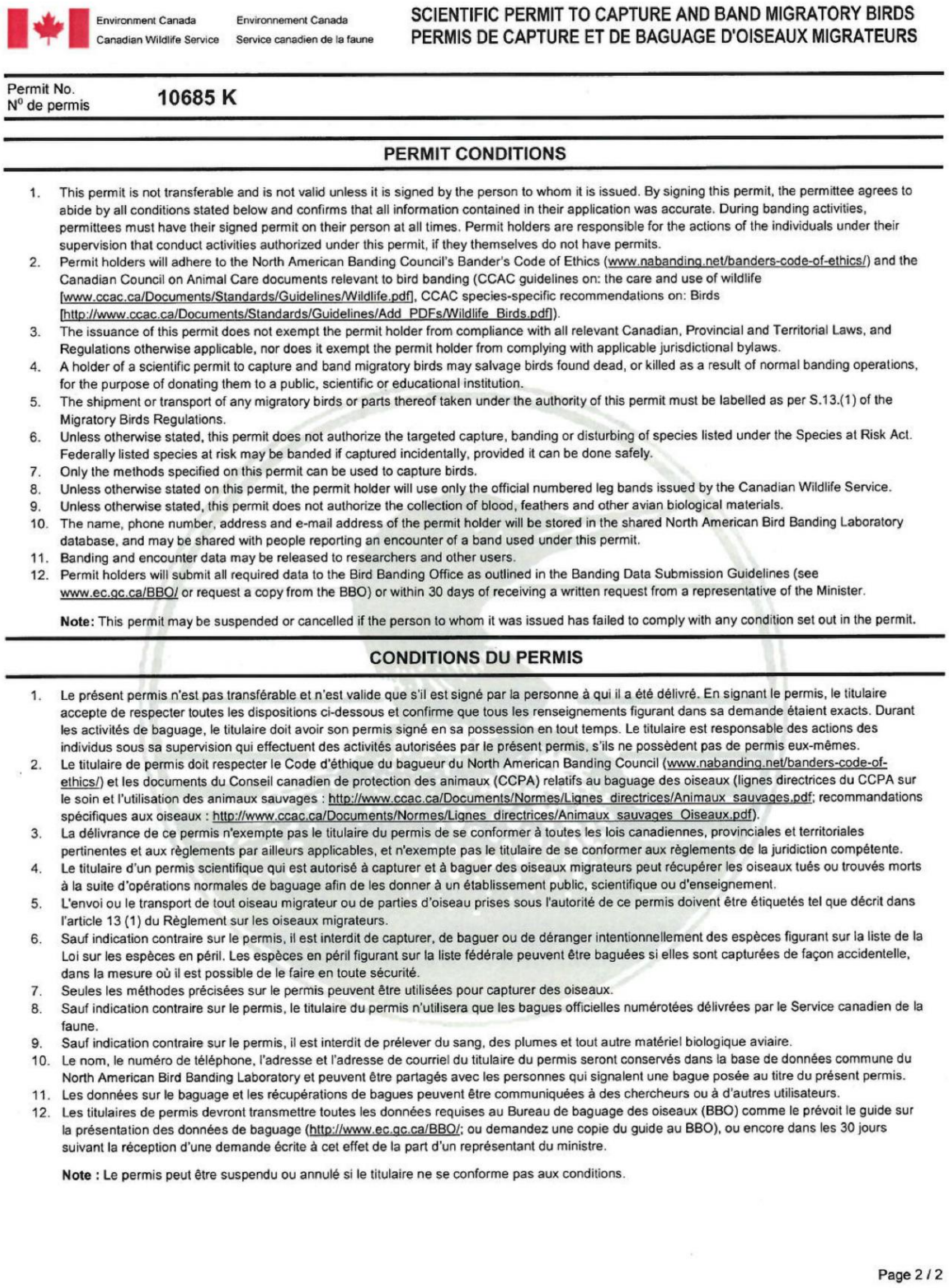
Signature [redacted]

AUTHORIZATIONS -- AUTORISATIONS

Authorized to:

- Band chicks at nest site and monitor
- Band specific species CLSW and BARS
- Hand capture
- Take, possess, and transport blood samples (from brachial vein) from CLSW & BARS adults and nestlings (not to exceed 1% body mass; IF IN POSSESSION OF A VALID ANIMAL CARE COMMITTEE APPROVAL)
- Take, possess, and transport feather samples (1 central rectrix) from CLSW & BARS adults and nestlings (IF IN POSSESSION OF A VALID ANIMAL CARE COMMITTEE APPROVAL)
- Take, possess, transport other biological samples (opportunistic fecal samples) from CLSW & BARS nestlings, from up to 100 nests (includes claws, fat, fecal samples, etc.; IF IN POSSESSION OF A VALID ANIMAL CARE COMMITTEE APPROVAL)
- Use mist nets
- Use (75C) PIT/RFID tag (leg attachment) on Cliff Swallow (CLSW) (6120)
  on adults (0.095g) (marker and attachment materials not to exceed 3% total body weight; IF IN POSSESSION OF A VALID ANIMAL CARE COMMITTEE APPROVAL) in Ontario
- Use (81H) Radio Transmitter (incl. nanotags) on Cliff Swallow (CLSW) (6120)
  Lotek NTQB-2 nanotag (0.35g) on adults (leg-loop harness; marker and attachment materials not to exceed 4% total body weight; RADIO TRANSMITTER USE IS SUBJECT TO CERTIFICATION OF THE DEVICE BY INDUSTRY CANADA; IF IN POSSESSION OF A VALID ANIMAL CARE COMMITTEE APPROVAL) in Ontario
- Use (75C) PIT/RFID tag (leg attachment) on Barn Swallow (BARS) (6130)
  on adults (0.095g) (marker and attachment materials not to exceed 3% total body weight; IF IN POSSESSION OF A VALID ANIMAL CARE COMMITTEE APPROVAL) in Ontario
- Use (81H) Radio Transmitter (incl. nanotags) on Barn Swallow (BARS) (6130)
  Lotek NTQB-2 nanotag (0.35g) on adults (leg-loop harness; marker and attachment materials not to exceed 4% total body weight; RADIO TRANSMITTER USE IS SUBJECT TO CERTIFICATION OF THE DEVICE BY INDUSTRY CANADA; IF IN POSSESSION OF A VALID ANIMAL CARE COMMITTEE APPROVAL) in Ontario

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



Environment Canada Environnement Canada
Canadian Wildlife Service Service canadien de la faune

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

Permit No.
N^o de permis **10685 K**

PERMIT CONDITIONS

1. This permit is not transferable and is not valid unless it is signed by the person to whom it is issued. By signing this permit, the permittee agrees to abide by all conditions stated below and confirms that all information contained in their application was accurate. During banding activities, permittees must have their signed permit on their person at all times. Permit holders are responsible for the actions of the individuals under their supervision that conduct activities authorized under this permit, if they themselves do not have permits.
2. Permit holders will adhere to the North American Banding Council's Bander's Code of Ethics (www.nabanding.net/banders-code-of-ethics/) and the Canadian Council on Animal Care documents relevant to bird banding (CCAC guidelines on: the care and use of wildlife [www.ccac.ca/Documents/Standards/Guidelines/Wildlife.pdf], CCAC species-specific recommendations on: Birds [http://www.ccac.ca/Documents/Standards/Guidelines/Add_PDFs/Wildlife_Birds.pdf]).
3. The issuance of this permit does not exempt the permit holder from compliance with all relevant Canadian, Provincial and Territorial Laws, and Regulations otherwise applicable, nor does it exempt the permit holder from complying with applicable jurisdictional bylaws.
4. A holder of a scientific permit to capture and band migratory birds may salvage birds found dead, or killed as a result of normal banding operations, for the purpose of donating them to a public, scientific or educational institution.
5. The shipment or transport of any migratory birds or parts thereof taken under the authority of this permit must be labelled as per S.13.(1) of the Migratory Birds Regulations.
6. Unless otherwise stated, this permit does not authorize the targeted capture, banding or disturbing of species listed under the Species at Risk Act. Federally listed species at risk may be banded if captured incidentally, provided it can be done safely.
7. Only the methods specified on this permit can be used to capture birds.
8. Unless otherwise stated on this permit, the permit holder will use only the official numbered leg bands issued by the Canadian Wildlife Service.
9. Unless otherwise stated, this permit does not authorize the collection of blood, feathers and other avian biological materials.
10. The name, phone number, address and e-mail address of the permit holder will be stored in the shared North American Bird Banding Laboratory database, and may be shared with people reporting an encounter of a band used under this permit.
11. Banding and encounter data may be released to researchers and other users.
12. Permit holders will submit all required data to the Bird Banding Office as outlined in the Banding Data Submission Guidelines (see www.ec.gc.ca/BBO/ or request a copy from the BBO) or within 30 days of receiving a written request from a representative of the Minister.

Note: This permit may be suspended or cancelled if the person to whom it was issued has failed to comply with any condition set out in the permit.

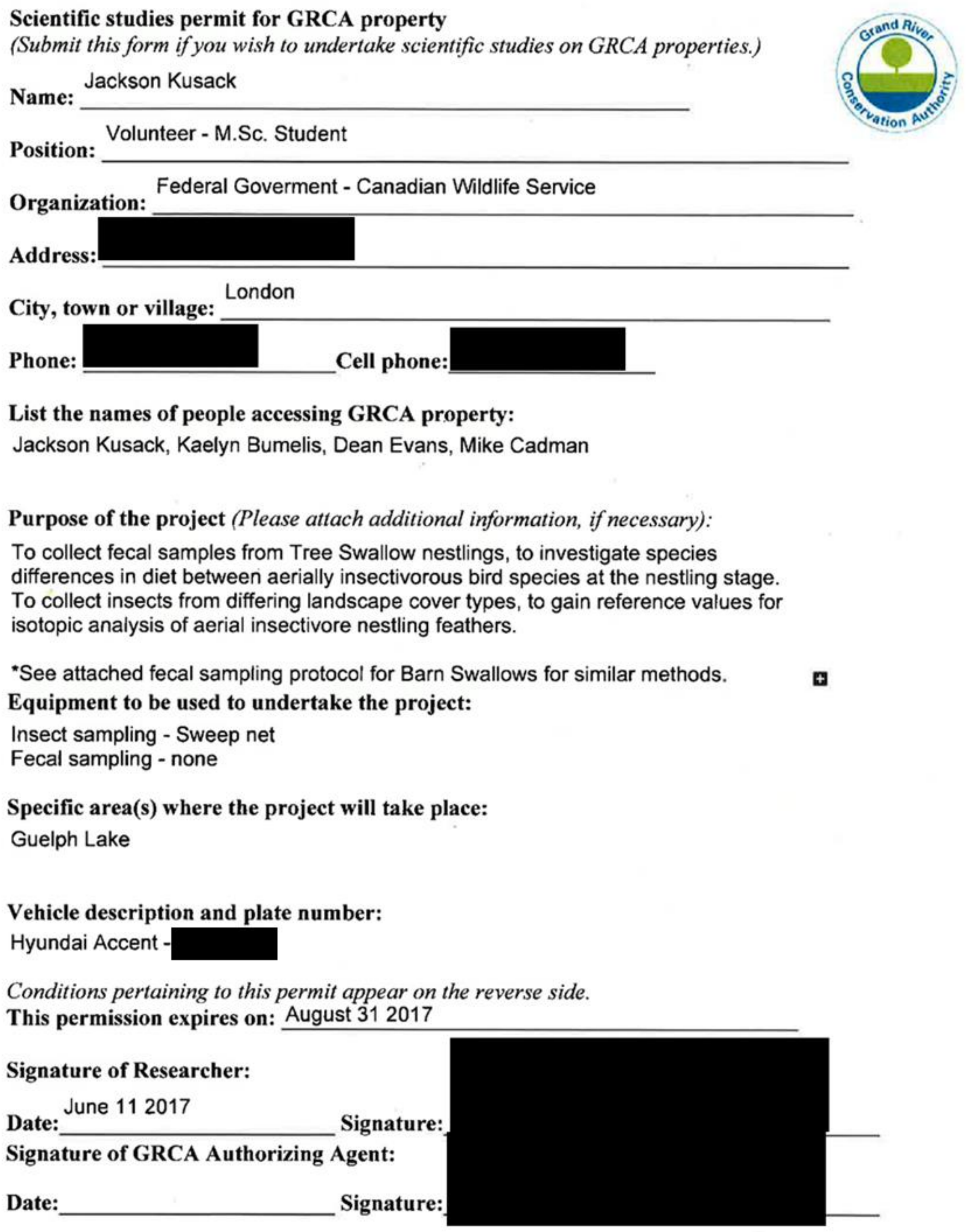
CONDITIONS DU PERMIS

1. Le présent permis n'est pas transférable et n'est valide que s'il est signé par la personne à qui il a été délivré. En signant le permis, le titulaire accepte de respecter toutes les dispositions ci-dessous et confirme que tous les renseignements figurant dans sa demande étaient exacts. Durant les activités de baguage, le titulaire doit avoir son permis signé en sa possession en tout temps. Le titulaire est responsable des actions des individus sous sa supervision qui effectuent des activités autorisées par le présent permis, s'ils ne possèdent pas de permis eux-mêmes.
2. Le titulaire de permis doit respecter le Code d'éthique du bagueur du North American Banding Council (www.nabanding.net/banders-code-of-ethics/) et les documents du Conseil canadien de protection des animaux (CCPA) relatifs au baguage des oiseaux (lignes directrices du CCPA sur le soin et l'utilisation des animaux sauvages : http://www.ccac.ca/Documents/Normes/Lignes_directrices/Animaux_sauvages.pdf; recommandations spécifiques aux oiseaux : http://www.ccac.ca/Documents/Normes/Lignes_directrices/Animaux_sauvages_Oiseaux.pdf).
3. La délivrance de ce permis n'exempte pas le titulaire du permis de se conformer à toutes les lois canadiennes, provinciales et territoriales pertinentes et aux règlements par ailleurs applicables, et n'exempte pas le titulaire de se conformer aux règlements de la juridiction compétente.
4. Le titulaire d'un permis scientifique qui est autorisé à capturer et à baguer des oiseaux migrateurs peut récupérer les oiseaux tués ou trouvés morts à la suite d'opérations normales de baguage afin de les donner à un établissement public, scientifique ou d'enseignement.
5. L'envoi ou le transport de tout oiseau migrateur ou de parties d'oiseau prises sous l'autorité de ce permis doivent être étiquetés tel que décrit dans l'article 13 (1) du Règlement sur les oiseaux migrateurs.
6. Sauf indication contraire sur le permis, il est interdit de capturer, de baguer ou de déranger intentionnellement des espèces figurant sur la liste de la Loi sur les espèces en péril. Les espèces en péril figurant sur la liste fédérale peuvent être baguées si elles sont capturées de façon accidentelle, dans la mesure où il est possible de le faire en toute sécurité.
7. Seules les méthodes précisées sur le permis peuvent être utilisées pour capturer des oiseaux.
8. Sauf indication contraire sur le permis, le titulaire du permis n'utilisera que les bagues officielles numérotées délivrées par le Service canadien de la faune.
9. Sauf indication contraire sur le permis, il est interdit de prélever du sang, des plumes et tout autre matériel biologique aviaire.
10. Le nom, le numéro de téléphone, l'adresse et l'adresse de courriel du titulaire du permis seront conservés dans la base de données commune du North American Bird Banding Laboratory et peuvent être partagés avec les personnes qui signalent une bague posée au titre du présent permis.
11. Les données sur le baguage et les récupérations de bagues peuvent être communiquées à des chercheurs ou à d'autres utilisateurs.
12. Les titulaires de permis devront transmettre toutes les données requises au Bureau de baguage des oiseaux (BBO) comme le prévoit le guide sur la présentation des données de baguage (http://www.ec.gc.ca/BBO/; ou demandez une copie du guide au BBO), ou encore dans les 30 jours suivant la réception d'une demande écrite à cet effet de la part d'un représentant du ministre.

Note : Le permis peut être suspendu ou annulé si le titulaire ne se conforme pas aux conditions.

Page 2 / 2

Appendix I. Scientific studies permit for Grand River Conservation Authority



Scientific studies permit for GRCA property
(Submit this form if you wish to undertake scientific studies on GRCA properties.)

Grand River Conservation Authority

Name: Jackson Kusack

Position: Volunteer - M.Sc. Student

Organization: Federal Goverment - Canadian Wildlife Service

Address: [redacted]

City, town or village: London

Phone: [redacted] **Cell phone:** [redacted]

List the names of people accessing GRCA property:

Jackson Kusack, Kaelyn Bumelis, Dean Evans, Mike Cadman

Purpose of the project *(Please attach additional information, if necessary):*

To collect fecal samples from Tree Swallow nestlings, to investigate species differences in diet between aerially insectivorous bird species at the nestling stage. To collect insects from differing landscape cover types, to gain reference values for isotopic analysis of aerial insectivore nestling feathers.

*See attached fecal sampling protocol for Barn Swallows for similar methods.

Equipment to be used to undertake the project:

Insect sampling - Sweep net
Fecal sampling - none

Specific area(s) where the project will take place:

Guelph Lake

Vehicle description and plate number:

Hyundai Accent - [redacted]

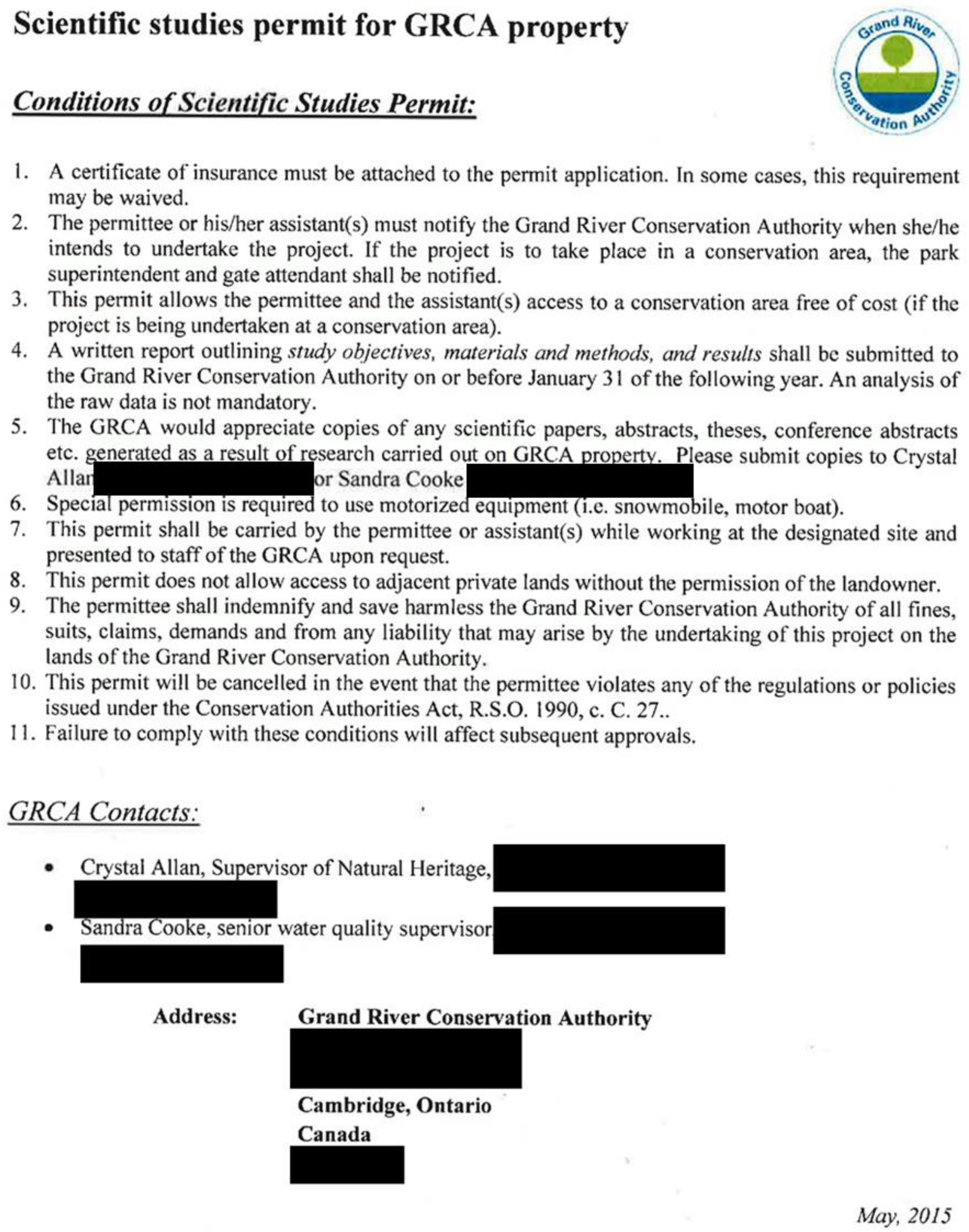
Conditions pertaining to this permit appear on the reverse side.
This permission expires on: August 31 2017

Signature of Researcher:

Date: June 11 2017 **Signature:** [redacted]

Signature of GRCA Authorizing Agent:

Date: **Signature:** [redacted]



Scientific studies permit for GRCA property

Conditions of Scientific Studies Permit:

1. A certificate of insurance must be attached to the permit application. In some cases, this requirement may be waived.
2. The permittee or his/her assistant(s) must notify the Grand River Conservation Authority when she/he intends to undertake the project. If the project is to take place in a conservation area, the park superintendent and gate attendant shall be notified.
3. This permit allows the permittee and the assistant(s) access to a conservation area free of cost (if the project is being undertaken at a conservation area).
4. A written report outlining *study objectives, materials and methods, and results* shall be submitted to the Grand River Conservation Authority on or before January 31 of the following year. An analysis of the raw data is not mandatory.
5. The GRCA would appreciate copies of any scientific papers, abstracts, theses, conference abstracts etc. generated as a result of research carried out on GRCA property. Please submit copies to Crystal Allan [redacted] or Sandra Cooke [redacted]
6. Special permission is required to use motorized equipment (i.e. snowmobile, motor boat).
7. This permit shall be carried by the permittee or assistant(s) while working at the designated site and presented to staff of the GRCA upon request.
8. This permit does not allow access to adjacent private lands without the permission of the landowner.
9. The permittee shall indemnify and save harmless the Grand River Conservation Authority of all fines, suits, claims, demands and from any liability that may arise by the undertaking of this project on the lands of the Grand River Conservation Authority.
10. This permit will be cancelled in the event that the permittee violates any of the regulations or policies issued under the Conservation Authorities Act, R.S.O. 1990, c. C. 27..
11. Failure to comply with these conditions will affect subsequent approvals.

GRCA Contacts:

- Crystal Allan, Supervisor of Natural Heritage, [redacted]
- Sandra Cooke, senior water quality supervisor [redacted]

Address: **Grand River Conservation Authority**
[redacted]
Cambridge, Ontario
Canada
[redacted]

May, 2015

Curriculum Vitae

Jackson W. Kusack

EDUCATION

M.Sc. in Biology
Western University London, ON 2016 – Present
Completed courses: Movement behaviour and analysis; Stable isotope applications; Insect Biology

B.Sc. w/ Honours, Major in Animal Biology – April 2016
Thompson Rivers University Kamloops, B.C. 2012 –2016

University of the Fraser Valley Abbotsford, B.C. 2011 –2012

RESEARCH EXPERIENCE

Western University London, ON, CA May 2016 – Present
Master of Science – Thesis Student
Supervisor: Dr. Keith Hobson Co-supervisor: Dr. Greg Mitchell

Canadian Wildlife Services London, ON, CA May 2016 – Aug 2016
Field Technician
Supervisor: Dr. Greg Mitchell Supervisor: Dr. Mike Cadman

Thompson Rivers University Kamloops, BC, CA June 2015 – April 2016
Undergraduate – Honours Student
Supervisor: Dr. Matthew Reudink Co-supervisor: Dr. Nancy Flood

Thompson Rivers University Kamloops, BC, CA May 2015 – Aug 2015
Field Assistant

Thompson Rivers University Kamloops, BC, CA Jan 2015 – Aug 2015
Undergraduate – Directed Studies Student
Supervisor: Dr. Matthew Reudink Co-supervisor: Dr. Nancy Flood

PUBLICATIONS

LaZerte, S. E., Reudink, M. W., Otter, K. A., **Kusack, J.**, Bailey, J. M., Woolverton, A., Paetkau, M., de Jong, A., Hill, D. J. (2017). feedr and animalnexus.ca: A paired R package ad user-friendly Web application for transforming and visualizing animal movement data from static stations. Ecology and Evolution, 7(19): 7884 - 7896.

CONFERENCES AND MEDIA

International Ornithological Congress (IOC) 2018 Vancouver, BC, CA
Aug 2018 – Conference: Poster
Title: Agricultural intensity and diet of Barn Swallow (Hirundo rustica) nestlings: Insights from fecal DNA and stable isotope analyses.

Ontario Ecology, Ethology, and Evolution Colloquium 2018 London, ON, CA
May 2018 – Conference: Talk
Title: Agricultural intensity and diet of Barn Swallow (Hirundo rustica) nestlings: Insights from fecal DNA and stable isotope analyses.

Joint Ornithological Meeting 2017 (AOS, SCO-SOC) Lansing, MI, USA
Aug 2017 – Conference: Talk
Title: The effect of agricultural intensity on the diet of Barn Swallow (*Hirundo rustica*) nestlings.

North American Ornithological Conference VI (NAOC VI) Washington, DC, USA
Aug 2016 – Conference: Poster
Title: Monitoring House Finch movements across a variable landscape using radio-frequency identification technology.

TRU Undergraduate Research and Innovation Conference Kamloops, BC, CA
Mar 2016 – Conference: Poster and Talk
Title: Chasing HOFI: An RFID Approach to Tracking Movement and Behaviour in the House Finch.

TRU Newsroom Article [http://inside.tru.ca/2015/08/25/songbird-research-ureap/]
Aug 2015 – News article
Article Title: Pathways to learning: Songbird research

Ornithology Meeting 2015 (AFO, SCO-SOC, WOS) Wolfville, NS, CA
July 2015 – Conference: Poster
Title: Evolution of moult strategies in Nearctic-Neotropical long-distance migratory songbirds.

TRU Undergraduate Research and Innovation Conference Kamloops, BC, CA
Mar 2015 – Conference: Poster
Title: Evolution of moult strategies in Nearctic-Neotropical long-distance migratory songbirds.

TEACHING EXPERIENCE

Western University London, ON, CA Sept 2016 – Present

Graduate Teaching Assistant – Analysis and Interpretation of Biological Data

- Winner of *Graduate Student Teaching Award* May 2018

VOLUNTEER

Canadian Wildlife Service 2016 and 2017

Bank Swallow Monitoring Volunteer

- Canoeing to remote locations on the Saugeen River to count Bank Swallow (a threatened species) nesting cavities

Bird Studies Canada – Citizen Science London, ON, CA May 2018 – June 2018

Swift Watch Volunteer

- Monitored known roosts (chimneys) for migrating Chimney Swifts (a threatened species), counting individuals and identifying roost locations.

AWARDS AND CERTIFICATES

BSC-SCO/SOC Student Travel Award	2018
Graduate Teaching Award – Western University	2018
Leadership in Environmental Sustainability Certificate	2016
SOC-SCO Student Poster Award - Ornithology Meeting	2015
AFO / SOC-SCO / WOS Student Travel Award	2015
Undergraduate Research Experience Award	2015