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Niche segregation among three sympatric species of swallows in southern Ontario

Kaelyn H. Bumelis, *The University of Western Ontario*

Supervisor: Hobson, Keith A., *The University of Western Ontario*
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Abstract

Barn Swallows (*Hirundo rustica*), Cliff Swallows (*Petrochelidon pyrrhonota*) and Tree Swallows (*Tachycineta bicolor*) breed sympatrically in southern Ontario but it is unclear how these species differ ecologically, and their coexistence implies niche segregation. I investigated potential interspecific differences in nestling diet and post-fledging movements. Using DNA barcoding of nestling feces and stable isotope analysis (δ^2H, δ^{13}C, δ^{15}N) of nestling feathers, I found evidence of differences in dietary sources of provisioned young. Barn Swallows showed evidence of provisioning more terrestrial-based prey, Cliff Swallows provisioned an intermediate diet, and Tree Swallows the most aquatic-based diet. To determine post-fledging movements, fledglings were tracked using automated telemetry. Cliff Swallow fledglings differed from the other two species in their post-fledging residency time at the natal site. This information may help to identify potential factors contributing to differential declines operating on the breeding grounds.

Keywords

niche segregation, diet, stable-isotopes, DNA barcoding, aerial insectivore, Barn Swallow, Cliff Swallow, Tree Swallow, post-fledging movement, automated telemetry

Summary for Lay Audience

Rehabilitating populations of threatened species often requires an understanding of the interactions of those species with others in the community. When closely related or similar species occupy the same habitat, it is expected they use resources in slightly different ways which reduces competition. Aerial insectivores are migratory birds which catch and eat flying insects. These birds' populations have been declining throughout North America. Evidence suggests that the time from hatching until migration is a vulnerable period and might affect aerial insectivore population trends. My study investigated three species of aerial insectivores which can be found breeding in the same area in southern Ontario. Typically, Barn Swallows, Cliff Swallows, and Tree swallows can be found nesting in agricultural areas. Since these three species share their habitat and diet, I predicted there would be key differences among them which facilitated coexistence. I looked specifically at the diet of nestlings, as well as movements of young once they left the nest. This has been documented to be an important stage, and so any differences might give insights into differential population declines. Nestling diet was determined by extracting insect DNA from the nestlings' feces and comparing the results to a DNA database. Stable-isotopes were also used to determine diet. Stable isotopes of an element have varying atomic mass, molecules containing heavier stable isotopes will move slower than their lighter counterpart. These isotopes vary across the environment in predictable ways and are integrated into animal tissues from their diet. I determined that the three species are feeding different prey to their young. I tracked movements of the young by outfitting them with a radio-transmitter which could be detected by automated receiving towers that are located across southern Ontario. I found that Cliff Swallows that hatch later in the season significantly decrease the time spent in their natal area compared to Barn and Tree swallows.

Co-Authorship Statement

This thesis was conceived and designed by Kaelyn H. Bumelis 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 Kaelyn H. Bumelis with the help of Michael D. Cadman of the Canadian Wildlife Service. All analyses and writing were done by Kaelyn H. Bumelis. Dr. Keith A. Hobson assisted writing by providing feedback and edits. Any resulting publications will be published with Keith A. Hobson, Greg W. Mitchell, and Michael D. Cadman.

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List of Abbreviations

‰ – Parts per thousand

AICc - Akaike information criterion, corrected for small sample size

AIR – Atmospheric N_2 used as an isotopic standard

BARS – Barn Swallow

BLAST - Basic local alignment search tool

BOLD – Barcode of Life Database

BWBIII – Bowhead whale baleen

C – Carbon

^oC – 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

CBS – Caribou Hoof Standard

CLSW – Cliff Swallow

CO_2 – Carbon dioxide gas

COI - Cytochrome *c* oxidase I

Db-RDA – Distance-based redundancy analysis

DNA – Deoxyribonucleic acid

ECCC – Environment and Climate Change Canada

g – grams

^{2}H – deuterium

δ^2H – Stable-hydrogen isotopes

KHS – Kudu horn standard

LMM – Linear mixed effect model

LSIS - AFAR – Laboratory for Stable Isotope Research - Advanced Facility for Avian
Research

mm, m, km – millimeters, meters, kilometers

m/s – meters per second

N_2 – Nitrogen gas

^{15}N – Nitrogen-15

δ^{15}N – Stable-nitrogen isotopes

NY – New York

ON – Ontario

PCR - Polymerase chain reaction

PGM – Personal Genome Machine

SD – Standard deviation

SE – Standard error

SK - Saskatchewan

TRES – Tree Swallow

USA – United States of America

VPDB – Vienna Pee Dee Belemnite

VSMOW – Vienna Standard Mean Ocean Water

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Chapter 1

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1   General Introduction

1.1   Community ecology

Biological communities can be complex but studies of their structure and potential mechanisms allowing coexistence provides insight into their evolution and ultimate conservation. Rehabilitating populations of threatened species often requires an understanding of the interactions of that species with other sympatric species (Simberloff 2004). Community ecology focuses on the abundance, diversity and interactions of species at a particular place. Species in communities may interact in numerous ways. However, consumer-resource relationships and competition are the focus of many community studies. Consumer-resource interactions typically benefit the consumer but can also negatively impact the resource. These interactions can include predation, parasitism, and herbivory. Competition, which results in both organisms being negatively impacted by each other, may take many different forms (Schoener 1983; Morin 2011).

1.1.1   Species competition and coexistence

Interspecific competition involves an interaction between two or more species wherein both can experience reduced fitness through lower fecundity and survivorship (Petchey *et al.* 2010; Morin 2011). These interactions typically involve closely related or similar species and can generally be grouped into interference or exploitative competition. Interference competition occurs when species interact in a way that negatively affects the competitors. These can include territorial interactions such as displacing competitors for reproductive territory. Exploitative competition occurs when species deplete a shared resource. For example, one species may consume the same food resource as another, making it scarcer (Schoener 1983; Morin 2011; Le Bourlot *et al.* 2014). Furthermore, indirect encounters when foraging between competitors may cause individuals to relocate, or to stop foraging altogether. This wastes time and energy that could be used for foraging or reproduction (Morin 2011).

The *competitive exclusion principle* states that species which occupy the same ecological niche are unable to coexist as one is bound to outcompete the other (Hardin 1960) except when resources are abundant (Hairston *et al.* 1960). When closely related species occupy the same habitat, it is expected that niche segregation allows for coexistence (Hutchinson 1957). This has been expanded to more fully represent the complexity of species interactions in communities. In order for potential competitors to coexist, species population growth rates must be reduced more than they are able to reduce the population growth rates of potential competitors (Chesson 2000). This concept is linked to the realized niche, which is defined as the range of environmental conditions under which an organism can survive and reproduce after considering the constraints imposed by other species (Hutchinson 1957). The realized niche may encompass important ecological differences in spatial and temporal patterns, or resource use among competitors. Species may have different responses to the environment around them, resulting in spatiotemporal differences among potential competitors (Chesson 2000) that can change the local density of organisms competing for the same resources, thereby reducing potential encounters (Jeltsch *et al.* 2013). For competitors occurring sympatrically, coexistence may be facilitated by partitioning resources such as food or territory.

1.2   Aerial insectivores

Aerial insectivores are a guild of migratory birds which consume flying insects. These include swallows (*Hirundinidae*), swifts (*Apodidae*), and nightjars (*Caprimulgidae*). North American populations of these birds have experienced substantial declines since the 1980's with the northeastern portion of North America having the greatest population reductions (Nebel *et al.* 2010). In addition, aerial insectivores in North America have been declining at different rates (Michel *et al.* 2016). There are many theories for these declines and several factors may be responsible such as climate change (Balbontín *et al.* 2009), reductions in fledging success (Cox *et al.* 2018), habitat loss (Grüebler *et al.* 2010) and loss of high-quality prey (Benton *et al.* 2002; Twining *et al.* 2016; Spiller and Dettmers 2019).

In southern Ontario, three aerial insectivore species - Barn Swallows (*Hirundo rustica*), Cliff Swallows (*Petrochelidon pyrrhonota*) and Tree Swallows (*Tachycineta bicolor*)

occur in sympatry during the breeding season, generally in agricultural areas. Barn and Cliff swallows are both long-distance migrants; these birds breed as far north as Alaska and winter as far south as Argentina (Brown *et al.* 2017; Brown and Brown 2019). In agricultural areas, Barn and Cliff swallows typically build mud nests inside barns or other human structures. Tree Swallows are short-distance migrants, they also breed as far north as Alaska, but overwinter as far south as the Gulf of Mexico. When breeding in agricultural areas, Tree Swallows nest in boxes provided by humans, or in natural cavities (Winkler *et al.* 2011). Barn, Cliff, and Tree swallows have similar clutch sizes; however, Barn Swallows may produce a second clutch, but this is rare for Cliff and Tree swallows (Winkler *et al.* 2011; Brown *et al.* 2017; Brown and Brown 2019). These three species are also declining at different rates. According to breeding bird survey data, in the lower Great Lakes region of Ontario, Barn Swallows have decreased 68%, Cliff Swallows 80% and Tree Swallows 56% from 1970 – 2017 (Smith *et al.* 2019). Differences in their life history may be key in determining potential causes of differential population declines.

1.3   Diet

Diet has a considerable impact on the life cycle of songbirds, including but not limited to reproductive success. These factors in turn can affect the population growth rates of aerial insectivores (Cox *et al.* 2018). Flying insects, the main source of diet for aerial insectivores, have been declining along with many other insect species (Hallmann *et al.* 2017; reviewed in Sánchez-Bayo and Wyckhuys 2019). Recently, research has also found that the diet composition of aerial insectivores has been changing over the past several decades (Nocera *et al.* 2012; Pomfret *et al.* 2012), which has been suggested as a potential cause for population declines. Previous studies have found differences in the diets of sympatric aerial insectivores (Waugh 1978; Orłowski and Karg 2013; Orłowski *et al.* 2015). Reasons for these differences have been attributed to variance in foraging height, foraging location, and species morphology. The latter can directly influence which prey each bird is able to capture (Waugh 1978). Examining how similar species utilize different resources can give researchers insight on how competitors are able to coexist. In addition, this information may be a basis for future studies assessing differential declines as a function of differences in diet.

Early studies on avian diet were relatively invasive, these included ligatures being placed on nestlings to prevent them from swallowing so that food may be removed from the mouth (Waugh 1978). Adults were also captured to remove bolus from their mouths as they returned to feed their young (McCarty and Winkler 1999). More presently, non-invasive techniques include opportunistic sampling of aerial insectivore gut contents post-mortem (Law *et al.* 2017), analyzing nestling fecal samples (Orlowski and Karg 2011, 2013; Orlowski *et al.* 2015) and stable isotope analyses (Kusack 2018).

1.3.1   Stable isotope analysis

Isotopes of an element have the same number of protons but a different number of neutrons. This means that they will have varying atomic mass, which will cause them to behave differently kinetically whereby molecules containing heavier stable isotopes will move slower than their lighter counterpart. Ratios of heavy to light stable isotopes can be used to infer diets of organisms, as they move through the environment in predictable ways (Peterson and Fry 1987; Fry 2006; Inger and Bearhop 2008). The information provided by stable isotope analyses depends on the tissues sampled as well as the isotopes being analyzed. The tissues used will determine what timescale the analysis will reflect, as some tissues have faster or slower turnover rates. For example, liver or blood have a fast turnover rate and will represent short-term diet compared to bone collagen which has a slower turnover rate. Additionally, metabolically inert tissues such as feathers have no turnover, so they will represent assimilated diet of the period they were grown (Hobson and Clark 1992). Stable isotopes commonly used for food web analyses include ^{2}H, ^{13}C, and ^{15}N. Stable isotope ratios are typically expressed in delta (δ) notation, as parts per thousand (‰) deviation from designated standards:

$$\delta^{Heavy}\text{X} = \left[\left(\frac{RSample}{RStandard}\right) - 1\right] \times 1000$$

Where R = ^{Heavy}X / ^{Light}X

Stable hydrogen isotope ratios ($\delta^{2}H$) can be used to differentiate between aquatic and terrestrial sources of diet. Tissues from organisms feeding in terrestrial systems tend to be enriched in ^{2}H when compared to aquatic food webs. Primary producers may influence

the δ^2H values in terrestrial and aquatic food webs. Terrestrial plants undergo transpiration, which releases the lighter hydrogen isotope resulting in enrichment of ^{2}H in terrestrial plants compared to aquatic plants (Wershaw *et al.* 1966; Doucett *et al.* 2007; Voigt *et al.* 2015). In addition, aquatic algae discriminate against the heavier isotope more so than terrestrial plants (Doucett *et al.* 2007). Stable hydrogen isotope ratios in aquatic food webs may be affected by evaporation as well as inflow to the system. Evaporating water vapor is depleted in ^{2}H causing the remaining water to be more enriched, this process increases with increasing temperature and aridity (Ehhalt *et al.* 1963). The amount of water inflow from other sources determines the influence evaporation has on ^{2}H enrichment – systems with low inflow will be more influenced by evaporation than systems with high inflow (Gibson and Edwards 2002).

Carbon stable isotope ratios are typically associated with primary producers in food webs. These can be influenced by different fractionation occurring in C3 or C4 photosynthetic pathways (Bender 1968), resulting in C4 plants being more enriched in ^{13}C (average -14‰) than C3 plants (average -28‰) (O'Leary 1988). Carbon stable isotope ratios may also differ between freshwater and terrestrial environments, as plants and algae from freshwater sources may differ in their carbon uptake when compared to terrestrial counterparts (France 1995; Doucett *et al.* 1996). Differences between carbon stable isotope ratios in marine versus terrestrial systems occur because carbon enters terrestrial food chains from atmospheric CO_2 with δ^{13}C around -7‰, whereas dissolved carbonates enter marine food webs with δ^{13}C around 0‰ (Hobson and Sealy 1991). Measurements of δ^{13}C are often used in conjunction with those of δ^{15}N in dietary studies of food webs.

Nitrogen stable-isotope ratios (δ^{15}N) are useful indicators of trophic position as they typically become more enriched with increasing trophic level (Hobson and Welch 1992; Hobson *et al.* 1994). However, agricultural practices involving the use of fertilizer can cause an enrichment in ^{15}N that may alter the isotopic composition of the regional food web for decades (Szpak 2014). Manure-based fertilizer tends to be higher in ^{15}N than synthetic fertilizer. Synthetic fertilizers typically have δ^{15}N values of approximately 0‰ whereas manure-based fertilizers are 10-25‰ (Hebert and Wassenaar 2001). Once

fertilizer is applied, ammonia volatilization may cause nitrogen from the application to be lost into the environment (Ma *et al.* 2010). This reaction results in a loss of isotopically light ammonia gas, which leaves the remaining soils enriched in ^{15}N (Hobson 1999; Pardo and Nadelhoffer 2010). Additionally, nitrogen concentrations in ground- and surface-waters have increased due to leaching, runoff, and atmospheric deposition from agricultural practices, as well as emissions from motor vehicles and industrial processes (Vitousek *et al.* 1997; Pardo and Nadelhoffer 2010).

Similar to Hutchinson's (1957) theory of an ecological niche being an n-dimensional space with axes that represent environmental components, isotopic data may also be presented in multivariate space, or δ-space, with axes representing isotopic values of tissues (Bearhop *et al.* 2004; Newsome *et al.* 2007; Jackson *et al.* 2011). This δ-space has been useful in conservation biology through identifying important habitat and diet resources, as well as detecting shifts in resource use resulting from disturbance (Newsome *et al.* 2007). However, isotopic data is limited as it cannot provide specific taxonomic information. For this reason, it is beneficial to combine stable isotope analyses with other approaches to gain more specific dietary information.

1.3.2 Fecal analysis

Fecal analysis is a useful tool in determining diet, as it is less invasive than some previously used methods and can give finer-scale taxonomic information. Fecal analyses can be done by inspecting the fragmented prey items in feces visually, or by using DNA barcoding. For DNA barcoding of aerial insectivore feces, a 157-base pair region of the mitochondrial cytochrome *c* oxidase subunit 1 (COI) gene (Hebert *et al.* 2003) is amplified using PCR. The COI gene is used because it shows relatively high interspecific variation, and relatively low intraspecific variation (Hebert *et al.* 2003). The 157 base-pair region used is arthropod-specific and contains fragments that are expected to remain post-digestion (Zeale *et al.* 2011). This coupled with a reference database such as the Barcode of Life Database (BOLD Systems, www.boldsystems.org; Ratnasingham and Hebert 2007) is used in order to identify taxa.

Visual fecal analysis is typically limited by the ability to correctly identify remains of prey. As a result, fecal DNA analyses are able to identify prey items at lower taxonomic levels than visual analysis. Furthermore, when identifying prey of aerial insectivores, fecal DNA analyses are able to identify prey that may be visually unidentifiable post-digestion (Zeale *et al.* 2011). DNA analyses have been successfully used to identify diet composition of avian species (Jedlicka *et al.* 2013; Galimberti *et al.* 2016; Moran *et al.* 2019) including aerial insectivores (Kusack 2018; McClenaghan *et al.* 2019). However, more research on diet composition of aerial insectivores using DNA barcoding has been on bats (e.g. Zeale *et al.* 2011; Gonsalves *et al.* 2013; Long *et al.* 2013). Studying differences in the prey of these species could help understand if these sympatric swallows are partitioning their resources and potentially offer insight on differential declines that are being experienced amongst these species.

1.4   Movement

A notable movement difference among Barn, Cliff, and Tree swallows is their migration strategy. Tree Swallows typically migrate to southern USA or the Gulf of Mexico whereas Barn and Cliff swallows migrate as far south as Argentina. However, at finer scales, differences in movements are relatively unknown. These movements may lead them to make different pre-migratory decisions or make them susceptible to environmental factors which affect survival. Like many avian species, the post-fledging period plays an important role in population growth rates for aerial insectivores due to high mortality (Naef-Daenzer *et al.* 2001; Cox *et al.* 2014; Cox *et al.* 2018; Evans *et al.* 2019). Fledgling survival is the lowest immediately post-fledging (Evans *et al.* 2019). During this time young are extremely conspicuous, perching in exposed sites and making begging calls (Vitz and Rodewald 2010; Cox *et al.* 2014), making them vulnerable to predation. After this period, fledglings become independent and eventually disperse. This independent phase is also associated with high mortality as young must learn to navigate unknown landscapes, forage for themselves, and avoid predation (Grüebler and Naef-Daenzer 2010). So, discerning differences in regional movements at this stage may serve as a starting point in conservation efforts.

Efforts to understand movements during the post-fledging period have yielded multiple hypotheses. First, the habitat optimization hypothesis typically refers to fine-scale movements made for food and shelter from predators (Brown and Taylor 2015). The migration hypothesis suggests that individuals make movements toward their migration route without entering a migratory physiological state (Rappole and Ballard 1987; Mitchell *et al.* 2010; Brown and Taylor 2015). Finally, the exploration hypothesis proposes that movements are made in order to gain cues for the following year. These include searching for future breeding habitats or searching for navigational landmarks to aid in returning during spring migration (Baker 1993; Brown and Taylor 2015; Cormier and Taylor 2019). Examining how movements differ between these three species could lend itself to better understanding the current incongruent population declines of aerial insectivores.

Previous attempts to study movements of songbirds have been difficult, as common methodology involved banding and recapture, which may not be reliable if individuals disperse and are not recaptured (Cox *et al.* 2014). Rate of recapture is also an issue with geolocators, as these units need to be retrieved in order to acquire movement data. Other tracking technology, such as global positioning systems (GPS), are typically too cumbersome for small songbirds (Taylor *et al.* 2017). Instead, radio-tagging and tracking of individuals has proven to be a useful method for studying movements of songbirds. Modern versions of these units are light enough to be used on songbirds, and individuals do not need to be recaptured in order to attain the data. Typically, for radio telemetry, very high frequency (VHF) radio transmitters are attached to the organism of interest. These transmitters each emit a unique signal in the VHF range (30 – 300 MHz) which can then be detected by a radio antenna and receiver. However, this method historically required researchers to detect animals through homing in on their location, e.g. by foot or aircraft, all while cycling through frequencies in order to detect the transmitters (Withey *et al.* 2001). More recently, automated telemetry towers have facilitated research focusing on movements of songbirds. Similar to previous radio telemetry methods, automated telemetry uses antennae and receivers to detect radio signals. These are typically affixed to a tower, building, or other structure. Moreover, radio transmitters are now coded with a unique output on the same frequency, so manual and automated receivers are able to

detect more transmitters and log their detections when they are within range. (Taylor *et al.* 2017).

The Motus Wildlife Tracking System (Motus) is a collaborative project which involves the use of automated telemetry towers to track small flying organisms (Taylor *et al.* 2017). What makes Motus an especially powerful tool is the number of automated receivers in the array. The Motus array consisted of 394 automated receivers in 2018 (Motus, wwww.motus.org) and continues to grow as new projects incorporate automated receiving towers into their research. Each tower is managed by its project owner. Nevertheless, transmitters may be detected on another projects' tower, in which case each project receives information for their own transmitters from all automated receivers in the array. These towers are useful for studying broad-scale movements of both adult and juvenile songbirds and have been used to compare movement differences among groups. For example, Brown and Taylor (2015) examined differential movements between adult and juvenile Blackpoll Warblers (*Setophaga striata*) tagged on Bon Portage Island, NS, Canada, and found juveniles made indirect movements and travelled more distance than adults prior to migration. Cormier and Taylor (2019) followed up by comparing post-fledging movements of Blackpoll Warblers to those of the Yellow-rumped Warbler (Myrtle subspecies; *Dendroica coronata coronata*) and found that fledglings of the two species showed differences in departure timing and movement patterns. Additionally, Evans (2018) used the Motus Wildlife Tracking System to evaluate the pre-migratory movements and survivorship of first- and second-brood Barn Swallow fledglings in southern Ontario. No evidence was found to suggest differences in survivorship between the two broods; however, second brood fledglings moved less distance and migrated younger than first brood fledglings. Determining the consequences of various human actions on biodiversity requires life history information at various spatial scales. Understanding post-fledging movements may give insight as to different spatiotemporal limitations being placed on the swallow species during this time.

1.5 Objectives and hypotheses

The objective of my thesis was to evaluate differences between three sympatric species of aerial insectivores in southern Ontario, specifically focusing on nestling diet and post-

fledging movements. I tested the hypothesis that sympatric Barn Swallows, Cliff Swallows, and Tree Swallows would show differences in their behaviors on their breeding grounds. This research is divided into two chapters; in Chapter 2 I investigated whether Barn, Cliff, and Tree swallows showed evidence of partitioning of prey provisioned to nestlings. I tested the hypothesis that the three swallow species partition their resources, which may reduce interspecific competition during chick-rearing. In Chapter 3 I used the Motus Wildlife Tracking system to investigate if and how post-fledging movements differed among the three species.

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Chapter 2

2 Dietary differences among nestling Barn, Cliff, and Tree swallows

2.1 Introduction

The fundamental niche describes the range of environmental conditions required for an organism to survive and reproduce. However, this range may be influenced by interactions with conspecifics and other species (Hutchinson 1957). The competitive exclusion principle states that organisms which occupy the exact same ecological niche are unable to coexist as one is bound to outcompete the other (Hardin 1960), except when resources are abundant (Hairston *et al.* 1960). Therefore, when closely related species occupy the same habitat, it is expected that niche segregation allows coexistence (Hutchinson 1957). Resource partitioning can include both spatial and temporal components and is often associated with partitioning among diets. Partitioning can be dynamic and may be influenced by environmental limitations affecting resource availability at various stages, or by increased energy demands (e.g. chick rearing) that ultimately determines the level of competition. For example, Barger *et al.* (2016) found that Common Murres (*Uria aalge*) and Thick-billed Murres (*Uria lomvia*) on Bogoslof Island, Alaska USA, shared common food resources during incubation but during chick-rearing their diets diverged.

Barn Swallows (*Hirundo rustica*), Cliff Swallows (*Petrochelidon pyrrhonata*) and Tree Swallows (*Tachycineta bicolor*) are passerine birds which breed in sympatry in southern Ontario. On their breeding grounds, these three species of swallows may occur in agricultural areas. In such cases, Barn and Cliff swallows build their nests inside barns and other human structures, whereas Tree Swallows rely on nesting boxes provided by humans or natural cavities. These swallows also share a food source, as they are all aerial insectivores - a guild of migratory birds which catch and eat flying insects on the wing. North American populations of aerial insectivores have been experiencing substantial declines since the 1980's (Nebel *et al.* 2010). Theories addressing this include climate change (Balbontín *et al.* 2009), land use and loss of insect prey due to pesticides (Benton

et al. 2002) among others. Swallow population declines are heaviest in the northeastern portion of North America, (Nebel *et al.* 2010), but are also inconsistent among species of aerial insectivores (Michel *et al.* 2016).

Evidence suggests there has been changes in diet composition of aerial insectivore species over the past several decades (Nocera *et al.* 2012; Pomfret *et al.* 2012). Diet can impact many aspects of a species' life cycle including fledging success and post-fledging survival, which are also key factors in aerial insectivore population growth rates (Cox *et al.* 2018). Poor diet has been attributed to poor nestling growth and body condition (Twining *et al.* 2016) which can lead to lower survival rate (Naef-Daenzer *et al.* 2001; Evans *et al.* 2019). Such studies highlight the importance of research into potential resource partitioning amongst these sympatric swallow species to determine if there is a link to the differential declines of aerial insectivores.

Previous studies have shown differences in nestling diet composition among sympatric aerial insectivore species. Orłowski and Karg (2013) found differences in diet diversity as well as weight of prey consumed, with some overlap in diet resulting from an overly abundant agricultural pest. Prey partitioning of sympatric aerial insectivores has been attributed to potential differences in foraging height (Samuel 1971; Orłowski *et al.* 2015) and body morphology. These include differences in bill shape which affect the ability to handle different prey sizes efficiently, as well as body, wing, and tail shape which influence flight maneuverability. These morphological adaptations, in turn, affect prey that can be captured while flying (Waugh 1978). Differences in diet composition have been linked to differential uptake of contaminants in aerial insectivorous bird species, which in turn can affect the rate at which toxicity may occur due to biomagnification along the food chain (Orłowski *et al.* 2015).

 Early techniques for determining aerial insectivore diet have included using ligatures to prevent nestlings from swallowing prey items (Waugh 1978), or catching adults on their way to provision their young and removing prey from their mouth (McCarty and Winkler 1999). While these studies provided useful, detailed information, these methods are avoided if possible due to their invasive nature. Instead, researchers may consider less

invasive methods. Stable isotope analyses and fecal analyses provide a less invasive alternative. DNA barcoding of nestling feces is a non-invasive method that has been successfully used to identify diet composition of avian species (Jedlicka et al. 2013; Galimberti et al. 2016; Moran et al. 2019) including aerial insectivores (Kusack 2018; McClenaghan et al. 2019). When identifying prey groups of aerial insectivores, fecal DNA analyses are able to overcome potential limitations of visual fecal analyses that result from differing digestion rates of parts from various prey groups. Generally, visual analysis has yielded varying results (Rosenberg and Cooper 1990; Tryjanowski *et al.* 2003; Orłowski and Karg 2011). In comparison to visual fecal analysis, DNA barcoding is able to identify soft-bodied prey that may be visually unidentifiable post-digestion.

Stable isotope analysis may also be used to infer diet (Peterson and Fry 1987; Fry 2006; Inger and Bearhop 2008) over various timescales (Hobson and Clark 1992). Specifically, stable-isotope ratios of hydrogen (δ^2H) and carbon (δ^{13}C) can been used to differentiate prey originating from aquatic vs. terrestrial sources (France 1995, Doucett *et al.* 1996; Doucett *et al.* 2007). Tissues from organisms feeding in aquatic systems tend to be depleted in ^{2}H when compared to terrestrial food webs (Wershaw *et al.* 1966; Doucett *et al.* 2007; Voigt *et al.* 2015). Differences in δ^2H signatures between aquatic and terrestrial sources may occur due to algae discriminating against the heavier isotope which results in depleted ^{2}H, or due to isotopic fractionation that takes place during the transpiration of water from the leaves of terrestrial plants, resulting in enrichment of ^{2}H (Wershaw *et al.* 1966; Doucett *et al.* 2007; Voigt *et al.* 2015). Stable carbon isotope ratios may also differentiate between primary producers with C_3, C_4 or CAM photosynthetic pathways (Bender 1968). Nitrogen stable-isotope ratios (δ^{15}N) are useful indicators of trophic position as they typically become more enriched with increasing trophic level (Hobson and Welch 1992; Hobson *et al.* 1994). Stable-nitrogen isotope values can also be influenced by variation in land-use practices and the use of fertilizers (Hobson 1999). Using a combination of stable isotope analyses, it is possible to construct an organism's isotopic niche. An isotopic niche is isotopic data presented in multivariate space, or δ-space, with axes representing isotopic values of tissues. This is comparable to Hutchinson's (1957) idea of an ecological niche being an n-dimensional space with axes representing environmental components of the organism's niche (Bearhop *et al.* 2004;

Newsome *et al.* 2007; Jackson *et al.* 2011). Determining the isotopic niche can show evidence of dietary overlap or partitioning among species.

I aimed to evaluate the diets fed to nestlings of three sympatrically breeding birds of the same foraging guild in southern Ontario. I tested whether Barn, Cliff, and Tree swallows partition their dietary resources, which may reduce interspecific competition during chick-rearing. To test this hypothesis, I analyzed nestling fecal sacs for prey DNA, as well as stable isotope ratios (δ^2H, δ^{13}C, and δ^{15}N) in nestling feathers for evidence of dietary segregation.

2.2   Methods

2.2.1   Study sites

Fieldwork was conducted at nine farms from May-July 2018 within Wellington County, near Guelph, ON (43.55° N, 80.25° W) (Figure 2.1). These locations were grouped into seven sites since two farms were adjacent to each other and so considered the same site. Each of these sites had all three species of swallow breeding sympatrically (average clutch initiation was May 25, 2018 for Barn Swallows, May 29, 2018 for Cliff Swallows, and May 24, 2018 for Tree Swallows). However, Guelph Lake Conservation Area only had Tree Swallows. All Barn Swallow and Cliff Swallow colonies were located inside barns, whereas Tree Swallows were in nesting boxes outside.
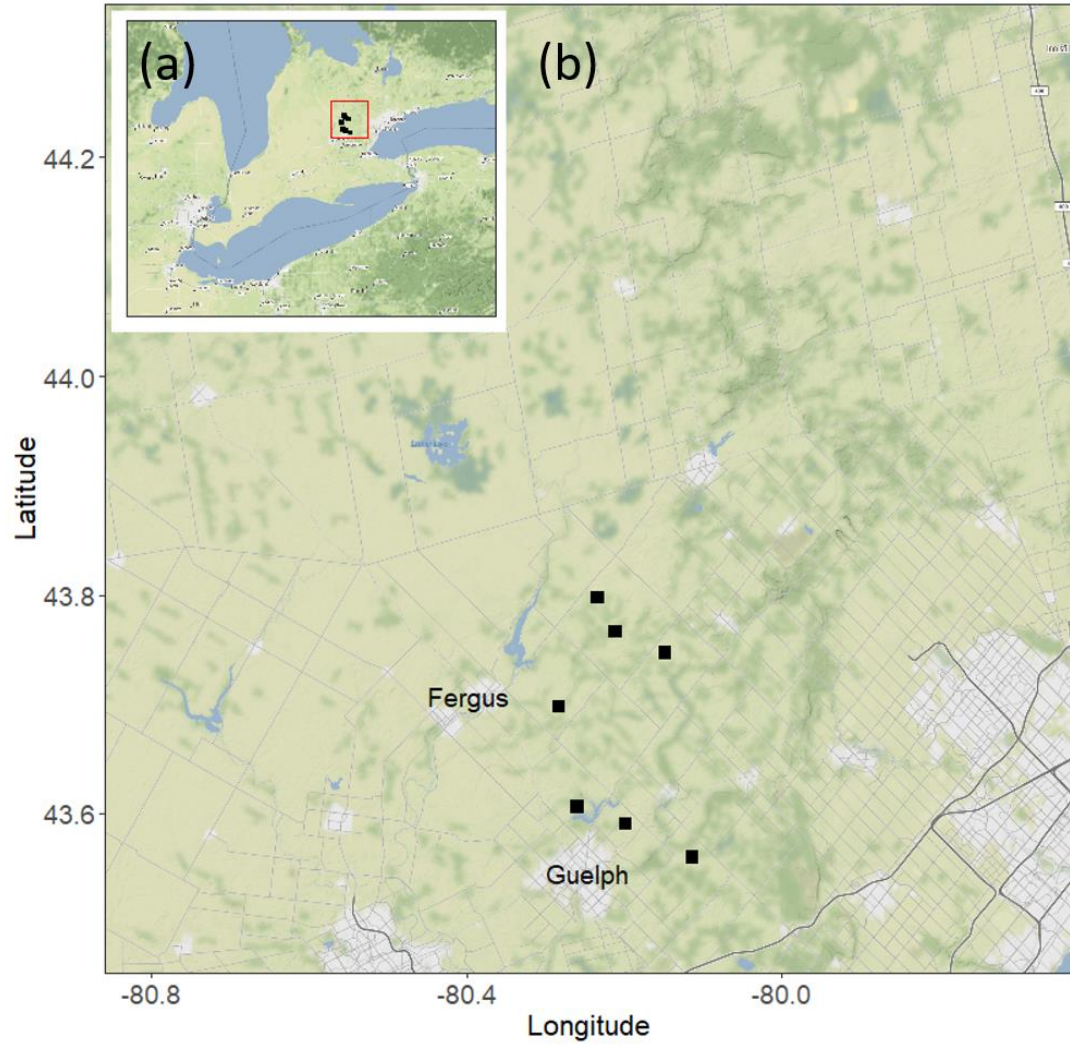
Figure 2.1 The location of study sites (squares) in 2018 shown in (a) southern Ontario, and (b) Wellington County.

2.2.2   Nest monitoring and sampling

Nest monitoring began in early May and involved visiting sites one to two times weekly to establish the approximate onset of laying; if eggs were present upon arrival, and clutch was not complete, it was assumed that one egg had been laid per day for all three species (Winkler *et al.* 2007; Brown *et al.* 2017; Brown & Brown 2019). Once clutch initiation date was approximated, nests were monitored at least twice per week to determine final clutch size and hatch date. Timing of hatching was predicted based on a 14-day incubation period after the penultimate egg was laid for Barn Swallows (Brown & Brown 2019), Cliff Swallows (Brown *et al.* 2017) and Tree Swallows (Winkler *et al.* 2007). To determine hatch day as accurately as possible, nests were visited before predicted hatch day and every few days thereafter. Hatch Day was assigned based on evidence of hatching; this included eggshells present, unhatched eggs remaining, and nestlings still being wet. Hatch Day was considered Day Zero. For nests where hatch day could not be assigned, nestlings were aged by feather tract development (Stoner 1935; Stoner 1945; Marsh 1980).

All nests were visited between Day Six and Ten after hatching, during which Tree Swallow and Barn Swallow nestlings were banded with a uniquely numbered United States Geological Survey (USGS) aluminum leg band. For each nestling, mass, age and length of wing at rest (length from the wrist joint to the longest primary) were documented. Fecal samples were collected by holding a clean piece of paper under the young as they were removed from their nest, these samples were grouped by nest. Cliff Swallow nestlings were not accessible for banding and therefore cardboard was placed beneath the nest for roughly 30 minutes to collect fecal samples while we processed other nestlings from the same site.

Barn Swallow and Tree Swallow nests were ideally visited and measurements taken when the young were 15 days old (see Appendix A for measurements summary). It was not possible to visit all nests at Day 15 therefore some Tree Swallows were measured at day 16 and 17. At that time, feathers were taken from all but one nestling per nest for stable isotope analyses. Hatch-year Cliff Swallows were challenging to access due to their elongated mud entrance tube. Cliff Swallow nests were visited at roughly Day 20

and nests were examined using a flashlight and dental mirror. During inspection some nestlings may fledge the nest and so mistnets were put up to catch them. If the entrance to the nest was not elongated, nestlings could be removed from the nest. Otherwise, the entrance was manually shortened. At this point they were also banded, weighed, measured and had a central tail feather taken for stable isotope analyses, then returned to their nests. After sampling, young were expected to fledge within 1 - 7 days. Average fledging age is 19-20 days, 20-21 days, and 18-22 days for Barn Swallows (Brown and Brown 2019), Cliff Swallows (Brown *et al.* 2017), and Tree Swallows (Winkler *et al.* 2007), respectively. Nests were ideally revisited within one week after the estimated fledging date to determine whether young had fledged. This was done by checking inside and beneath nests for any dead young.

2.2.3   Stable isotope analyses

Juvenile tail feathers were soaked with 2:1 chloroform:methanol overnight and left to dry in a fumehood at ambient temperature for 24 hrs. Samples analyzed for stable hydrogen (δ^2H) isotopes were weighed out to 0.35mg in silver capsules using the feather barbs only. Capsules were compressed and submitted to Dr. Hobson for δ^2H analyses at the LSIS-AFAR stable isotope facility at the University of Western Ontario. Samples were loaded into a Uni-prep carousel (Eurovector®, Milan, ITA) held at 60ºC, evacuated and flushed with dry helium and then combusted in a Eurovector 3000 elemental analyzer (Eurovector, Milan) pyrolytically on glassy carbon at 1350ºC. Separated H_2 was analyzed using a Thermo Delta V Plus (Thermo scientific®, Bremen, DEU) continuous-flow isotope ratio mass spectrometer via a Conflo device (Thermo Scientific, Bremen, DEU). Sample results were expressed in the standard delta (δ) notation in parts per thousand (‰) deviation from the Vienna Standard Mean Ocean Water (VSMOW) standard. In-house keratin standards (CBS: -197‰; KHS: -54.1‰) were used in order to derive the δ^2H value of the non-exchangeable H fraction according to the comparative equilibration approach (Wassenaar and Hobson 2003). Based on within-run (n=5 each) keratin standards, measurement error was estimated to be ±2‰.

Samples analyzed for stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values were weighed out to 1.0mg in tin capsules using feather barbs and part of the rachis with a high

precision balance (Mettler Toledo® XP6 Excellence Plus XP Micro Balance, Greifensee, CHE). The capsule was compressed and placed into numbered wells in a sample tray. Feathers were assayed for $\delta^{13}C$ and $\delta^{15}N$ at the Environment and Climate Change Canada stable isotope laboratory in Saskatoon, SK. Samples were combusted at 1030°C in a Carlo Erba NA1500 (Thermo Scientific; Waltham, United States) or Eurovector 3000 (Eurovector, Milan) elemental analyser. The resulting N_2 and CO_2 were separated chromatographically and introduced into an Elementar Isoprime (Elementar; Langenselbold, Germany) or a Nu Instruments Horizon (Nu Instruments Ltd.; Wrexham, United Kingdom) isotope ratio mass spectrometer. Sample results were expressed in the standard delta (δ) notation in parts per thousand (‰) deviation from international standards (Vienna Pee Dee Belemnite [VPDB] and AIR for $\delta^{13}C$ and $\delta^{15}N$, respectively). Internal laboratory calibration standards were BWBIII keratin ($\delta^{13}C$ = -20.18, $\delta^{15}N$ = +14.31 ‰) and Pugel ($\delta^{13}C$ = -13.64, $\delta^{15}N$= +5.07 ‰). Measurement precision was based on replicate (n = 5) within-run measurements of internal reference material and estimated to be ±0.1 ‰ for both $\delta^{13}C$ and $\delta^{15}N$.

2.2.4   Fecal DNA analyses

Fecal samples were collected into scintillation vials which contained 95% ethanol. Upon returning from the field the samples were immediately frozen. Samples were processed at the Canadian Centre for DNA Barcoding (Guelph, Canada). Samples were amplified separately, using arthropod-specific primers targeting a 157 base pair region of the mitochondrial cytochrome *c* oxidase subunit 1 (COI) gene (Hebert *et al.* 2003). Amplified samples were pooled and sequenced using an Ion Torrent PGM high-throughput sequencer (Thermo Fisher Scientific), trimmed to remove the primer, and filtered for a minimum size of 100 base pairs. Filtered reads were queried against the Barcode of Life Database (BOLD; www.boldsystems.org) reference using a basal local alignment search tool (BLAST) algorithm to assign taxonomic identity. Results were accepted to be true if they had a minimum of 50 reads that matched reference sequence with at least 95% identity across at least 100 base pairs.

2.2.5   Statistical analyses

All statistical analyses were done using R Studio (Version 1.2.1335) and R (Version 3.5.3; RStudio Team 2015; R Core Team 2019). To test for differences in the diets of nestling Barn, Cliff, and Tree swallows, I used three separate linear mixed-effects models (LMM) with the feather stable isotope values (δ^2H, δ^{13}C, δ^{15}N) as response variables (R package nlme; Pinheiro *et al.* 2019). The global models for all three included species and sampling date as predictor variables, and site as a random effect. Sampling date was included to account for any seasonal variability in diet that might influence feather stable isotope ratios. To test for the effect of diet on growth of nestling Barn, Cliff, and Tree swallows, I used a linear mixed-effects model (LMM) with mass(g) / wing length (mm) as an index for condition at Day 15-20 as the response variable. The global model included species, hatch date (day of year), and feather stable isotope values (δ^2H, δ^{13}C, δ^{15}N) as predictor variables, as well as site as a random effect. In each case the best model was determined through backward selection using the lowest Akaike information criterion for small sample size (AICc) value, except when ΔAICc < 2 in which case the simplest model was chosen (model selection tables are in Appendix B).

To test whether short-term diet composition differed between nestling Barn, Cliff and Tree swallows, I used distance-based redundancy analysis (db-RDA; package ade4; Dray and Dufour 2007). Distance measures for the presence-absence family matrix were calculated using the Jaccard method (Jaccard 1912). Predictors in the global model included species, as well as date and site to account for any seasonal or site-specific effects on prey composition. Model selection was done using stepwise deletion of predictor variables determined by significance level.

2.3   Results

2.3.1   Stable isotopes

Feather isotope values differed significantly for the three swallow species. One Tree Swallow sample was removed from all analyses as it was a significant outlier (δ^2H = -112‰, δ^{13}C = -27.1‰, δ^{15}N = 12.49‰). Tree Swallow feathers showed the lowest δ^2H values (-100‰ to -79‰), followed by Cliff Swallows (-96‰ to -75‰) and Barn

Swallows (-92‰ to -69‰) (Table 2.1). The best-fitting model indicated that feather δ^2H values were best predicted by species (LMM; $F_{2,63}$ = 23.56, p = < 0.0001) and date of sampling (LMM; $F_{1,63}$ = 13.97, p = 0.0004) (Table 2.2; Figure 2.2). The species – date interaction was removed during model selection. There was a negative linear relationship between sampling date and feather δ^2H values (-0.27 ± 0.072‰), indicating that values were more negative later in the season.

Figure 2.2 Scatterplot of nestling Barn Swallow (n=28), Cliff Swallow (n=24), and Tree Swallow (n=21) feather δ^2H values plotted by collection date (day of year). Feather samples were collected near Guelph, ON, in the breeding season of 2018.

Table 2.1 Species-specific summary for stable isotopes within nestling Barn, Cliff, and Tree swallow feathers. Stable isotope values are provided as mean isotope values ± standard deviation of raw values.

Species	n	$\delta^{13}C \pm SD‰$	n	$\delta^2H \pm SD‰$	n	$\delta^{15}N \pm SD‰$
Barn Swallow	40	-23.0 ± 0.5	28	-78 ± 6	40	11.5 ± 0.7
Cliff Swallow	24	-23.9 ± 0.5	24	-87 ± 6	24	10.0 ± 0.5
Tree Swallow	31	-24.4 ± 0.7	21	-88 ± 6	31	10.5 ± 0.7

Table 2.2 Post-hoc test results for linear mixed effect models of isotope values (δ^2H, $\delta^{13}C$, $\delta^{15}N$) from Barn, Cliff, and Tree swallow nestling feathers collected near Guelph, ON, in the breeding season of 2018.

Response	Contrast	n	Estimate	SE	t	p-value
δ^2H	BARS - CLSW	(28 – 24)	6	1.62	3.415	0.0032
	BARS - TRES	(28 – 21)	11	1.66	6.676	< 0.0001
	CLSW - TRES	(24 – 21)	6	1.91	2.895	0.0142
	*Random ~ Site			3		
	*Residuals			5		
$\delta^{13}C$	BARS - CLSW	(40 – 24)	0.7	0.12	5.697	< 0.0001
	BARS – TRES	(40 – 31)	1.3	0.12	10.788	< 0.0001
	CLSW – TRES	(24 – 31)	0.6	0.13	4.535	0.0001
	*Random ~ Site			0.5		
	*Residuals			0.4		
$\delta^{15}N$	BARS - CLSW	(40 – 24)	0.9	0.13	7.005	< 0.0001
	BARS - TRES	(40 – 31)	0.9	0.11	8.032	< 0.0001
	CLSW – TRES	(24 – 31)	0.02	0.13	- 0.119	0.9922
	*Random ~ Site			0.6		
	*Residuals			0.4		

*These terms are expressed with standard deviation

Tree Swallow feathers showed the lowest $\delta^{13}C$ values (-25.9‰ to -22.7‰), followed by Cliff Swallows (-24.9‰ to -22.9‰) and Barn Swallows (-24.1‰ to -21.8‰) (Table 2.1). The species – date interaction, as well as date as a fixed effect were removed during model selection. The best-fitting model indicated that feather $\delta^{13}C$ values were best predicted by species (LMM; $F_{2,86} = 59.27$, $p = < 0.0001$). Tukey's post-hoc test indicated differences of feather $\delta^{13}C$ values between all three swallow species (Table 2.2, Figure 2.3). There was no evidence of a relationship between sampling date and feather $\delta^{13}C$ values.
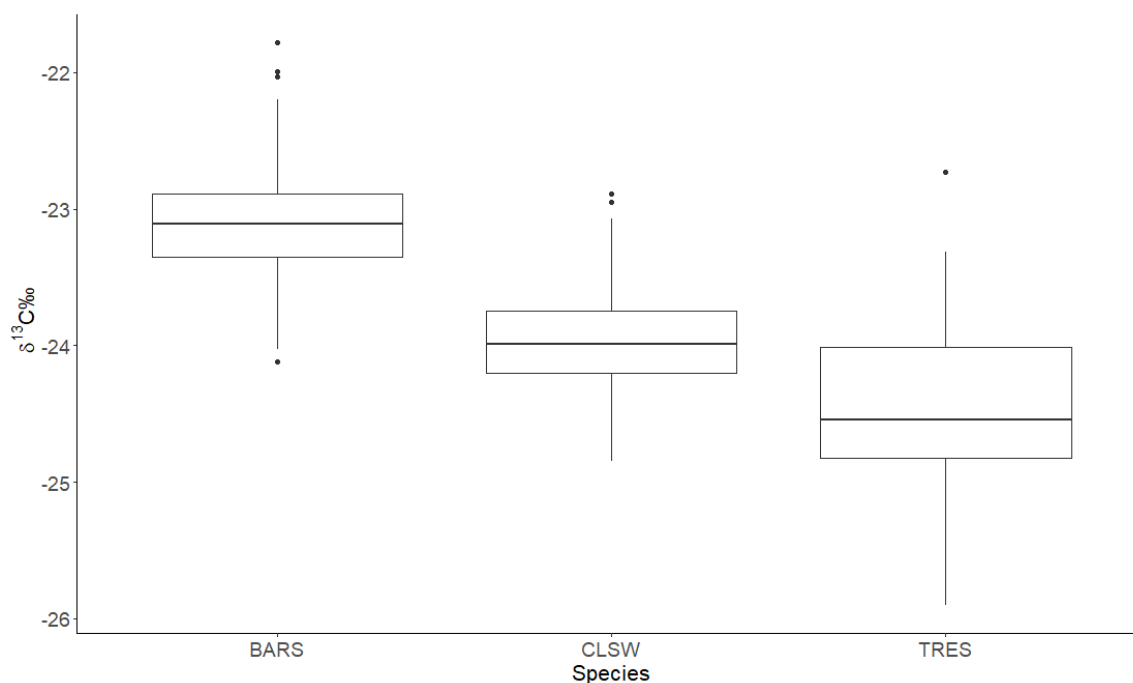
Figure 2.3 Boxplot of nestling Barn Swallow (n=40), Cliff Swallow (n=24), and Tree Swallow (n=31) feather $\delta^{13}C$ values. Feather samples were collected near Guelph, ON, in the breeding season of 2018. Boxes show the first quartile, median, and third quartile. Lines extending from boxes represent minimum and maximum. Points represent outliers.

The best-fitting model indicated that feather $\delta^{15}N$ values were best predicted by species (LMM; $F_{2,85} = 55.11$, p = < 0.0001) and date of sampling (LMM; $F_{1,85} = 11.24$, p = 0.001). There was a negative linear relationship between sampling date and feather $\delta^{15}N$ values (-0.016 ± 0.005‰), indicating that values were lower later in the season. The species – date interaction was non-significant and therefore removed. Barn Swallow feather $\delta^{15}N$ values (10.3‰ to 12.9‰) showed differences when compared to Cliff Swallows (9.1‰ to 11.1‰) and Tree Swallows (9.3‰ to 12.0‰). However, Cliff Swallows and Tree Swallows showed no differences in $\delta^{15}N$ values (Table 2.2, Figure 2.4).
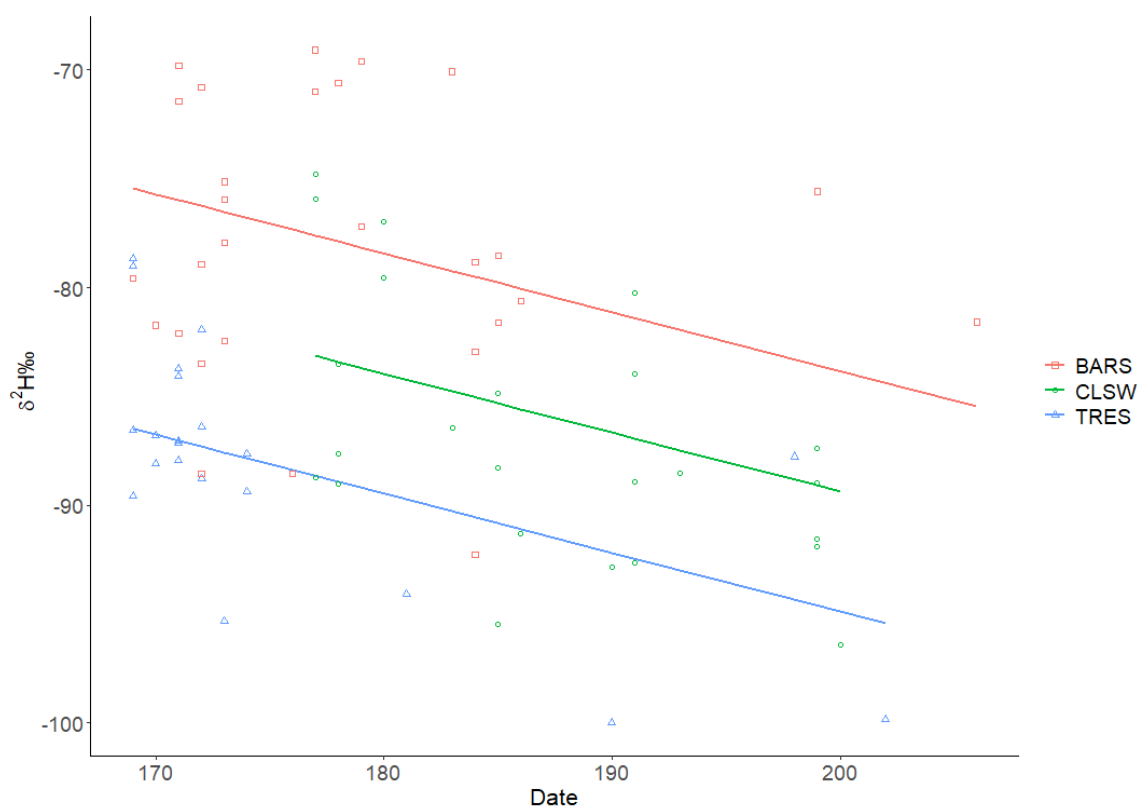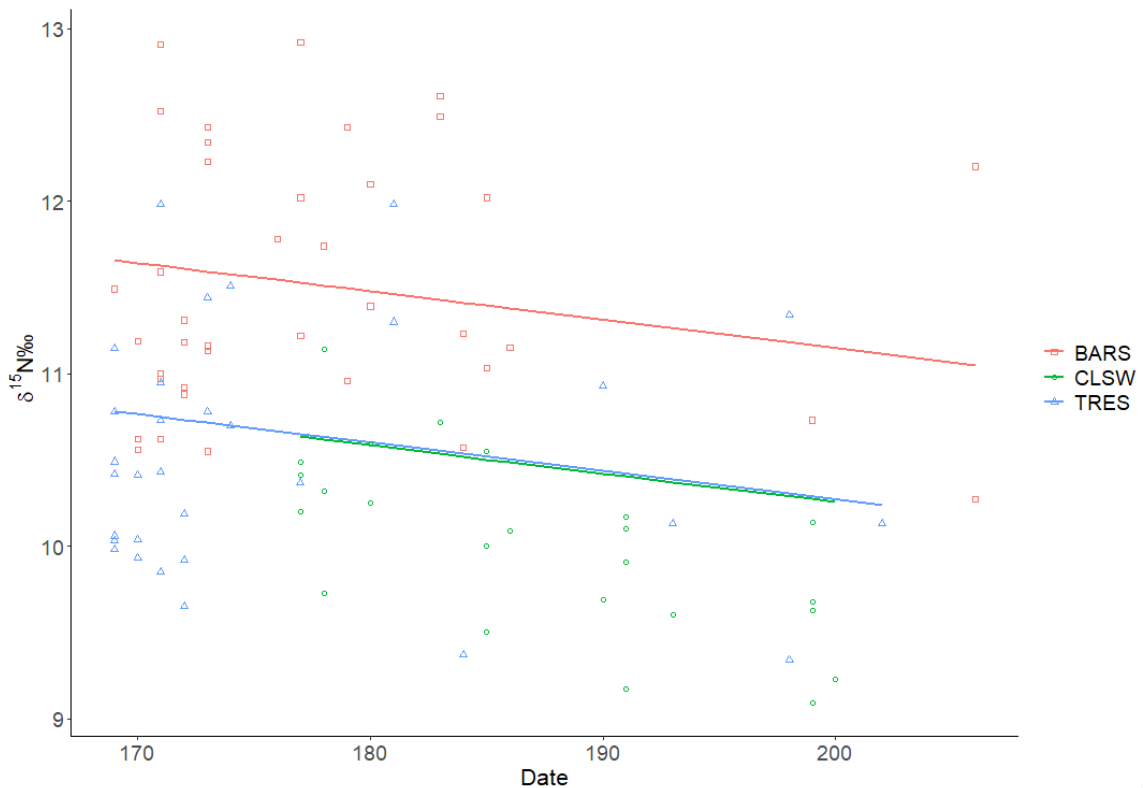

Figure 2.4 Scatterplot of nestling Barn Swallow (n=40), Cliff Swallow (n=24), and Tree Swallow (n=31) feather $\delta^{15}N$ values plotted by collection date (day of year). Feather samples were collected near Guelph, ON, in the breeding season of 2018.

The best model for pre-fledging body condition [mass(g) / wing(mm)] included species, hatch date, and feather δ^2H as predictor variables. The three swallow species differed significantly in their body condition index (Table 2.3), and there was a significant negative relationship between hatch date and body condition index. Feather δ^2H was included in the best model (Figure 2.5) but was not significant. Mass and wing measurements for individuals included in this analysis are in Table 2.4, table including all measured individuals can be found in Appendix A.
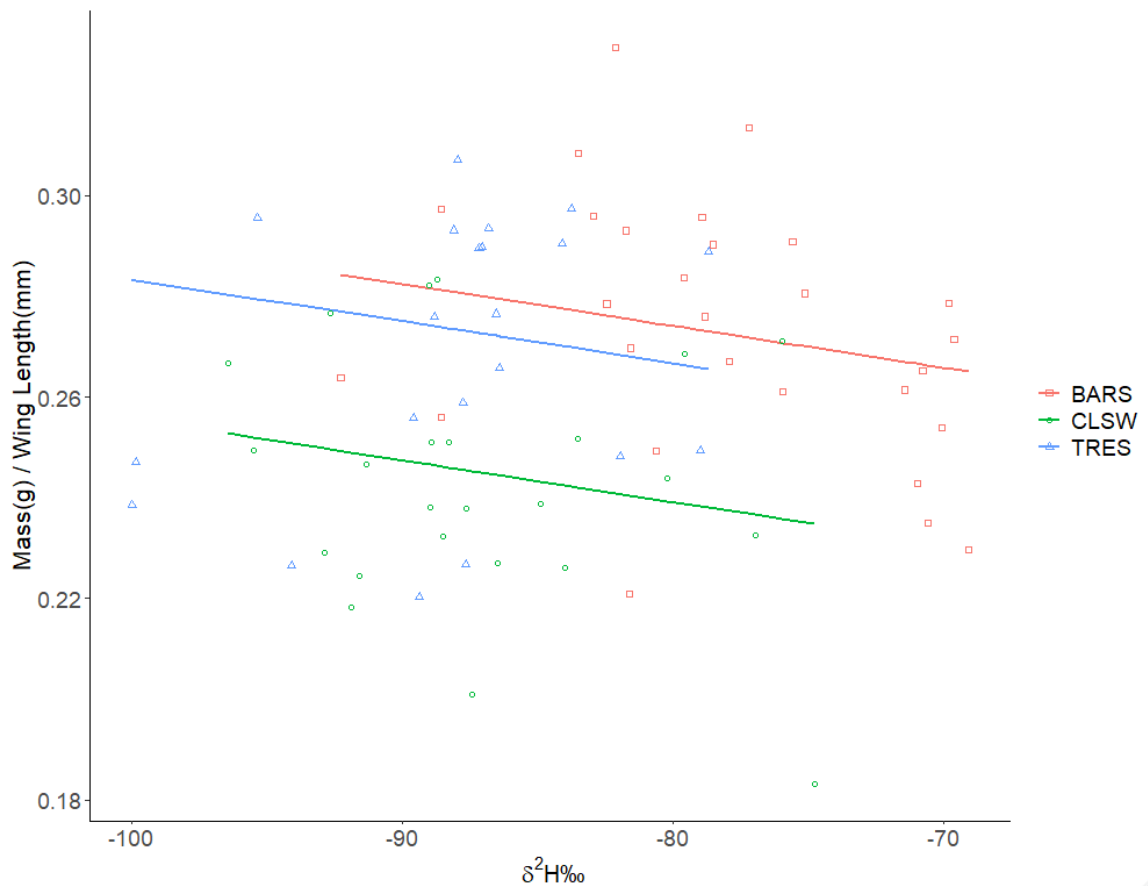
Figure 2.5 Scatter plot of nestling Barn Swallow (n=28), Cliff Swallow (n=24), and Tree Swallow (n=21) body condition index [mass(g)/wing(mm)] plotted by feather δ^2H values. Lines represent predicted values based on median hatch date (June 8 2018).

Table 2.3 Linear mixed effect model results for fledgling (Day 15 – 20) Barn Swallow (n = 28), Cliff Swallow (n = 24), and Tree Swallow (n = 21) mass. Fledglings were measured near Guelph, ON, in the breeding season of 2018.

Mass/Wing ~ Species + Hatch Date + δ^2H					
Terms	df	Estimate	SE	Likelihood Ratio	p-value
Species	2			21.837	<0.0001
Hatch Date	1	-0.00092	0.0003	6.425	0.011
δ^2H	1	-0.00084	0.0005	2.531	0.112
*Random~Site			0.014		
*Residuals			0.022		

*These terms are expressed with standard deviation

Table 2.4 Species-specific summary for measurements taken during banding at Day 15-20.

		Mass (g)			Wing (mm)	
Species	n	Mean	SD		Mean	SD
Barn Swallow	28	20.44	1.46		74.96	4.47
Cliff Swallow	24	22.70	1.60		93.79	4.87
Tree Swallow	21	20.54	1.96		76.76	5.47

2.3.2   Fecal DNA barcoding

DNA was successfully extracted and amplified from 67 fecal samples out of 101 samples across three species (39 Barn Swallows, 14 Cliff Swallows, 14 Tree Swallows). Of these samples, 140 taxa were identified from seven Orders and 28 Families (See Appendix A). Dipterans made up the majority of short-term nestling diet for Barn Swallows, Cliff Swallows, and Tree Swallows (94%, 92% and 91%, respectively; Figure 2.6). One Barn Swallow sample was removed from the redundancy analysis for being an outlier, this was the only sample which did not contain any families within the order Diptera, and was also the only sample which had the family Ichneumonidae – a parasitoid wasp. As a result, it was a highly influential point in the ordination. Using stepwise deletion of predictor variables, site was removed from the model, as it was non-significant. The model did not adequately capture the differences in eigenvalues (constrained 0.11, unconstrained 0.91).[1] The best model included species (db-RDA; $F_{2,62}$ = 2.23, p = 0.005) and date (db-RDA; $F_{1,62}$ = 2.64, p = 0.005; Figure 2.7).

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[1] Negative eigenvalues account for 0.02 of the model proportion, this occurs due to Jaccard distance being used rather than distance being represented in Euclidean space
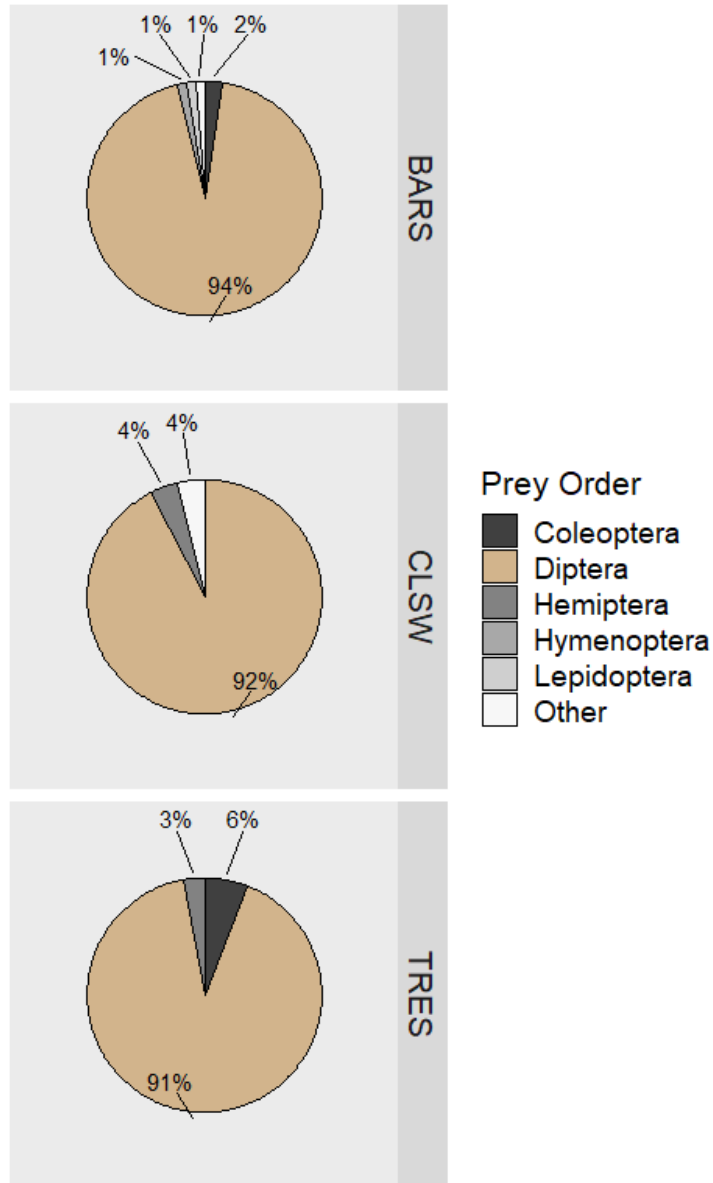
Figure 2.6 Pie charts showing orders of diets found from DNA sequencing of nestling fecal samples of Barn Swallows (n=38), Cliff Swallows (n=14), and Tree Swallows (n=14). Samples were collected during the breeding season of 2018, near Guelph, ON.
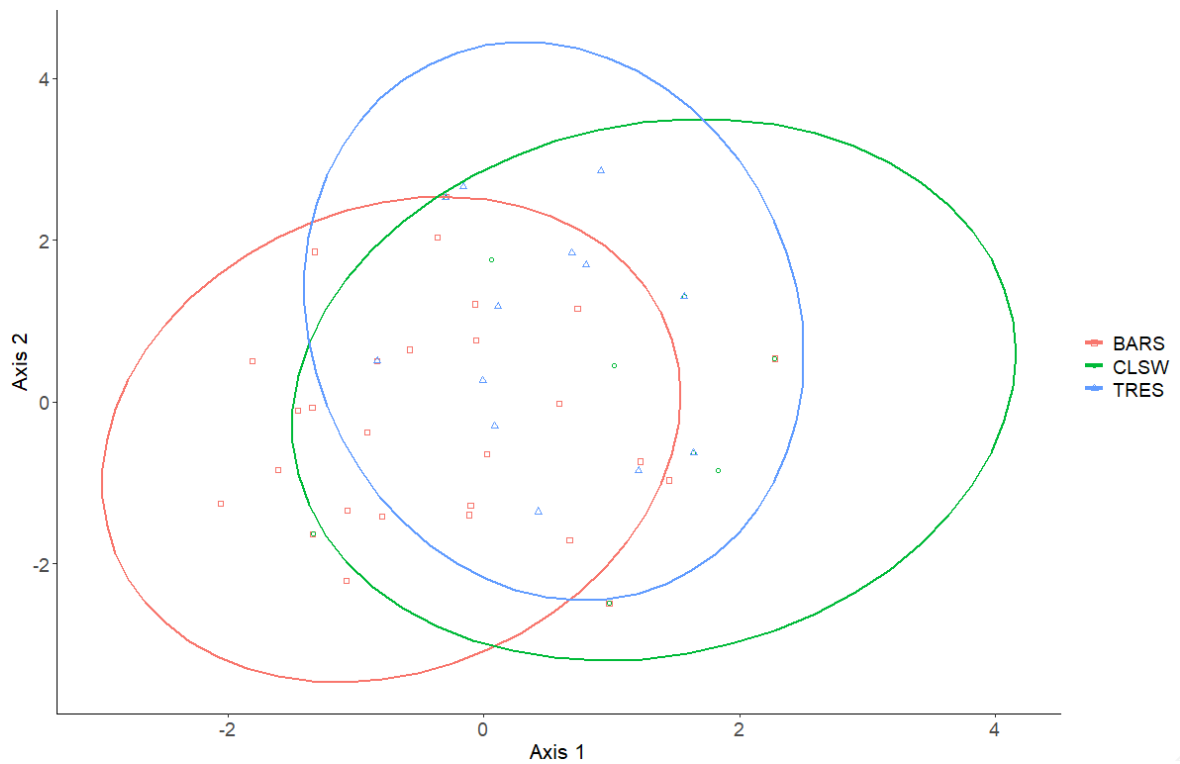
Figure 2.7 Biplot showing the diet of nestling Barn Swallows (n=38), Cliff Swallows (n=14), and Tree Swallows (n=14) based on prey family presence-absence data from DNA barcoding of nestling feces. Samples were collected near Guelph, ON, during the 2018 breeding season.

2.4   Discussion

Using DNA analyses of nestling fecal samples as well as stable isotope analyses of nestling feathers I was able to evaluate the diet of swallows breeding in sympatry in southern Ontario. I tested whether Barn Swallows, Cliff Swallows, and Tree Swallows would partition their dietary resources. Other studies of aerial insectivores occurring in sympatry have found evidence of diet partitioning via foraging distance, airspace segregation as well as differential prey preference (Samuel 1971; Waugh 1978; Orłowski and Karg 2013; Orłowski *et al.* 2015). Nestling feather stable isotope ratios (δ^{13}C, δ^{2}H, and δ^{15}N) showed differences among nestlings of the three swallow species. These results suggest Barn, Cliff and Tree swallows were provisioning different prey items or providing prey from different sources to their young. DNA barcoding of fecal matter showed potential differences between the swallow species, however the model failed to explain a majority of the variation in nestling diets. Overall, I found evidence that Barn, Cliff, and Tree swallow nestlings are likely being provisioned different diets, alluding to potential prey partitioning among species. This prey partitioning may facilitate coexistence between the three species on their breeding grounds.

Stable-hydrogen isotope values differed among feathers of all three species, of which Barn Swallows were the most enriched in the heavier isotope and Tree Swallows were the most depleted. This indicates Barn Swallows are likely less reliant on aquatic emergent prey than the other two species. Barn Swallows typically forage close to their nests (Samuel 1971) and will even forego foraging on larger-sized prey for proximity (Waugh 1978) which results in a faster provisioning rate than Tree Swallows and Cliff Swallows (Ramstack *et al.* 1998). If Barn Swallows were preferentially foraging close to their nests, they may be encountering more prey of terrestrial origin. Furthermore, Cliff Swallows have been documented using highly variable food sources (Brown 1986; Brown and Brown 1996; Ramstack *et al.* 1998) and foraging over much larger areas than sympatric Barn Swallows (Samuel 1971). This variability potentially explains the intermediate δ^{2}H values of nestling Cliff Swallow feathers. Tree Swallow feathers were the most depleted in ^{2}H, indicating more reliance on aquatic emergent prey. These findings are similar to other studies which found aquatic organisms to be an important

dietary source for Tree Swallows (McCarty and Winkler 1999; Quinney and Ankney 1985; Stanton *et al.* 2016). This also explains the individual Tree Swallow sample which needed to be removed from analyses - this individual was likely heavily reliant on aquatic prey, resulting in feather isotope values which were much lower in $\delta^{13}C$ and δ^2H when compared to other swallow feathers. For all three species, nestling feathers became more depleted of ^2H later in the breeding season. This could be due to higher amounts of precipitation causing the food web to become more depleted in ^2H, or due to shifts in diet toward more reliance on aquatic sources.

As well as being enriched in ^2H, Barn Swallow feathers were also the most enriched in ^{13}C. Differences in $\delta^{13}C$ values are strongly associated with primary producers in food webs. Differences in tissue $\delta^{13}C$ values may result from differences in photosynthetic pathways of the plants in the food web. In terrestrial food webs, C3 plants tend to be more depleted of ^{13}C whereas C4 plants tend to be more enriched (Hobson 1999). Diets originating from aquatic sources may also cause lower feather $\delta^{13}C$ values when compared to terrestrial food webs. These differences are highly site-specific (Peterson and Fry 1987; France 1995; Doucett *et al.* 1996; Doucett *et al.* 2007). However, δ^2H values are generally more reliable at differentiating between aquatic and terrestrial sources of diet (Doucett *et al.* 2007; Voigt *et al.* 2015) and the feather δ^2H and $\delta^{13}C$ values for the three species show similar trends wherein Barn Swallow feathers are most enriched and Tree Swallow feathers are most depleted.

Additionally, $\delta^{15}N$ values of nestling Barn Swallow feathers were more enriched than the other two swallow species. Stable nitrogen isotope ratios increase with trophic level (Hobson and Welch 1992, Hobson *et al.* 1994). However, tissues can also become more enriched in ^{15}N from agricultural land-use practices such as fertilizer application which increases environmental $\delta^{15}N$ values, and from tillage which brings minerals to the soil surface to be taken up by plants (Hobson 1999; Szpak 2014). Nitrogen from fertilizer application may also be lost into the environment through ammonia volatilization (Ma *et al.* 2010). Ammonia volatilization results in a loss of isotopically light ammonia gas, leaving the remaining soils enriched in ^{15}N. Barn Swallows typically forage close to their nests and as a result may consume organisms with higher $\delta^{15}N$ values when nesting in

agricultural areas. Orlowski *et al.* (2015) found Barn Swallows consumed high biomass of coprophilous insects, this could increase $\delta^{15}N$ values as the manure in which the insects thrive is enriched in ^{15}N compared to non-agricultural environments (Szpak 2014). Orlowski *et al.* (2015) also found that Barn Swallows took prey associated with crops which would likely have higher $\delta^{15}N$ values due to fertilizer inputs. Cliff Swallow and Tree Swallow feathers showed no difference in $\delta^{15}N$ values, this is likely the result of the two species foraging on different prey which have similar $\delta^{15}N$ signatures. The exact source of $\delta^{15}N$ signature is unknown. However, the differences in both $\delta^{13}C$ and $\delta^{2}H$ feather values between Cliff and Tree swallow nestlings indicate they are likely being provisioned different prey, or prey from different locations. Stable nitrogen isotopes of nestling feathers declined as the breeding season progressed for all three species. This may be due to timing of fertilization of agricultural lands contributing to higher $\delta^{15}N$ values earlier in the season.

There was a significant difference between the body condition index of the three swallow species. This was likely due to the different ages at which the swallows were sampled. Aerial insectivore nestling mass increases above adult mass and peaks at Day 12 - 15, then decreases prior to fledging (Stoner 1945; Ricklefs 1968). Barn and Tree swallows were measured at approximately peak mass, whereas Cliff Swallows were measured prior to fledging. Swallow nestling condition showed a negative relationship with hatch date as well as feather $\delta^{2}H$. Though not significant, the relationship between feather $\delta^{2}H$ values and nestling condition may indicate potential benefits of aquatic prey provisioned to nestlings. Twinning *et al.* (2016) found that a more aquatic-based diet improved the growth and body condition of nestling Tree Swallows.

Fecal DNA analysis indicated that there may be differences in prey composition between the three swallow species. However, the results are unreliable, as the model failed to capture the majority of the variation between samples. Dipterans were the most detected Order (>90%) for all three species. These findings are consistent with previous reports of nestling diet for swallows (Waugh 1978; McCarty and Winkler 1999; Kusack 2018; McClenaghan *et al.* 2019). However, most families occurred in five or less fecal samples, making comparisons of provisioned diet between swallow species difficult. In addition,

sample size was reduced as there were no prey detected for some fecal samples. Future analyses will involve analyzing nestling feces for dietary differences by splitting the prey families into functional groups, similar to previous studies of aerial insectivore diet (Orlowski and Karg 2013; Orlowski *et al.* 2015). I was unable to analyze diet beyond presence – absence data, as DNA barcoding does not give quantitative results for dietary analyses. Therefore, it is impossible to know whether any one of the swallow species is preferentially foraging on particular prey items.

2.5   Conclusions

My data suggest that Barn, Cliff and Tree swallows breeding in sympatry may be provisioning different prey to their young, alluding to resource partitioning. Partitioning may occur due to differences in foraging height (Brown *et al.* 2017; Brown and Brown 2019), morphology (Waugh 1978), or foraging distance from the nest (Samuel 1971; Brown and Brown 1996; Ramstack *et al.* 1998). Partitioning of resources is thought to facilitate coexistence between ecologically similar species (Hutchinson 1957). Additionally, loss of prey is believed to be a driver for aerial insectivore declines (Benton *et al.* 2002; Twining *et al.* 2016). Previous studies on Tree Swallows have found that diet quantity has had no significant effect on nestling growth (Twinning *et al.* 2016; Imlay *et al.* 2017) but rather diet quality may play an important role. As Twinning *et al.* (2016) suggest, aquatic diets contribute to improved nestling growth and condition as they contain more omega-3 fatty acids. Nestlings in better condition are more likely to fledge successfully and survive post-fledging (Naef-Daenzer *et al.* 2001; Evans *et al.* 2019), which is an important contributor to aerial insectivore population growth rates (Cox *et al.* 2014, Cox *et al.* 2018). This study emphasizes the importance of determining whether differential population declines in Barn, Cliff, and Tree swallows may be linked to differences in prey quality provisioned to nestlings.

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Chapter 3

3   Post-fledging movements of juvenile Barn, Cliff and Tree swallows

3.1. Introduction

The post-fledging period is defined as the time when young have fledged but have not yet migrated and is considered one of the most critical life stages for migratory songbirds (Cox *et al.* 2014; Naef-Daenzer and Grüebler 2016; Evans *et al.* 2019). This period is important as juveniles must navigate unknown habitats, fuel for migration, and prospect for future breeding sites all while avoiding predation. Following fledging, young stay close to the nest as they are initially dependent on adults. The period immediately following fledging is a time of high mortality, when young are most conspicuous to predators possibly due to their begging calls (Vitz and Rodewald 2010; Cox *et al.* 2014; Evans *et al.* 2019). After this period, fledglings become independent and eventually disperse. This independent phase is also associated with high mortality as young must avoid predators while learning to forage for themselves and navigate unknown landscapes. Due to the vulnerable nature of the post-fledging period, researchers have sought to gain more understanding of this period by tracking small-scale movements, as well as larger, more unknown movements made by fledglings (e.g. Baker 1993; Kershner *et al.* 2004; Cormier and Taylor 2019).

Fledglings may undertake extensive pre-migratory movements, for which there are many theories. These movements may occur when fledglings begin moving in the direction of their migratory path, without entering a migratory physiological state (Rappole and Ballard 1987; Mitchell *et al.* 2010; Brown and Taylor 2015) but have also been attributed to exploratory movements in order to search for future breeding sites (Rappole and Ballard 1987; Mitchell *et al.* 2010) or to find distinguishable landmarks, enabling them to relocate the natal region in the spring (Baker 1993; Mitchell *et al.* 2010; Brown and Taylor 2015; Cormier and Taylor 2019). Fledging success and fledgling survival are key factors in population growth rates of songbirds (Bonnot *et al.* 2013; Cox *et al.* 2014; Cox

et al. 2018). Beyond that, conservation of avian species as a whole is most effective with complete life history information.

Since the 1980's, aerial insectivores have been experiencing substantial population declines in North America (Nebel *et al.* 2010). These population declines differ among species and are the heaviest in the northeastern portion of North America (Nebel *et al.* 2010; Michel *et al.* 2016). Cox *et al.* (2018) indicated that fledging success and juvenile recruitment were important factors in the variation of population growth rates in Tree Swallows (*Tachycineta bicolor*) and could be a potential cause for aerial insectivore declines. As a result, understanding the post-fledging period may be an important step toward understanding the population dynamics of aerial insectivores.

Three avian aerial insectivore species—Barn Swallows (*Hirundo rustica),* Cliff Swallows (*Petrochelidon pyrrhonata)* and Tree Swallows —all share breeding grounds in southern Ontario. The most typical sites where all three species are found breeding in sympatry are agricultural areas. In these instances, Barn and Cliff swallows build their nests inside barns and other similar constructions, whereas Tree Swallows must find natural cavities or rely on nesting boxes provided by humans for their nests. These swallows also share a food source, as they are all aerial insectivores - a guild of migratory birds which catch and eat insects during flight. However, these species do not share all characteristics. Notably, Tree Swallows are short-distance migrants, unlike Barn and Cliff swallows which are long-distance migrants. In addition to this, a portion of Barn Swallows may nest twice during the breeding season, whereas Cliff and Tree swallows typically nest once.

Previous attempts to understand post-fledging movements of passerines have been difficult, as banding and recapture of fledglings may not be reliable if juveniles disperse and are not recaptured (Cox *et al.* 2014). Instead, radio-tagging and tracking of individuals has proven to be a useful method for studying the post-fledging period. This method has been successfully used to determine fine-scale movements (Kershner *et al.* 2004; Berkeley *et al.* 2007), as well as broad-scale movements (Brown and Taylor 2015; Cormier and Taylor 2019) in songbirds. The Motus Wildlife Tracking System is a

collaborative project which involves the use of automated telemetry towers to track small flying organisms (Taylor *et al.* 2017). These towers are useful for studying broad-scale movements of both adult and juvenile songbirds. Using this system, I aimed to evaluate the post-fledging movements of three sympatric avian aerial insectivores in southern Ontario. I examined whether sympatric Barn, Cliff, and Tree swallows show differences in their post-fledging movements. To do so, I radio-tagged nestlings of all three species and tracked their post-fledging movements using the Motus automated telemetry array.

Differences among the three swallow species during the post-fledging period may be critical in understanding differential population declines. Due to high mortality, this period is thought to be a population bottleneck for aerial insectivore species (Cox *et al.* 2018; Evans *et al.* 2019) as well as other songbirds (Naef-Daenzer and Gruebler 2016; Cox 2014). Longer parental care post-fledging has been associated with higher survival into the independent period (Grüebler and Naef-Daenzer 2010). So, if the swallow species spend varying amounts of time in their natal area, it may be contributing to differential declines. In addition, any differential post-fledging movements that the juveniles make may expose them to different threats during this vulnerable life-stage.

3.2. Methods

Post-fledging movements of juvenile swallows were studied by radio tagging nestlings at 9 farms from May-July 2018 within Wellington county, near Guelph, ON (43.55° N, 80.25° W) (Figure 3.1). These locations were grouped into seven sites as some farms were adjacent to one another. Each of these sites had all three species of swallow breeding sympatrically (average clutch initiation was May 25 2018 for Barn Swallows, May 29 2018 for Cliff Swallows, and May 24 2018 for Tree Swallows). However, Guelph Lake Conservation Area only had Tree Swallows. All Barn and Cliff swallow colonies were located inside barns, whereas Tree Swallows were in nesting boxes outside.
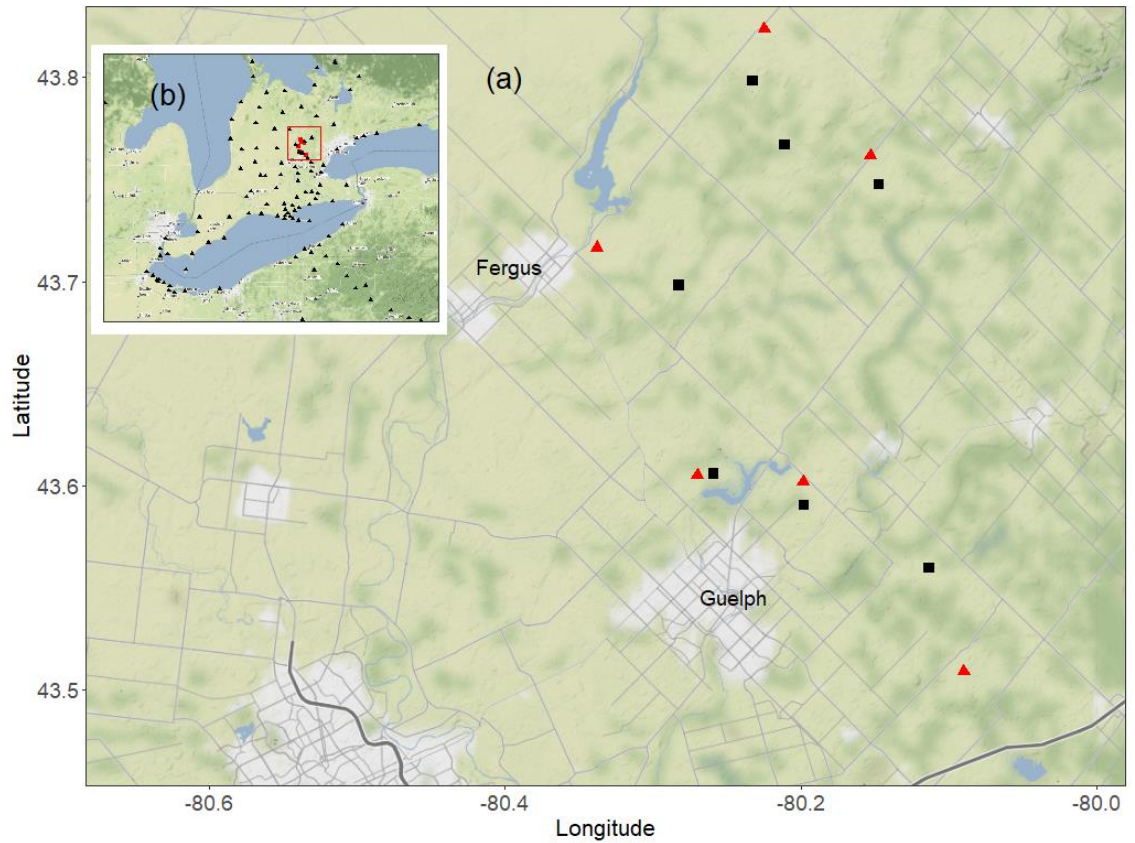
Figure 3.1 The location of study sites (squares) and automated receiving towers (triangles) in (a) southern Ontario, and (b) Wellington County from May – September 2018.

3.2.1.   Nest monitoring and radio tagging

Nest monitoring began in early May and involved one to two visits weekly to establish approximate onset of laying. If eggs were present upon arrival, it was assumed one egg was laid every 24 hours for all three species (Brown and Brown 2019; Brown *et al.* 2017; Winkler *et al.* 2007). Once clutch initiation was approximated, nests were monitored at least twice per week to estimate clutch size and hatch date. Timing of hatching was predicted based on a 14-day incubation period after the penultimate egg was laid for Barn Swallows (Brown and Brown 2019), Cliff Swallows (Brown *et al.* 2017) and Tree Swallows (Winkler *et al.* 2007). To determine hatch day as accurately as possible, nests were visited before predicted hatch day as well as every few days thereafter. Hatch day was assigned based on evidence of hatching (eggshells present, unhatched eggs remaining, and nestlings still being wet). Hatch day was considered day zero. For nests where hatch day could not be assigned, nestlings were aged based on feather tract development (Marsh 1980; Stoner 1935, 1945).

All nests were visited between Day Six and Ten after hatching, during which Barn and Tree swallow nestlings were banded with a uniquely numbered United States Geological Survey aluminum leg band. For each banded nestling, mass, age and length of wing at rest (from the wrist joint to the longest primary) were documented. Barn and Tree swallow nests were also ideally visited when the young were 15-days old, at which point the above-mentioned measurements were taken (see Appendix A for measurement summary). It was not possible to visit all nests at Day 15 therefore some Tree Swallows were measured on day 16 or 17. At this time, one nestling from each nest was outfitted with a radio transmitter. Hatch-year Cliff Swallows were challenging to access due to their elongated mud nest entrance-tube. Cliff Swallow nests were visited at roughly Day 20 and nests were examined using a flashlight and mirror. During inspection some nestlings may fledge the nest, and so mistnets were erected to catch them. If the entrance to the nest was not elongated, nestlings could be removed from the nest. Otherwise, the entrance was manually shortened. At this point Cliff Swallows were banded, weighed, measured and were fitted with a radio transmitter before being returned to their nests. After tagging, young were expected to fledge within 1 - 7 days. Average fledging age is

19-20 days, 20-21 days, and 18-22 days for Barn Swallows (Brown and Brown 2019),
Cliff Swallows (Brown *et al.* 2017), and Tree Swallows (Winkler *et al.* 2007)
respectively. Nests were ideally revisited within one week after the estimated fledging
date to determine whether young had fledged. This was done by checking inside and
beneath nests for any dead young. Each radio transmitter (Lotek, model NTQB2-2) was
programmed with a unique output which transmitted at a frequency of 166.38MHz every
9.7 – 10.1 seconds, resulting in an estimated life span of approximately 60 days
(www.lotek.com). Transmitters were fitted using a two leg-loop harness (Rappole and
Tipton 1991), made from elastic string.

3.2.2. Automated telemetry array

To determine post-fledging movements of the three swallow species, radio tagged
individuals were tracked using the Motus Wildlife Tracking System – an array of
automated telemetry units (www.motus.org). Each automated telemetry unit has 1-4
antennae which are connected to a SensorGnome receiver (Compudata, London Ontario).
When a radio transmitter is within range, the SensorGnome will record the tag identity,
which antennae it was detected on and signal strength, as well as GPS time and location.
Antennae can detect a radio transmitter up to 15km (Taylor *et al.* 2017) depending on
topography. The data output from each automated receiver in the Motus array is pooled
together and contains information on each detection for every active tag. This
information is filtered so each project receives information for their own transmitters
from all automated receivers in the array. In 2018, our project included five automated
receivers in the Wellington County region to increase detectability, Guelph Lake
Conservation Area also has their own automated receiver (Figure 3.2). The Motus array
consisted of 321 automated receivers from May – September 2018.

3.2.3. Data analysis

All data analysis was done using R Studio (Version 1.2.1335) and R (Version 3.5.3;
RStudio Team 2015; R Core Team 2019). Data was checked for potential false detections
by first removing those which had a run length of three (i.e. had only three bursts) or less
due to the high probability of being false detections. Distance between towers as well as

time between subsequent detections was calculated in order to determine the speed at which individuals were travelling. Any detections showing swallows travelling above maximum flight speed were removed (Barn Swallows 20m/s (Liechti and Bruderer 2002), Cliff Swallows 15.5m/s (Shelton *et al.* 2014), and Tree Swallows 10m/s (Bowlin and Winkler 2004)).

To calculate cumulative distance, the sum of between-tower distances for sequential detections was calculated. Distances of <15km were not included, to account for the possibility that a bird is being detected at two towers simultaneously. Cumulative distance is not an exact measure of distance, as individuals could be moving and not be detected by the array. To calculate distributions of the swallow species after they had dispersed from their natal site, first, daily centers of activity were calculated to account for differences in number of detections among individuals (package VTrack; Campbell *et al.* 2012). This is calculated as the mean of the receiver locations the individual is detected on, weighted by the number of detections on each receiver (Udyawer *et al.* 2018). Using the daily centers of activity, a 75% kernel utilization distribution was estimated for each of the three species (package adehabitatHR; Calenge 2006). The estimates of utilization distributions were then used to determine the extent of overlap the three swallow species had during the post-fledging period.

3.2.4.   Statistical analyses

Residency time at the natal site was analyzed using survival analysis (R package survival; Therneau 2015), the 'event' of interest was number of days until fledglings were first detected outside of their natal area. The timescale is the number of days past fledging age, as the young are unlikely to be detected outside of their natal area prior to fledging. Fledging age used was 19 days for Barn Swallows, 20 days for Cliff Swallows, and 18 days for Tree Swallows, as this is likely the earliest they would be detected outside their natal area. This is an approximate residency time as the fledglings could be moving outside the natal area and not be detected. Using a Weibull accelerated failure time model, the number of days fledglings spent at the natal site was compared for Barn, Cliff and Tree swallows. The model included site, species, and hatch day as predictor variables. For movement analyses, the best model was determined with backward

selection using the lowest Akaike information criterion for small sample size (AICc) value, except if ΔAICc < 2 in which case the simplest model was chosen.

3.3. Results

Of the 165 swallows that were tagged (50 Barn, 60 Cliff, and 55 Tree Swallows), 116 swallows were detected by the Motus automated telemetry array, these included 36 Barn Swallows, 51 Cliff Swallows, and 29 Tree swallows. Of these, 79 swallows were detected after dispersing from their natal area (21 Barn, 44 Cliff, and 14 Tree Swallows). The best-fitting survival model indicated an effect of site as well as an interaction between species and hatch date (Table 3.1; model selection in Appendix C). Regardless of hatch date, Barn Swallows and Tree Swallows showed no difference in the number of days spent in their natal area. In contrast, there was a significant negative relationship between hatch date and the number of days Cliff Swallow fledglings remained in their natal area, indicating that later-hatching Cliff Swallows left the natal area faster than early-hatching Cliff Swallows (Table 3.2). Early-hatching Cliff Swallows spent a similar amount of time in the natal area as Barn and Tree swallows. However, late-hatching Cliff Swallows were detected outside of their natal area at a younger age than Barn or Tree swallows (Figure 3.2).

Table 3.1 Results for significant terms of the Weibull survival analysis used to predict the number of days fledgling Barn Swallows (n = 36), Cliff Swallows (n = 51), and Tree Swallows (n = 29) would remain in their natal area. Swallows were radio-tagged near Guelph, ON, in the breeding season of 2018.

Terms	df	Deviance	Resid. Df	-2*LL	Pr(>Chi)
Species	2	9.00	114	531.77	0.011
Hatch	1	9.98	112	522.78	0.0016
Site	6	15.26	105	497.53	0.018
Species : Hatch	2	0.439	103	484.72	0.0016

Table 3.2 Post-hoc results for species-hatch day interaction of Weibull survival analysis, used to predict the number of days Barn Swallows (n = 36), Cliff Swallows (n = 51), and Tree Swallows (n = 29) would remain in their natal area. Swallows were radio-tagged near Guelph, ON, in the breeding season of 2018.

	Estimate	SE	z	p-value
BARS:Hatch	-0.013	0.024	-0.52	0.60
CLSW:Hatch	-0.15	0.032	-4.87	< 0.0001
TRES:Hatch	-0.041	0.049	-0.83	0.41
Scale	0.428			
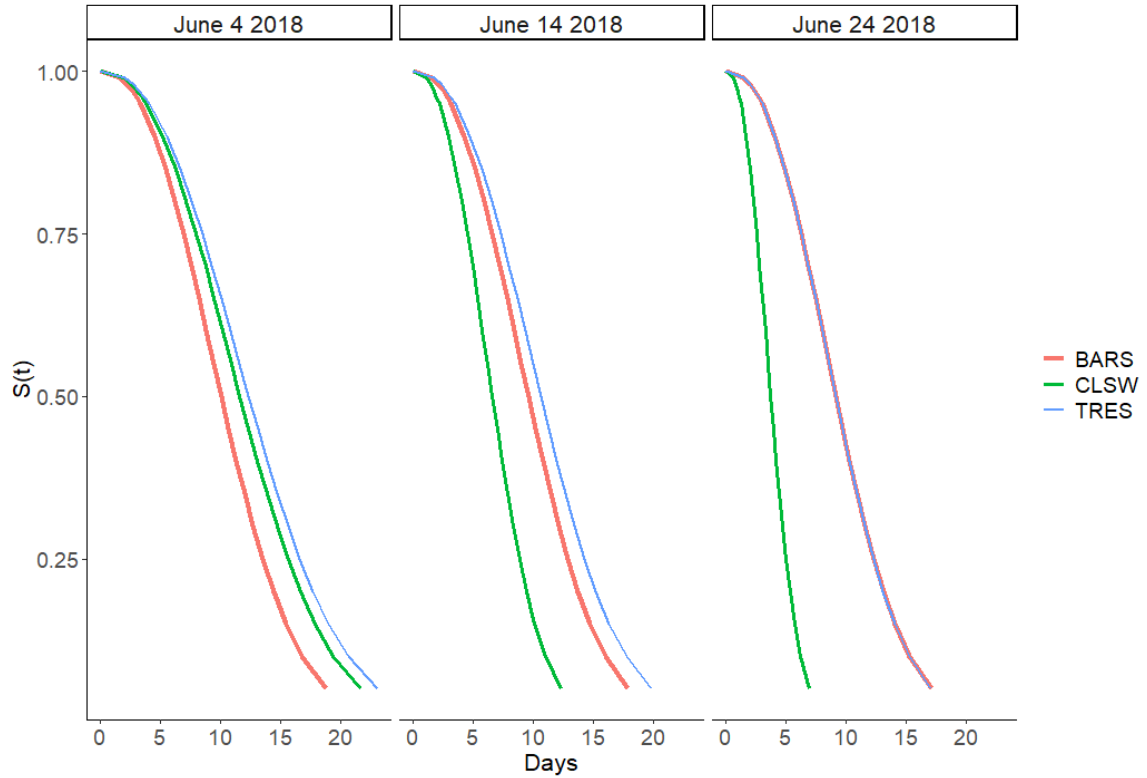
Figure 3.2 Predicted probability for Barn Swallows (n = 36), Cliff Swallows (n = 51), and Tree Swallows (n = 29) hatching on (a) 4 June 2018, (b) 14 June 2018, (c) 24 June 2018, to remain in their natal area dependent on age. Swallows were tagged near Guelph, ON, in the breeding season of 2018.

Barn Swallows (225.7 ± 216.1km), Cliff Swallows (287.3 ± 180.6km), and Tree Swallows (246.8 ± 157.2km) all showed substantial variation in cumulative distance travelled. Of the fledglings that were tracked until migration Barn Swallows travelled 357.61 ± 224.63km, Cliff Swallows travelled 386.02 ± 253.08, and Tree Swallows travelled 287.34 ± 134.93km. All distances are mean ± standard deviation. There was also overlap in the distributions of the three species, once they had dispersed from their natal area (Figure 3.3). Based on a 75% kernel density contour for each of the three species' daily centers of activity, Barn and Cliff swallows showed the most overlap (80.94%), followed by Barn and Tree swallows (63.18%), and finally Cliff and Tree swallows Showed the least overlap (58.21%).
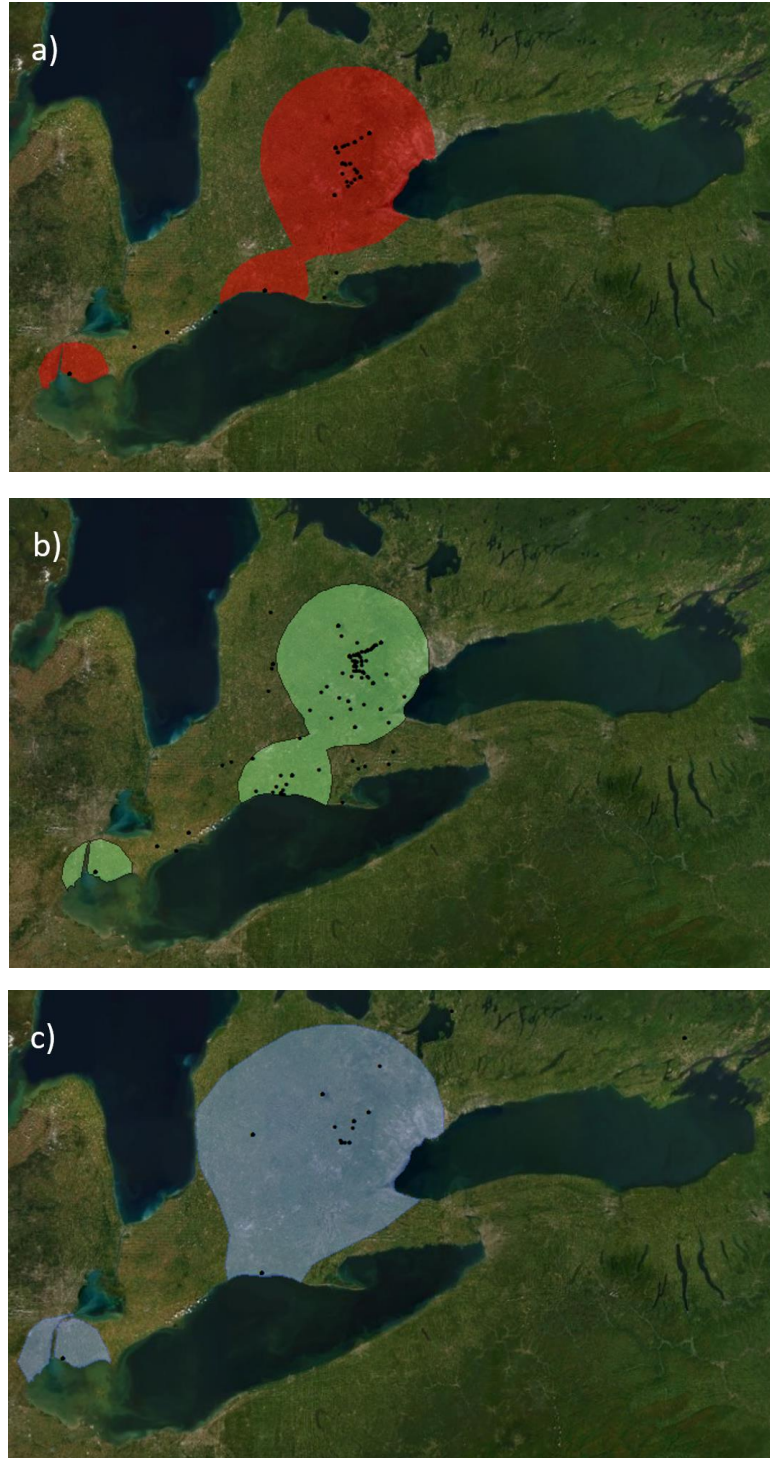
Figure 3.3. Map of the 75% kernel utilization density contours for a) Barn (n = 21), b) Cliff (n = 41), and c) Tree Swallow (n = 14) fledglings once they have departed their natal site. Kernel density is estimated using daily center of activity estimates.

3.4.   Discussion

With the use of the Motus Wildlife Tracking System, I was able to evaluate the post-fledging movements of sympatric swallows. Specifically, I tested whether sympatric Barn, Cliff, and Tree swallow fledglings showed differences in the time they spent at their natal site as well as the distance moved during the post-fledging period. Similar to other studies on migratory songbirds during the post-fledging period (Brown and Taylor 2015; Cormier and Taylor 2019; Evans 2018), total distance travelled by Barn Swallows (357.61 ± 224.63km), Cliff Swallows (386.02 ± 253.08km), and Tree Swallows (287.34 ± 134.93km) that were tracked until migration suggested that fledglings may be making extensive exploratory movements (Figure 3.4), as opposed to movements strictly toward their migratory route as the locations typically used to migrate south from southern Ontario are approximately 115km – 250km from the study area.
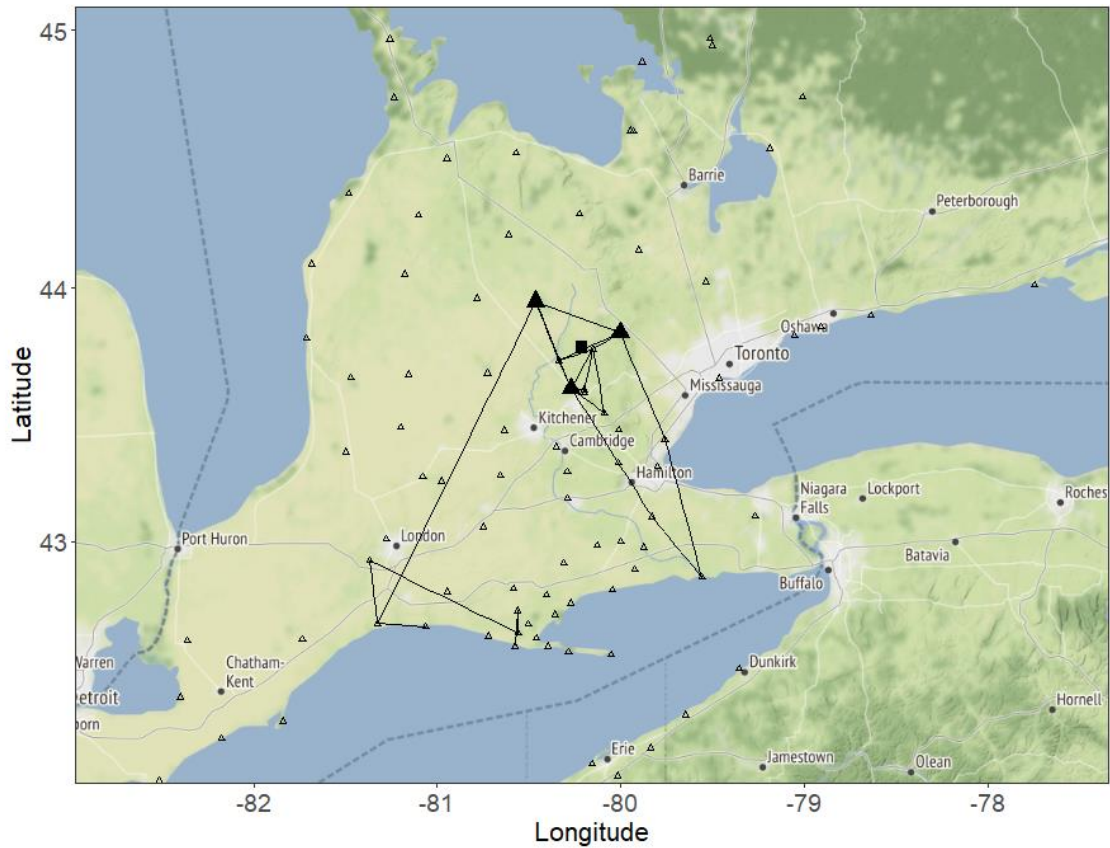
Figure 3.4 Post-fledging movements made by a fledgling Cliff Swallow tagged in Wellington County (black square), in the breeding season of 2018. Open triangles represent automated receiving towers. Closed triangles are conservation areas frequented by the fledgling.

Cliff Swallow fledglings showed changes in their duration at the natal site depending on timing of hatch. Earlier hatching Cliff Swallows stayed in their natal area as long as Barn and Tree swallows. However, later hatching Cliff Swallows were detected outside of their natal area after fewer days post-fledging than the other two species. Barn and Tree swallows showed no difference in the number of days they remained in their natal site, regardless of hatch date. Cliff Swallows are colonial, as a result they are often seen migrating in groups numbering into the thousands (Brown *et al.* 2017). If Cliff Swallows fledge early, they may be afforded more time in the natal area if they are waiting for a group movement. If Cliff Swallows leave at approximately the same time, later-hatching Cliff Swallows will inevitably be migrating younger. In general, later-hatching individuals have shorter post-fledging period. These individuals have been found to accelerate development and disperse at a younger age (Styrsky *et al.* 2004; Evans 2018). Evans (2018) found that second brood Barn Swallow fledglings migrate at a younger age than first broods, so if Barn Swallows stay in the natal area for the same duration regardless of hatch date they may be shortening another stage of the post-fledging period. Additionally, the present study aimed to avoid radio-tagging second brood individuals, and so there may not have been enough difference between hatch dates to see a change in residency time in the natal area. Historically, Barn Swallows and Tree Swallows have been solitary nesters (Brown and Brown 2019; Winkler *et al.* 2011); as a result, individuals of these species may show staggered dispersal from the natal area.

Detectability needs to be taken into consideration, as it may possibly affect total apparent distance travelled as well as the age in which fledglings are detected outside their natal site. Tree Swallows had much lower detectability than either Barn or Cliff Swallows, as only 14 of the 55 Tree Swallow fledglings were ever detected outside of their natal area. Also, adult Tree Swallows tagged in the same area had extremely low detection rates (M. Cadman, unpublished data). This could be occurring for multiple reasons. Low numbers of individuals being detected could be a result of tag loss, individual deaths, topography, or that the swallows are flying in a way that is not easily detected by automated towers. Cliff Swallows were detected the most, as 44 of the 60 individuals tagged were detected outside their natal area. These findings are consistent with Lenske and Nocera (2018)

who found that when comparing Cliff and Barn Swallows in an agricultural area near Peterborough, ON, Canada, Cliff Swallows tended to be detected more than Barn Swallows. This has been attributed to Cliff Swallows foraging at a higher elevation than Barn Swallows (Samuel 1971; Brown *et al.* 2017; Brown and Brown 2019).

In addition, this research has highlighted some potentially significant habitats for Barn, Cliff, and Tree swallows. Once fledglings have left their natal area, they appear to be using habitats with open water features (Figure 3.5). This may be contributing to the considerable overlap in the distribution among fledgling Barn, Cliff, and Tree swallows once they have left their natal area. The use of communal roosting sites near open water by aerial insectivorous species has been previously documented (Kirby 1978; Winkler 2006). However, the importance of these habitats has not been extensively explored in southern Ontario (but see Falconer *et al.* 2016). Sites with greater number of individuals detected include Luther Marsh Wildlife Management Area, Guelph Lake Conservation Area, Forks of the Credit Provincial Park, and Holiday Beach Conservation Area. A tower in Wellington County two kilometers from Belwood Lake Conservation Area also had a higher number of individuals detected. Though the towers can detect up to 15km (Taylor *et al.* 2017), it appears as though these habitats are attracting fledgling swallows.
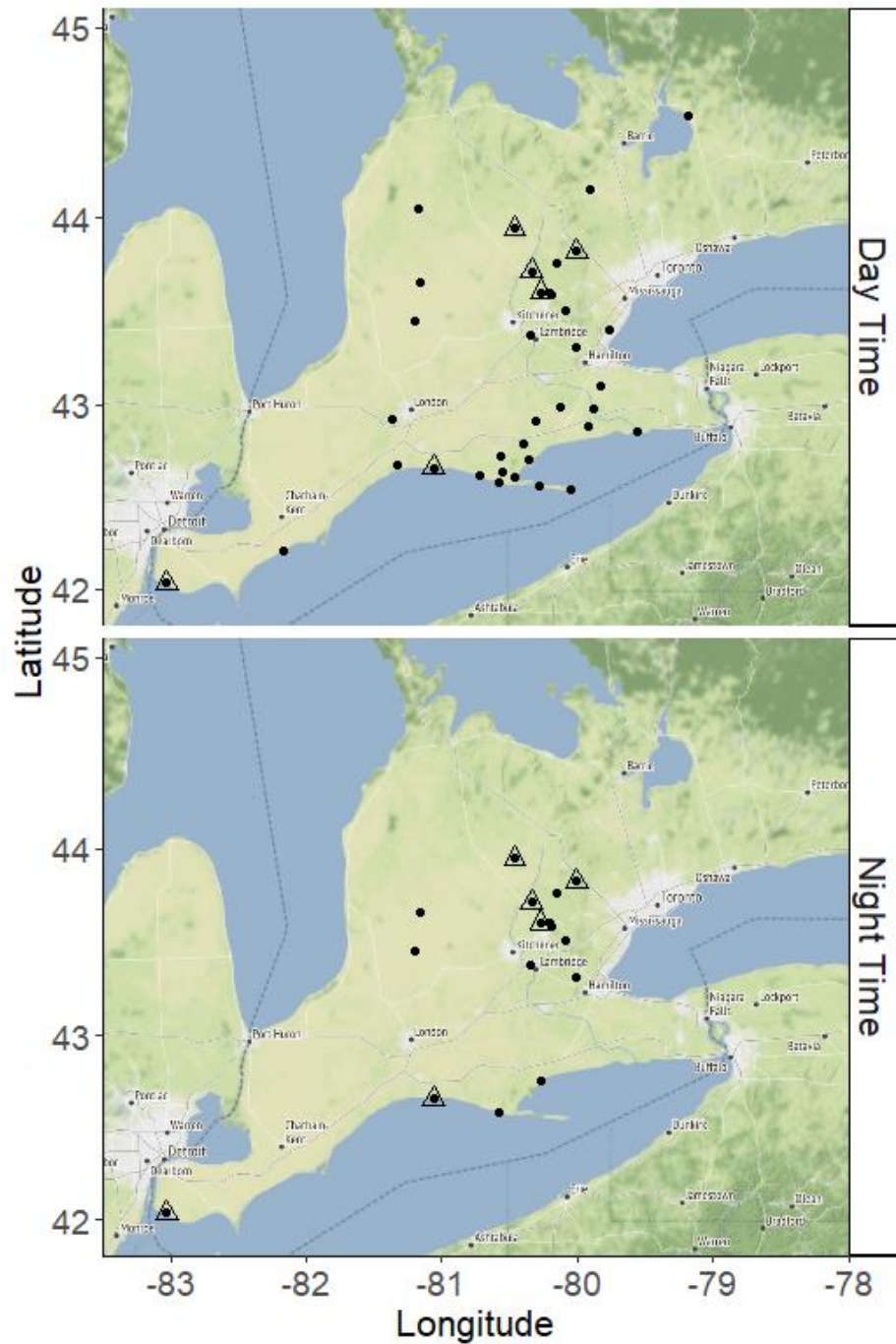
Figure 3.5. Maps of southern Ontario showing the hourly detection locations of fledgling Barn, Cliff, and Tree swallows during the day time (6am – 8pm) and the evening time (9pm – 5am). Swallows were tagged in the breeding season of 2018 near Guelph, ON.

3.5.　　Conclusions

The differential detectability of Barn, Cliff and Tree swallows limited comparisons that could be made regarding their post-fledging movements. However, I found evidence that Cliff Swallow fledglings which hatched later in the season spent less time in their natal area. Brown and Brown (1996) found that later-hatching Cliff Swallows showed lower first-year survival. These individuals may experience negative effects due to accelerated development (Styrsky *et al.* 2004), or have a shorter dependent phase, which has been linked to lower survival (Grüebler and Naef-Daenzer 2010). In addition, this study presents new information as to potential key habitats for fledgling swallows. Such information may be important for advising future conservation efforts of aerial insectivores by demonstrating the need for vital communal roosting sites.

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Chapter 4

4 General Discussion

4.1 Key findings

4.1.1 Nestling diet source

This research suggests that sympatric Barn, Cliff, and Tree swallows are partitioning their resources by provisioning different prey items or providing prey from different sources to their young. Stable isotope analyses (δ^2H, δ^{13}C, and δ^{15}N) of nestling feathers indicate Barn Swallows rely on a more terrestrial-based diet, Cliff Swallows an intermediate diet, and Tree Swallows the most aquatic-based diet. These results are similar to other studies of aerial insectivore diets. Aerial insectivores occurring in sympatry have previously been recorded partitioning diet resources (Samuel 1971; Waugh 1978; Orłowski and Karg 2013; Orłowski *et al.* 2015). Barn Swallows typically forage close to their nests (Samuel 1971; Waugh 1978), and as a result may encounter more terrestrial prey. Previous research in Ontario has shown Barn Swallows take prey commonly associated with agriculture (Kusack 2018; McClenaghan *et al.* 2019). Cliff Swallows will congregate in patches, depleting prey within 20-30 minutes before moving on to another patch, resulting in high spatiotemporal variability in foraging (Samuel 1971; Brown 1986; Brown and Brown 1996; Ramstack *et al.* 1998) this may explain the intermediate δ^2H values of nestling feathers. Tree Swallows are known to take aquatic prey items (Quinney and Ankney 1985; McCarty and Winkler 1999; Mengelkoch *et al.* 2004; Stanton *et al.* 2016), and have been thought to travel larger distances to forage than Barn Swallows (Ramstack *et al.* 1998). DNA barcoding of fecal matter showed the three swallow species take prey predominantly from the order Diptera. These findings are consistent with previous research on these swallow species (Waugh 1978; Brown and Brown 1996; McCarty and Winkler 1999; Mengelkoch *et al.* 2004; Kusack 2018; McClenaghan *et al.* 2019). At the family level, DNA barcoding of nestling feces showed potential differences between the swallow species; however, the model failed to explain a majority of the variation in nestling diets, may be due to reduced sample sizes. Overall, I found evidence

that Barn, Cliff, and Tree swallow nestlings are likely being provisioned different diets, alluding to potential prey partitioning between species.

4.1.2   Post fledging movements

Barn, Cliff, and Tree swallows showed vast differences in their detectability by automated receiving towers. Of the nestlings that were radio tagged, 21 Barn Swallows, 44 Cliff Swallows, and 14 Tree Swallows were detected outside of their natal area. Previous research on these species using automated telemetry has yielded similar results (Lenske and Nocera 2018; M.Cadman unpublished data). In terms of cumulative distance travelled, Barn Swallows (357.61 ± 224.63km), Cliff Swallows (386.02 ± 253.08), and Tree Swallows (287.34 ± 134.93km) that were tracked until migration showed evidence of making exploratory movements, as the locations typically used to migrate south from southern Ontario are approximately 115km – 250km from the study area. Other studies on migratory songbirds have also found fledglings make extensive exploratory movements (Brown and Taylor 2015; Cormier and Taylor 2019; Evans 2018). Cliff Swallow fledglings showed changes in their duration at the natal site depending on timing of hatch. Earlier hatching Cliff Swallows stayed in the natal area as long as Barn and Tree swallows. However, later hatching Cliff Swallows spent less time in their natal area than the other two species. Barn and Tree swallows showed no difference the amount of time they spent at their natal site, regardless of hatch date. Unlike Barn and Tree swallows, Cliff Swallows are highly colonial and often migrate in large groups (Brown and Brown 1996). This may result in fledglings leaving the natal area with the colony, regardless of age. Cliff Swallows had a higher detectability, and therefore perceived residency time was likely more accurate, as they were more likely to be detected once they left the natal area. Fledglings of the other species may have left the area and not been detected for days after they had left. In general, later-hatching individuals have a shorter post-fledging period, these individuals have been found to accelerate development and disperse at a younger age (Styrsky *et al.* 2004; Evans 2018). Evans (2018) found that second brood Barn Swallow fledglings left for migration at a younger age than first broods. The present study aimed to avoid radio-tagging second brood individuals, and so there may not have been enough difference between hatch dates

to see a change in residency time in the natal area. Overall, there was inadequate evidence to suggest differences in post-fledging movements among the three swallow species, as detectability among species limited the comparisons that could be made.

4.2   Conservation implications

Aerial insectivore populations have been declining in North America, especially in the northeastern regions (Michel *et al.* 2016). In Canada, Barn Swallows have declined at a higher rate than Cliff or Tree swallows (Smith *et al.* 2019). As a result, they have been listed as threatened since 2017, and are protected under the Species at Risk Act. However, according to breeding bird survey data for the lower Great Lakes region of Ontario, Canada, where this study was conducted, Barn Swallows have decreased by 68%, Cliff Swallows by 80% and Tree Swallows by 56% from 1970 – 2017 (Smith *et al.* 2019). The post-fledging period has been identified as an important determinant in songbird population trends (Cox *et al.* 2014; Cox *et al.* 2018). Survival during the post-fledging period can be influenced by factors in the nest, such as pre-fledging condition resulting from diet (Twining *et al.* 2016; Twining *et al.* 2018; Evans *et al.* 2019). For these reasons, attaining information regarding the time from hatching to migration can contribute to future conservation efforts.

This research suggests that swallow species are not provisioning the same prey to their young. Instead, they vary in their use of aquatic and terrestrial prey sources. Barn Swallows showed evidence of a more terrestrial-based diet, Cliff Swallows showed an intermediate diet, and Tree Swallows a more aquatic-based diet provisioned to young. More reliance on aquatic prey has been linked to improved nestling growth and condition as they contain more omega-3 fatty acids (Twining *et al.* 2016; Twining *et al.* 2018). There is likely no single cause for the decline of aerial insectivores, but these results show the importance of continued research comparing nestling condition and fledging success of aerial insectivores as a function of diet quality. In addition, this research has highlighted some potentially significant habitats for Barn, Cliff, and Tree swallows. Once fledglings have left their natal area, many are detected in natural areas with wetlands. Sites with increased number of individuals detected include Luther Marsh Wildlife

Management Area, Guelph Lake Conservation Area, Forks of the Credit Provincial Park, and Belwood Lake Conservation Area (Figure 4.1).
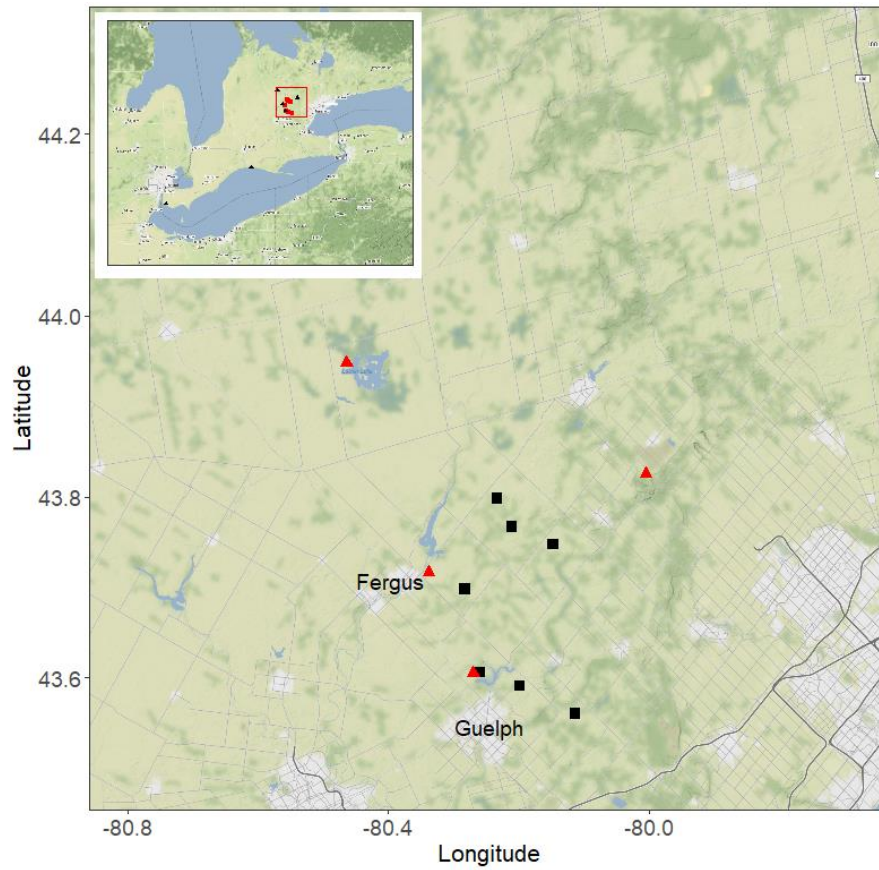
Figure 4.1 Maps of southern Ontario showing conservation areas with wetland habitat near tagging locations (squares) used by fledgling Barn, Cliff, and Tree swallows. Swallows were tagged in the breeding season of 2018 near Guelph, ON.

4.3   Study assumptions and limitations

In terms of diet analyses, it would have been beneficial to sample insects to determine their relative contributions of diet using stable isotope mixing models. However, due to many of the study sites being active farms, setting up malaise or conical traps daily would not have been feasible. Additionally, if swallows are foraging higher up in the air, or at greater distances from the nest, there are limitations as to the portion of their diet that would be represented by insects caught in these traps. The results from the isotope analyses suggested dietary differences among the three swallow species. These results could be expanded upon with fecal DNA analyses, however, reduced sample sizes limited the taxon-specific conclusions that could be made about nestling diet.

The use of automated telemetry also comes with limitations. During this study period, two towers were vandalized, compromising potential additional detections had they been fully operational. First, the northern-most tower (43.49°N, 80.13°W) was found to be vandalized on June 8th, 2018, and was not put back online due to concerns about future vandalism. This tower could have been a valuable tool in determining residence time at a finer scale for the more northern sites in the study. However, the northern-most tower had relatively fewer detections than the others in the Guelph array (Dean Evans, pers. obs). The second tower that was vandalized during the study period was the tower located at the Guelph Lake Conservation Area (43.36°N, 80.16°W). The discovery of this vandalized tower was made on April 25th, and it was brought back online on June 4th, 2018. No swallows were tagged before this tower was back online.

Differences in the detection range of the towers also pose limitations on the study findings. The detectability of fledglings can vary from site to site; towers were arranged in the best possible way to allow for the best coverage, but still some sites experienced greater coverage than others. Location precision for detections is low, as the towers in the Motus array can detect at distances up to 15km (Taylor *et al.* 2017). The large tower coverage makes determining exact locations difficult, and because of this, the calculated distance moved is in fact minimum distance moved, as swallows can also be making movements that are not detected by the array. This issue is worsened by differences in

detectability among species. Tree Swallows were the least detected and Cliff Swallows were the most detected, meaning Tree Swallows are likely moving without being detected by the array and therefore their estimates of total movement may be underestimated and estimates of residency time may be overestimated. These differences limit the comparisons that can be made between the three species. In relation to this, calculating the home range at the individual level was not possible due to a low number of detections for many individuals.

4.4   Future directions

Future research on aerial insectivore diets should consider a more detailed assessment of diet quality and the impact it has on juvenile body condition and fledging success. This information would prove valuable for determining any effects that differences in nestling diet may be having on differential declines of aerial insectivore species. Attaining more fecal data could aid in determining taxon-specific information regarding the diet of the different swallow species. Additionally, future research sorting prey from fecal DNA results into functional groups (similar to Orłowski and Karg 2013; Orłowski *et al.* 2015) may simplify finding any associations of the swallow species with their prey. Information regarding functional prey groups can be used to compare specific diets relative to nestling body condition and fledging success amongst the species.

Future studies should also investigate key areas used by juvenile aerial insectivores. Assessing habitat surrounding towers that prominently detect fledglings may be a first step in determining habitat requirements for aerial insectivores in one of their most vulnerable life stages (Cox *et al.* 2018). The data from the automated receivers can also be used to determine survivorship of fledgling swallows (e.g. Evans *et al.* 2019). Cliff Swallows showed relatively high detectability in comparison to the other two swallow species. Using this information to assess the survival of the Cliff Swallow fledglings may give some insight as to the steep Cliff Swallow population declines in this region (Smith *et al.* 2019). In addition, identifying potential sources of mortality for fledgling swallows would be imperative to determining the reasoning for any reductions in survivorship.

4.5   Conclusions

The aim of this research was to assess differences between sympatric aerial insectivore species during a vulnerable life stage. The time from hatching until migration is thought to be critical for aerial insectivores. The post-fledging period is a key determinant in population growth rates (Cox *et al.* 2014; Cox *et al.* 2018). Diet quality of nestlings ultimately affects survival, as high-quality diets with more omega-3 fatty acids lead to increased growth and better body condition pre-fledging (Twining *et al.* 2016; Twining *et al.* 2018), which are key factors in fledging success and survival (Naef-Daenzer *et al.* 2001; Evans *et al.* 2019). I present evidence of dietary differences among Barn, Cliff and Tree swallow nestlings. Ultimately, this may contribute to future research focused on whether ecological differences between species during the first few months after hatching are contributing to differential population declines of aerial insectivores. In addition, I found little evidence to suggest differences in fledgling movements during the post-fledging period. However, I present new information as to potential key habitats for fledgling swallows. Such information may be important for advising future conservation efforts of aerial insectivore post-fledging habitat.

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Appendices

Appendix A. Summary tables

Table A.1. Species-specific summary for measurements taken during banding, as well as during collection of feathers and application of radio transmitter.

			Mass (g)		Wing (mm)	
Species	Age (days)	n	Mean	SD	Mean	SD
BARS	6-10	436	16.86	3.22	36.26	9.03
	15	247	19.99	1.55	72.88	5.63
CLSW	~20	61	22.31	1.72	92.24	5.35
TRES	6-10	141	18.12	3.79	35.39	10.57
	15	138	20.23	2.49	73.21	7.36

Table A.2. Site-specific summary for stable isotopes within nestling Barn Swallow, Cliff Swallow, and Tree Swallow feathers.

Site	n	Mean $\delta^{13}C \pm$ SD‰	Min $\delta^{13}C$‰	Max $\delta^{13}C$‰	n	Mean $\delta^2H \pm$ SD‰	Min δ^2H‰	Max δ^2H‰	n	Mean $\delta^{15}N \pm$ SD‰	Min $\delta^{15}N$‰	Max $\delta^{15}N$‰
CK	18	-23.9 ± 0.6	-24.8	-23.1	14	-87 ± 7	-96	-70	18	10.5 ± 0.8	9.2	11.7
CT	5	-24.6 ± 1.3	-25.9	-22.6	4	-79 ± 6	-86	-71	5	10.5 ± 0.4	10.1	11.0
GL	6	-24.4 ± 0.3	-24.9	-24.0	5	-92 ± 5	-100	-88	7	11.2 ± 1.0	9.3	12.5
HI	9	-23.7 ± 0.8	-25.3	-23.0	4	-81 ± 6	-89	-75	9	11.7 ± 0.4	11.1	12.2
HM	26	-23.9 ± 0.7	-25.5	-23.0	21	-83 ± 7	-91	-70	26	10.3 ± 0.6	9.1	11.2
MF	11	-22.4 ± 0.4	-23.3	-21.8	7	-76 ± 6	-84	-69	11	12.4 ± 0.4	11.3	13.0
NE	20	-23.7 ± 0.6	-25.1	-22.9	18	-85 ± 7	-100	-75	20	10.5 ± 0.5	9.6	11.8

Table A.3. Summary of all detected arthropod prey items, across all samples. Freq is the frequency of detection, Reads is the number of reads during sequencing

Order	Family	Species	Freq.	Reads
Coleoptera	Carabidae	*Amara familiaris*	1	150
	Curculionidae	*Tychius picirostris*	2	1500
	Dermestidae	*Anthrenus scrophulariae*	1	456
Diptera	Anthomyiidae	*Anthomyiinae sp.*	1	99
		Delia florilega	3	1152
	Asilidae	*Eudioctria propinqua*	6	19,949
	Bibionidae	*Dilophus femoratus*	2	427
	Calliphoridae	*Pollenia sp.*	2	102
		Pollenia pediculata	7	3439
	Carnidae	*Carnus hemapterus*	1	83
	Chironomidae	*Microtendipes pedellus*	1	57
	Culicidae	*Aedes provocans*	2	381
	Dolichopodidae	*Dolichopus sp.*	1	109
	Empididae	*Empididae sp.*	1	178
	Ephydridae	*Athyroglossa ordinata*	1	74
	Limoniidae	*Dicranomyia sp.*	1	810
		Euphylidorea platyphallus	1	2536
		Limoniidae sp.	10	4415
		Ormosia affinis	2	335
		Rhipidia maculata	1	437
	Muscidae	*Muscidae sp.*	1	98
	Psychodidae	*Psychodidae sp.*	1	81
	Sarcophagidae	*Boettcheria bisetosa*	1	51
		Sarcophaga aldrichi	1	724
		Sarcophaga polistensis	1	74
		Sarcophaga subvicina	9	5653
	Scathophagidae	*Scathophaga stercoraria*	1	258
	Syrphidae	*Chalcosyrphus nemorum*	1	65
		Syrphus vitripennis	1	92
	Tabanidae	*Hybomitra sp.*	5	2520
		Hybomitra lasiophthalma	2	272
		Hybomitra zonalis	2	807
	Tachinidae	*Belvosia sp.*	1	84
		Chrysoexorista	1	114
		Dinera grisescens	2	683

		Exoristinae sp.	2	8941
		Lydina americana	1	3239
		Patelloa leucaniae	1	311
		Platymya confusionis	2	3033
		Tachinidae sp.	1	1637
		Winthemia sp.	1	82
		Winthemia rufopicta	5	2428
		Winthemia sinuata	3	3905
	Tephritidae	*Urophora cardui*	1	147
		Urophora cf. lopholomae	2	2457
		Urophora ivannikovi	1	64
	Tipulidae	*Angarotipula illustris*	10	11,254
		Angarotipula rubzovi	1	58
		Nephrotoma ferruginea	6	3658
		Tipula ignobilis	1	1005
		Tipulidae sp.	2	236
Hemiptera	Miridae	*Lygus lineolaris*	2	2144
Hymenoptera	Ichneumonidae	*Tryphon seminiger*	1	131
Lepidoptera	Geometridae	*Trichodezia albovittata*	1	479
Orthoptera	Acrididae	*Chorthippus curtipennis*	1	175
Plecoptera	Chloroperlidae	*Sweltsa mediana*	1	94

Table A.4. Detection summary for individual fledgling Barn, Cliff, and Tree swallows

Species	Tag	Number of Detections	Number of Receivers	Days Detected
BARS	306	234	3	15
	307	61	2	7
	321	1	1	1
	323	311	7	37
	329	2	2	2
	330	3	2	2
	334	25	3	5
	339	13	3	7
	344	39	2	7
	347	211	5	16
	361	10	5	3
	363	102	1	7
	367	4	3	3
	372	10	2	5
	380	3	2	2
	383	30	1	6
	388	11	3	2
	392.1	42	2	14
	393	70	1	7
	396	13	1	2
	398	20	1	3
	399	25	4	8
	401	122	3	11
	407	1	1	1
	408	156	2	12
	412.1	117	1	12
	413	18	1	3
	413.1	319	7	19
	417	167	7	28
	419	1	1	1
	422	168	4	24
	425	48	1	7
	426	30	2	8
	427	1	1	1
	429	161	5	18
	430	43	2	7
CLSW	296	7	2	4
	298	2	1	2
	300	4	3	3
	308	2	2	2
	312	15	2	7

CLSW	314	1	1	1
	315	26	4	7
	316	19	1	2
	318	1	1	1
	320	49	3	9
	322	50	4	10
	324	24	1	6
	325	6	2	2
	326	4	1	3
	327	5	3	3
	328	7	2	2
	331	1	1	1
	332	54	3	8
	335	104	6	27
	336	150	20	31
	337	1	1	1
	338	3	1	2
	340	38	2	4
	341	104	2	18
	342	31	3	7
	346	79	17	18
	348	1	1	1
	350	14	2	6
	351	41	6	9
	353	3	2	3
	355	4	2	3
	356	3	2	3
	370	4	2	4
	373	3	2	3
	377.1	18	1	2
	379.1	23	2	4
	380.1	34	3	8
	381.1	1	1	1
	386.1	117	3	11
	387.1	96	7	12
	388.1	18	9	6
	390.1	11	2	3
	393.1	133	2	12
	395.1	42	2	6
	398.1	124	4	12
	402.1	8	4	3
	405.1	62	5	11
	430.1	1	1	1
	431.1	2	2	2

CLSW	432.1	1	1	1
	433.1	46	1	6
TRES	305	26	3	7
	309	2	2	2
	310	44	1	3
	311	61	2	5
	313	28	2	6
	333	4	2	4
	343	155	3	31
	345	49	2	5
	354	64	1	5
	368	52	3	6
	369	14	2	3
	371	49	1	4
	376	3	1	2
	378.1	319	2	16
	382.1	3	2	2
	384.1	85	1	6
	386	20	1	3
	389.1	26	6	12
	391	19	1	4
	392	21	1	3
	394	31	1	2
	394.1	1	1	1
	396.1	92	1	6
	397	5	1	2
	401.1	87	4	7
	404	1	1	1
	414	86	1	9
	423	3	1	1
	431	16	2	7

Appendix B. Chapter 2 model selection tables

Table B.1. Model selection table for linear mixed effect models of isotope values (δ^2H, δ^{13}C, δ^{15}N) from Barn, Cliff, and Tree swallow nestling feathers collected near Guelph, ON, in the breeding season of 2018. ΔAICc shown for most competitive models.

Model	df	AICc	ΔAICc
δ^2H ~ Species * Date (day of year)	8	461.982	-
δ^2H ~ Species + Date (day of year)	6	462.472	0.490
δ^2H ~ Species	5	473.503	
δ^2H ~ Date (day of year)	4	495.378	
NULL Model (δ^2H ~ Random Effect (Site))	3	501.923	
δ^{13}C ~ Species * Date (day of year)	8	144.290	-
δ^{13}C ~ Species + Date (day of year)	6	144.860	0.567
δ^{13}C ~ Species	5	142.595	2.265
δ^{13}C ~ Date (day of year)	4	218.978	
NULL Model (δ^{13}C ~ Random Effect (Site))	3	216.814	
δ^{15}N ~ Species * Date (day of year)	8	126.386	-
δ^{15}N ~ Species + Date (day of year)	6	127.465	1.079
δ^{15}N ~ Species	5	135.963	
δ^{15}N ~ Date (day of year)	4	188.055	
NULL Model (δ^{15}N ~ Random Effect (Site))	3	200.427	

Table B.2. Model selection table for linear mixed effect models of Barn (n = 28), Cliff (n = 24), and Tree Swallow (n = 21) pre-fledging condition [mass(g)/wing(mm)]. Nestlings were measured and feathers collected near Guelph, ON, in the breeding season of 2018. (Only competitive models shown)

Predictors	df	AICc	ΔAICc
Species +Hatch Date + δ^2H	7	-326.757	-
Species + Hatch Date +	6	-326.676	0.081
Species + Hatch Date * δ^2H	8	-326.080	0.677
Species + Hatch Date + δ^{15}N	7	-325.592	1.165
Species + Hatch Date + δ^2H + δ^{15}N	8	-325.374	1.383
Species + Hatch Date * δ^2H + δ^{15}N	9	-325.013	1.744
Species	5	-324.831	1.926
Species + Hatch Date + δ^{13}C	7	-324.777	1.98
NULL Model	3	-306.061	20.969

Table B.3. Model selection table of distance-based redundancy analysis on the diet of nestling Barn Swallows (n=38), Cliff Swallows (n=14), and Tree Swallows (n=14) based on prey family presence-absence data from DNA barcoding of nestling feces. Samples were collected near Guelph, ON, during the 2018 breeding season.

	Predictor	df	F	Pr>F
Species * Date + Site	Species:Date	2	0.9065	0.575
	Site	7	1.283	0.205
Species + Date + Site	Species	2	1.7776	0.025
	Date	1	2.0441	0.035
	Site	7	1.1501	0.175
Species + Date	Species	2	2.2308	0.005
	Date	1	2.6391	0.005
Species	Species	2	2.5641	0.005
Date	Date	1	3.2762	0.005

Appendix C. Chapter 3 model selection table

Table C.1. Model selection table for the Weibull survival analysis used to predict the number of days fledgling Barn Swallows (n = 36), Cliff Swallows (n = 51), and Tree Swallows (n = 29) would remain in their natal area. Swallows were radio-tagged near Guelph, ON, in the breeding season of 2018.

Predictors	df	AICc	ΔAICc
Species * Hatch Date + Species * Site	25	522.153	
Species * Site + Hatch Date	23	525.602	
Species * Hatch Date + Site	13	514.296	5.823
Species * Hatch Date	7	508.473	-
Species + Hatch Date	5	523.339	
Species	4	531.136	
Hatch Date	3	534.037	
NULL Model	2	535.877	

Appendix D. Animal use protocol approval

Western

2017-005:1:

AUP Number: 2017-005
AUP Title: Ecology of Migratory Songbirds in North America
Yearly Renewal Date: 03/01/2019

**The YEARLY RENEWAL to Animal Use Protocol (AUP) 2017-005 has been approved by the Animal Care Committee (ACC),
and will be approved through to the above review date.**

Please at this time review your AUP with your research team to ensure full understanding by everyone listed within this AUP.

As per your declaration within this approved AUP, you are obligated to ensure that:

1) Animals used in this research project will be cared for in alignment with:
        a) Western's Senate MAPPs 7.12, 7.10, and 7.15
http://www.uwo.ca/univsec/policies_procedures/research.html
        b) University Council on Animal Care Policies and related Animal Care Committee procedures
http://uwo.ca/research/services/animalethics/animal_care_and_use_policies.html

2) As per UCAC's Animal Use Protocols Policy,
        a) this AUP accurately represents intended animal use;
        b) external approvals associated with this AUP, including permits and scientific/departmental peer approvals, are complete and accurate;
        c) any divergence from this AUP will not be undertaken until the related Protocol Modification is approved by the ACC; and
        d) AUP form submissions - Annual Protocol Renewals and Full AUP Renewals - will be submitted and attended to within timeframes outlined by the ACC.
http://uwo.ca/research/services/animalethics/animal_use_protocols.html
3) As per MAPP 7.10 all individuals listed within this AUP as having any hands-on animal contact will
        a) be made familiar with and have direct access to this AUP;
        b) complete all required CCAC mandatory training ([training@uwo.ca] training@uwo.ca); and
        c) be overseen by me to ensure appropriate care and use of animals.
4) As per MAPP 7.15,
        a) Practice will align with approved AUP elements;
        b) Unrestricted access to all animal areas will be given to ACVS Veterinarians and ACC Leaders;
        c) UCAC policies and related ACC procedures will be followed, including but not limited to:
                i) Research Animal Procurement
                ii) Animal Care and Use Records
                iii) Sick Animal Response
                iv) Continuing Care Visits

5) As per institutional OH&S policies, all individuals listed within this AUP who will be using or potentially exposed to hazardous materials will have completed in advance the appropriate institutional OH&S training, facility-level training, and reviewed related (M)SDS Sheets, http://www.uwo.ca/hr/learning/required/index.html

Submitted by: Copeman, Laura
on behalf of the Animal Care Committee
University Council on Animal Care

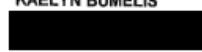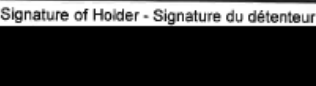Research - University Secretariat - Western University
www.uwo.ca
Research Section 7. 7.0 Academic Integrity in Research Activities; 7.1 Sundry Donations for Research; 7.2 Consulting Fees Paid for Services of a Researcher

The University of Western Ontario
Animal Care Committee / University Council on Animal Care
London, Ontario Canada N6A 5C1
519-661-2111 x 88792 Fax 519-661-2028
[auspc@uwo.ca]auspc@uwo.ca
http://www.uwo.ca/research/services/animalethics/index.html

Appendix E. Sub-banding Permit

| Environment and Climate Change Canada / Environnement et Changement climatique Canada | 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	Permit No. / N⁰ de permis
Ontario	**10685 L**

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	Issue Date / Date d'émission	
KAELYN BUMELIS		**2018/05/14**
	Expiration Date / Date d'expiration	**2020/12/31**

Signature of Holder - Signature du détenteur	For the Minister - Pour le Ministre Name (Print) - Nom (Lettres moulées)	Signature
	L. LAURIN	

AUTHORIZATIONS -- AUTORISATIONS

Authorized to:

- Band nestlings at nest site and monitor
- Band SARA listed species Barn Swallow (BARS) (6130) in collaboration with permit 10613 (under the authority of the Species at Risk Act (SARA) sections 73 and 74)
- Band specific species CLSW and TRES, in collaboration with permit 10613
- Hand capture
- Take, possess, and transport feather samples (R1 & R2) from adult and nestling TRES, CLSW and, SAR BARS, in collaboration with permit 10613 (if in possession of a valid Animal Care Committee Approval).
- Take, possess, transport other biological samples (fecal samples) collected opportunistically from adult and nestling TRES, CLSW and SAR BARS, in collab with permit 10613 (includes claws, fat, fecal samples, etc.; if in possession of a valid Animal Care Committee Approval).
- Trap at cavity, burrow or nest box
- Use mist nets
- Use traps
- Use (81H) radio transmitter (incl. nanotags) on Cliff Swallow (CLSW) (6120)
  Lotek NTQB-2 nanotag (0.35g) to adults and 15 day-old nestlings, in collaboration with permit 10613 (leg-loop harness; marker and attachment materials not to exceed 3% 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 (81H) radio transmitter (incl. nanotags) on Barn Swallow (BARS) (6130)
  Lotek NTQB-2 nanotag (0.35g) to adults and 15 day-old nestlings, in collaboration with permit 10613 (leg-loop harness; marker and attachment materials not to exceed 3% 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 (81H) radio transmitter (incl. nanotags) on Tree Swallow (TRES) (6140)
  Lotek NTQB-2 nanotag (0.35g) to adults and 15 day-old nestlings, in collaboration with 10613 (leg-loop harness; marker and attachment materials not to exceed 3% 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

Appendix F. Scientific studies permit for the Grand River Conservation Authority

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

Name: Kaelyn Bumelis

Position: M.Sc Candidate

Organization: Western University

Address: ███████████████

City, town or village: London, ON

Phone: _____ **Cell phone:** ███████████

List the names of people accessing GRCA property:
Kaelyn Bumelis
Shelby Law

Purpose of the project *(Please attach additional information, if necessary):*
To study potential sources of declines in aerial insectivores. In particular I am hoping to collect fecal samples as well as deploy radio transmitters on Tree Swallows (and also potentially collect fecal samples from Barn Swallows, if present). I have attached a copy of my proposal.

Equipment to be used to undertake the project:
NA

Specific area(s) where the project will take place:
Guelph Lake Conservation Area

Vehicle description and plate number:
TBA (rental)

Conditions pertaining to this permit appear on the reverse side.
This permission expires on: July 30 2018

Signature of Researcher:

Date: May 4 2018 _____ **Signature:** ████████████

Signature of GRCA Authorizing Agent:

Date: May 15, 2018 _____ **Signature:** ████████████

Curriculum Vitae

Kaelyn H.A. Bumelis

Education

University of Western Ontario	London, ON	September 2017 – present

MSc– Biology

University of Western Ontario   London, ON   September 2012 – April 2017
BSc – Specialization in Environmental Science, Major in Ecosystem Health

Work Experience

University of Western Ontario   London, ON   Jan – April 2018; 2019
Teaching Assistant – Wildlife Ecology and Management (Biology 3446)

University of Western Ontario   London, ON   Sept – Dec 2017; 2018
Teaching Assistant – Environmental Science (Environmental Science 1021)

Environment Canada   Burlington, ON   April – Aug 2016; 2017
Wildlife Technician

Environment Hamilton   Hamilton, ON   May – July 2015
Summer Intern

Conference Participation

AOS Annual Meeting   Alaska, USA   June 2019
Poster presentation;
Niche segregation among three sympatric species of swallows in southern Ontario

Biology Graduate Research Forum   London, ON   November 2018
Poster presentation;
Niche segregation among three sympatric species of swallows in southern Ontario

Awards

AOS Student Travel Award (2019)
Biology Graduate Research Forum – Best Poster Presentation (2018)
University of Western Ontario – Dean's Entrance Scholarship (2012)