UNDERSTANDING THE DRIVERS OF POPULATION DECLINES FOR SWALLOWS (FAMILY: HIRUNDINIDAE) THROUGHOUT THE ANNUAL CYCLE

by

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Submitted in partial fulfilment of the requirements
For the degree of Doctor of Philosophy

at

Dalhousie University
Halifax, Nova Scotia
July 2018

This thesis is dedicated to my daughter, Ceilidh Robin McGlay,

for whom, I hope, there were always be swallows.

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Abstract

Swallows and other aerial insectivores are experiencing steep population declines, potentially as a result of decreased insect availability during breeding and poor non-breeding conditions. To determine the likely drivers of decline for Bank *Riparia riparia*, Barn *Hirundo rustica*, Cliff *Petrochelidon pyrrhonoto* and Tree Swallows *Tachycineta bicolor* and Purple Martins *Progne subis* and whether they were common to multiple species, I: 1) examined the relationships between insect abundance and swallow breeding success (2014-2015); 2) compared breeding phenology and performance before (1962-1972) and after (2006-2016) the onset of population declines; 3) examined relationships between non-breeding conditions and potential carry-over effects (2014-2016); 4) identified winter locations; and 5) reviewed the effect of several threats on adult survival.

Insect abundance was not related to Barn, Cliff and Tree Swallow nestling survival or mass suggesting that it did not limit breeding success. Between 1962-1972 and 2006-2016, I found that Barn, Cliff and Tree Swallows bred 8-10 days earlier and had unchanged or higher performance. In contrast, Bank Swallows did not breed earlier and had lower performance. Poor non-breeding conditions, particularly low rainfall, resulted in carry-over effects during breeding (i.e., lower mass, later breeding or lower performance) for Barn and Cliff Swallows; these conditions were related to higher mass, but later breeding and lower performance for Bank Swallows. Stable isotope and geolocator results indicated that Bank, Barn and Cliff Swallows likely winter throughout Brazil, Bolivia, Paraguay, Uruguay and Argentina. While little information is available on relationships between threats and adult survival, poor weather is related to lower survival for all species except Purple Martins.

Low insect abundance during the breeding season is likely not contributing to population declines for Barn, Cliff and Tree Swallows, but, for Bank Swallows, declines may be partly due to a mis-timing between food availability and breeding. Also, for Bank, Barn and Cliff Swallows, poor non-breeding conditions are associated with carry-over effects on breeding, including lower success. Poor non-breeding conditions may also contribute to population declines through lower adult survival. While there are some similarities in the response of many species to different potential drivers, Bank Swallows often differed in their response.

Acknowledgements

Rarely does a single name as author represent the total intellectual and physical efforts, and emotional support associated with producing a thesis. Therefore, I would like to thank the following people and organizations for their contributions to this thesis.

First and foremost, I would like to thank my supervisor, Marty Leonard, for her intellectual and emotional support throughout my degree. With her guidance, I have developed my abilities to plan, conduct and communicate my research. I have also learned a great deal about conservation through our many discussions.

Secondly, I would like to thank my committee members and collaborators, Frédéric Angelier, Glenn Crossin, Hilary Mann, Keith Hobson, Gabriella Mastromonaco, Joanna Mills Flemming, Leslie Phillmore, Amélie Roberto-Charron and Sarah Saldanha who provided much assistance with analyzing samples, data analysis and/or revising manuscripts. I'd also like to mention Andy Horn who was always willing to review manuscripts, Becky Whittam who supported my initial idea to do research on population declines for Maritime swallows, and Peter Thomas who helped out in numerous ways as the work progressed. Many thanks also to Keven Kardynal and Steven VanWilgenburg for providing R scripts and support for the stable isotope assignment.

I would like to thank the many, many field staff and volunteers for their invaluable assistance with collecting and compiling data: Sue Abbot, Emma Beaton, Ty Bryant, Lauren Burke, Maia Courtenay, Brody Crosby, Danny Farrar, Sallie Lau, Andrew MacDonald, Ashleigh McKeen, Julie McKnight, Donavon Nickerson, Karen Potter and Nooshin Sobhani; and the volunteers who contributed swallow nesting observations to the Maritime Nest Records Scheme.

I would not have been able to do this work without the permission of many landowners and organizations, who allowed me to conduct research on their properties (even at 3 am!): Reinhardt Degenhardt and family, Ducks Unlimited Canada, Robert and Gladys Estabrooks, Environment and Climate Change Canada, Faye Hansen and family, Parks Canada, Sid McWhirter and family, Kathy Truman and family, Joan and John Vogul, Roland, Nettie, Elizabeth and Kyle Wells, and Dieter and Sabina Wilz. Many of whom made sure we were well fed during the field season. I would also like to thank the Canadian Wildlife Federation, Environment and Climate Change Canada, the Natural Science and Engineering Research Council, New Brunswick Wildlife Trust Fund, Nova Scotia Habitat Conservation Fund and Wildlife Preservation Canada, for providing financial assistance.

Finally, I'd like to thank my family and friends who have been willing to listen to me talk about swallows for the last five years. In particular, my partner, Miles McGehee has been nothing short of completely supportive with my long days and, often, extended absences.

Chapter 1. Introduction

BIODIVERSITY CONSERVATION

Across taxa, many species are facing increased risk of extinction (Di Marco et al. 2014; Dulvy et al. 2014; Purcell et al. 2014; Paleczny et al. 2015). This includes steep population declines for a large number of previously common species with widespread populations (Conrad et al. 2006; Vickery et al. 2014; Inger et al. 2015). In North America alone, 37% of migratory bird species require urgent conservation action and this list includes many species with large populations and broad distributions (North American Bird Conservation Initiative 2016). Declines in these widespread, common species are particularly concerning as these species are often more important for ecosystem structure and function than rare species (Gaston & Fuller 2008; Inger et al. 2015), and the declines suggest that many ecosystems are changing on a broad scale (Gaston & Fuller 2008). For many species, it has been easier to demonstrate that population declines have occurred than to determine why (Faaborg et al. 2010), and this information is critical for conservation effects.

Two different approaches to understanding population declines may be taken. The first approach is to examine correlations between population trends and limiting factors or threats. While strong correlations between population trends and limiting factors indicate that the two are related, the actual cause of decline may be due to other underlying relationships (Green 1999). This correlative approach is also not effective if declines are due to several, poorly quantified factors (Green 1999), or if the factors have several indirect effects on populations that are difficult to separate (Newton 2004). The second approach is to identify the effect of limiting factors on demographic processes (i.e., breeding success, recruitment, survival, immigration and emigration) throughout the annual cycle. Given population trends are driven by these process, understanding the relationship between limiting factors and demographic processes could help identify how these factors drive population declines (Rappole & McDonald 1994; Sherry & Holmes 1996; Selwood et al. 2015; Rushing et al. 2016). This approach is also more useful for focusing conservation efforts on the factors and demographic processes that have the strongest effect on population declines.

For migratory birds, determining the relationships between demographic processes and limiting factors presents unique challenges as breeding and wintering locations are often separated by thousands of kilometres, making it challenging to examine these relationships during all stages of the annual cycle (Sherry et al. 2005; Webster & Marra 2005). Furthermore, the effects of limiting factors in one stage of the annual cycle may carry-over and affect subsequent stages (Norris et al. 2004; Norris & Taylor 2006; Harrison et al. 2011). Since population declines may be driven by limiting factors during a particular stage of the annual cycle and/or carry-over effects from one stage to subsequent stages, it is important to consider the role of limiting factors on demographic processes throughout the annual cycle when determining the cause of population declines.

POPULATION DECLINES IN AERIAL INSECTIVORES

Avian aerial insectivores (i.e., birds that feed mid-air), a group that includes swallows, swifts, nightjars and flycatchers, are experiencing steep and widespread population declines across North America (Nebel et al. 2010; Shutler et al. 2012; Smith et al. 2015; Michel et al. 2016). While the cause of these population declines is unknown, similarities in population trends within this group have resulted in two likely hypotheses to explain population declines among the broader group of aerial insectivores. The first hypothesis suggests that because most of the species within this group solely feed on aerial insects, declines are driven by reductions in insect abundance (Nebel et al. 2010). This would be consistent with research demonstrating declines in insect abundance across many taxa (Conrad et al. 2006; Shortall et al. 2009; Hallmann et al. 2017) and dietary shifts for several aerial insectivores (Nocera et al. 2012; Pomfret et al. 2014; English et al. 2018). The second hypothesis suggests that conditions on the wintering grounds and/or migration routes are affecting overwintering survival and/or resulting in carry-over effects on migration or breeding. This is consistent with greater population declines for long-distance migrants (those that travel to South America) than short-distance migrants (those that travel to the southern USA and Central America) (Nebel et al. 2010), and the observed decrease in adult spring mass of one aerial insectivore, the Tree Swallow *Tachycineta bicolor*, attributed to poor non-breeding conditions (Rioux Paquette et al. 2014). These hypotheses are not mutually exclusive, and it is likely that declines in aerial insectivores are driven by a variety of other factors throughout their annual cycle.

In addition to these likely hypotheses for population declines among aerial insectivores, it has been suggested that the declines may be driven by a common factor(s) that affects all species in a similar manner (Nebel et al. 2010; Smith et al. 2015). This idea of a common driver for declines is largely due to the reliance of these species on a common food source (i.e., aerial insects), and a common negative change point in population trends during the mid-1980s for most aerial insectivores, especially swallows, swifts and nightjars (Nebel et al. 2010; Smith et al. 2015). However, for at least some species, there is considerable spatial variability in population trends, suggesting that the declines are potentially the result of several complex, broad-scale factors (Michel et al. 2016). If a single driver of population declines for aerial insectivores is identified, then conservation efforts addressing this driver would benefit a broad suite of species. Therefore there is a need for comparative research among different species of aerial insectivores to determine if there is support for these species responding in a similar manner to potential threats.

Therefore, the overarching goal of my thesis is to determine likely driver(s) of population declines for a group of aerial insectivores (i.e., swallows, Family Hirundinidae) throughout their annual cycle by examining the evidence for the two hypotheses described above. I take a multi-species, comparative approach to understand whether species exhibit a similar response to these factors, suggesting a common driver. My work was conducted in a region where population declines for aerial insectivores are particularly steep (Table 1), so if these potential limiting factors are driving population declines, then I expect to observe those relationships.

My thesis is divided into five chapters. In Chapter 2, I determine if food availability is limiting success, by examining relationships between insect availability and breeding success for Maritime populations of Barn *Hirundo rustica*, Cliff *Petrochelidon pyrrhonota* and Tree Swallows *Tachycineta bicolor*. In Chapter 3, I determine if changes in breeding performance across a 57-year time period, potentially as a result of changes in breeding phenology, could explain population declines in the

Maritimes for Bank *Riparia riparia*, Barn, Cliff and Tree Swallows. In Chapter 4, I determine if non-breeding conditions result in carry-over effects during the breeding season. I examine the relationships between non-breeding habitats (inferred through stable isotopes) and non-breeding stress (determined through feather corticosterone and telomere dynamics) on potential carry-over effects, like spring mass, breeding phenology and performance, for Maritime populations of Bank, Barn and Cliff Swallows. In Chapter 5, since I observe carry-over effects from non-breeding to breeding, I determine wintering locations, migratory connectivity and fidelity for Maritime populations of Bank, Barn and Cliff Swallows. Finally, in Chapter 6, I review the literature to summarize and assess the effects of threats on adult survival for five species of well-studied swallows (Bank, Barn, Cliff, Tree and Purple Martin *Progne subsis*).

Ultimately, my results provide insight into the demographic drivers of population declines for North American swallows through examining the two mostly likely hypotheses for these declines. My results will also help to determine if populations of different species are affected in similar ways.

STUDY SPECIES

Throughout this thesis, I focus on understanding the potential drivers of decline for five species of swallow (Family: Hirundinidae) that breed in North America. All five species are experiencing steep declines (Table 1) and two of these species, Bank and Barn Swallows, are presently listed as *Threatened* under the Canadian Species at Risk Act, SC 2002, c 29 (COSEWIC 2011, 2013). While all five species are aerial insectivores, the Tree Swallow also relies on berries throughout the non-breeding period

(Piland & Winkler 2015), potentially due to its more northerly winter distribution in the southern USA and northern parts of Central America (Winkler et al. 2011) where insects may be more scarce during the winter. The other four species migrate to South America, and southern parts of Central America during the winter (Brown & Bomberger Brown 1999a; Garrison 1999; Brown & Tarof 2013; Brown et al. 2017).

All five species are short-lived passerines with a high reproductive rate (Brown & Bomberger Brown 1999a; Garrison 1999; Winkler et al. 2011; Brown & Tarof 2013; Brown et al. 2017). The estimated annual adult survival rate of 0.35-0.62, and a maximum life span of 8-13 years. During the breeding season, Bank, Cliff and Tree Swallow, and Purple Martin pairs typically produce one brood each year (clutch size: 1-9 eggs), however 30-67% of pairs from the fifth species, Barn Swallow, may raise two broods in a single breeding season (clutch size: 3-7 eggs).

These species all utilize different nesting sites, although for four species, their most commonly used nesting sites throughout large areas of their range are artificial habitats. Bank Swallows are the only species that still largely nests in natural sites by digging a burrow into steeply eroding banks often adjacent to water (Garrison 1999). Barn and Cliff Swallows build mud nests in or under structures (e.g., buildings, bridges and culverts), although, in some areas, particularly for Cliff Swallows, there are many locations where they still nest in or on natural caves and cliffs, respectively (Brown & Bomberger Brown 1999a; Brown et al. 2017). Throughout much of their range Tree Swallows and Purple Martins nest in nest boxes or condos, respectively; their natural nest sites are hollow trees or tree cavities (Winkler et al. 2011; Brown & Tarof 2013). At their nesting sites, these species also vary in the degree to which they are colonial. Bank and

Cliff Swallows, and Purple Martins nest colonially, whereas Barn and Tree Swallows often appear to be colonial due to the patchy distribution of their artificial nesting sites. During the non-breeding season these species are commonly found in multi-species flocks where their migration and winter ranges overlap (Winkler 2006).

Table 1. Estimated annual rate of population change and the 95% credible interval from 1966-2015 for five species of swallows throughout their North American range, and in my study areas in New Brunswick, Nova Scotia and Prince Edward Island. Results from Sauer et al. 2017.

Species	Trend estimate (95% credible interval)		
	North America	New Brunswick	Nova Scotia & Prince Edward Island
Bank Swallow	-5.33 (-6.65, -3.80)	-9.35 (-11.69, -6.49)	-8.97 (-11.32, -6.70)
Barn Swallow	-3.32 (-3.69, -2.97)	-4.58 (-5.60, -3.52)	-4.29 (-5.27, -3.30)
Cliff Swallow	-2.81 (-4.49, -1.65)	-5.31 (-6.74, -3.77)	-4.82 (-7.58, -2.32)
Tree Swallow	-1.38 (-1.86, -1.04)	-2.68 (-3.52, -1.87)	-1.83 (-2.75, -0.87)
Purple Martin	-0.91 (-2.15, -0.55)	-10.16 (-14.08, -6.50)	_

Chapter 2. No Effect of Insect Abundance on Nestling Survival or Mass for Three Declining Aerial Insectivores

INTRODUCTION

Parental care affects the fitness of both adults and their young, and, for birds, parental care includes behaviours related to nest-site selection, nest building, incubation, brooding, predator deterrence and food provisioning (Owens & Bennett 1994; Soler et al. 1998; Lima 2009). These aspects of parental care are costly, so many species offset the demands of breeding by timing their breeding to occur during favourable conditions, like during periods of high food availability (Martin 1987). For some species, this can involve timing periods of high food demand from nestlings with short-lived peaks in food abundance (e.g., caterpillar emergence) (Both et al. 2006, 2009; Visser et al. 2006). For other species, however, such as some swallows, seasonal trends in food abundance may vary and have no discernable peaks (Hussell & Quinney 1987; Grüebler & Naef-Daenzer 2008; Dunn et al. 2011), making it difficult for birds to anticipate periods of high or low food abundance. Regardless of the trend in food availability, breeding that occurs when there are adequate food supplies for adults as well as their young will maximize reproductive success and survival.

For nestlings, food availability can impact growth, development and survival. Low food availability is associated with reduced nestling mass (Brzek & Konarzewski 2004; Burger et al. 2012), delayed feather growth resulting in shorter feathers at fledging (McCarty & Winkler 1999a; Hovorka & Robertson 2000), and reduced survival to fledging (Boulton et al. 2008). Low food availability during the nestling period can also negatively impact post-fledgling survival and recruitment because young fledge in worse condition than after periods of high food availability (Møller 1994; McCarty 2001a; Schwagmeyer & Mock 2008). In addition to food availability, quality can also affect nestling growth and development (e.g., growth rate, mass, condition, feather development and immunocompetence, de Ayala et al. 2006; Twining et al. 2016).

Swallows, along with other aerial insectivores, are experiencing severe and widespread population declines across most of North America, particularly in the northeast (Nebel et al. 2010; Smith et al. 2015; Michel et al. 2016). The temporal and spatial synchrony in population declines suggest that there is a common threat(s) affecting aerial insectivores (Nebel et al. 2010; Smith et al. 2015; but see Michel et al. 2015). The most obvious common factor is that these species all rely on aerial insects for food. Therefore, it has been hypothesized that reductions in insect abundance may be driving these trends (Nebel et al. 2010; Shutler et al. 2012). These reductions could be the result of a mis-timing between peak insect abundance and offspring demands. For instance, swallows in the Maritime provinces of Canada have advanced their breeding by 8-10 days over the last 57 years (Imlay et al. 2018; Chapter 3) providing the potential for mis-timing to occur (but see Dunn et al. 2011). Alternatively, reductions in insect abundance could be a result of changes to the ecosystem that have reduced overall abundance (Nebel et al. 2010). For example, agricultural intensification (i.e., conversion of hayfields and pastures to row crops) is associated with lower abundance of dipterans, a common swallow food item (Rioux Paquette et al. 2013).

Relationships between insect abundance and swallow breeding success, especially nestling and post-fledgling survival, have been investigated for Tree Swallows (e.g., Quinney et al. 1986; McCarty & Winkler 1999; Nooker et al. 2005) and to a lesser extent for other species (e.g., Grüebler & Naef-Daenzer 2008). However, research examining these relationships with multiple species simultaneously has not been conducted. Understanding if insect abundance has a consistent effect on breeding success across several species may help to determine if there is a common factor influencing declines. To that end, I examined the relationships between insect abundance and breeding success of Barn, Cliff and Tree Swallows in an area with steep population declines (Sauer et al. 2014). Specifically, I determined if the timing of breeding (i.e., hatching dates) was related to periods of low insect abundance during nestling rearing, and then determined if insect abundance during nestling rearing was related to nestling survival and mass, which serves as a proxy for post-fledging survival (reviewed in Naef-Daenzer & Grüebler 2016).

METHODS

In 2014 and 2015, I monitored Barn, Cliff and Tree Swallows at three sites within 30 km of Sackville, New Brunswick (45.9017°, -64.3631°). The first site (BEFV) was a mix of active hayfields (mowed at least once annually), old hayfields (not mowed during my study), wet meadows, and open, cattail wetlands. At this site, Barn Swallows nested in a barn, under a deck, and in a carport near the active and old hayfields. Tree Swallows nested in the nestboxes located at the periphery of the active hayfields and adjacent to cattail wetlands. The second site (JO) was a mix of actively grazed cattle pasture, and mostly grassy areas with a few shrubs adjacent to a lake and bordered by a narrow stand of coniferous trees. At this site, Barn Swallows nested in a barn and Cliff Swallows nested under the eaves of farm buildings surrounded by the pasture. Tree Swallows nested in 41 boxes in the area adjacent to the lake and near the pasture. The third site (WE) was a mix of actively grazed pasture for cattle and sheep, active hayfields and a wet meadow that was frequently flooded from a nearby open cattail wetland. Barn and Cliff Swallows nested in and under the eaves, respectively, of the farm buildings surrounded by pasture. Tree Swallows nested in 20 boxes located along the edges of the pasture, hayfield and wet meadow.

To determine hatching date and brood size, I typically checked swallow nests every 2-3 days during the breeding season, with more frequent checks (i.e., every two days) around the earliest projected hatching date. Since nests were not checked daily, hatching date was determined by the size and feather development of nestlings once hatched. In the event of asynchronous hatching, hatching date was defined as the day most young hatched (usually the first day of hatching). Nests were infrequently checked until nestling banding and the final check on day 12 post-hatch. Nestling survival after day 10 is high (≥ 95%) for these species (Brown & Bomberger Brown 1999b; Ambrosini et al. 2002), therefore the number of nestlings at day 12 should reflect fledging success. I banded nestlings with Canadian Wildlife Service aluminum bands and measured the mass of all nestlings at or near the point when growth rate was highest for each species (Barn: day 9 post-hatch; Cliff: day 10; Tree: day 12; Stoner 1935, 1945; Brown & Bomberger Brown 1996; McCarty 2001). Nestling mass is positively correlated with post-fledgling (i.e., juvenile) survival for Barn and Cliff Swallows (Brown & Bomberger Brown 1996; Naef-Daenzer & Grüebler 2016), therefore I used nestling mass as a proxy for post-fledgling survival. I recognize, however, that post-fledgling mass and fledging date (not measured during this study) may also affect post-fledgling survival (Raja-Aho et al. 2017).

Using similar methods to previous studies (Quinney et al. 1986; Hussell & Quinney 1987; Hussell 1988, 2012; Dunn et al. 2011), I measured insect abundance at my study sites by collecting two insect samples/day/site using two stationary conical nets. The insect sampling period included 10 June – 24 July 2014 and 8 June – 16 July 2015, and included samples from the first day swallow nestlings hatched to twelve days after the last of the first nests hatched. I did not collect insect samples during the nestling period of second nests either following a failed [all species] or successful [Barn] first nest. At each site, two nets were placed in open fields near wetlands, 5-20 m from the closest Tree Swallow nest box and 25-140 m from the closest farm buildings that provided nesting sites for Barn and Cliff Swallows. The nets were positioned 1.6 m above the ground and could rotate freely. A sample jar containing 100% ethanol was placed in the net between 06:00 and 10:00 and collected between 15:00 and 20:30, for an average sampling period of 8.57 ± 0.05 [SE] hours/day/jar. Each sample was air-dried for 24 hours and the dried mass was measured. I calculated an index of daily insect abundance at each site by dividing dried insect mass for each sample by the amount of time the jar was in place, averaging the results for both nets at the site and log transforming the mean to normalize the data. Using this method, previous studies have found relationships between mean daily insect abundance and Tree Swallow clutch initiation dates (Hussell & Quinney 1987; Dunn et al. 2011), clutch sizes (Hussell & Quinney 1987), nestling diets (Quinney & Ankney 1985), nestling begging (Hussell 1988), growth and survival (Quinney et al. 1986), and nest-box occupancy (Hussell 2012).

In 2014, I identified the insects to order. The most common insects at my site were (in order of greatest total mass) Diptera, Coleoptera and Hymenoptera; together these insects accounted for 86.5% of the mass in my samples. All three species of swallows forage on insects in these orders, but there is interspecific and geographic variation in the amount of insects consumed in each order (summarized in Brown & Bomberger Brown 1995, 1999b; Winkler et al. 2011). Some research has found selection for Hymenoptera by Barn Swallows (Law et al. 2017) and larger insects (>3 mm) by Tree Swallows (McCarty & Winkler 1999b), but it is unclear if prey selection is consistent across populations.

Data analysis

First, to determine if insect abundance during the nestling period varied with the timing of breeding (i.e., hatching date [HD]), I used a general linear model for each species. I considered the nestling period for each nest to be from the hatch date until the last nest check on day 12; insect abundance was averaged across these twelve days (IA_M). I compared eight different models including all possible combinations of HD, site and year, and a null model. If I found a seasonal decline in IA_M, then this could explain seasonal declines in breeding success (Møller 1994; Brown & Bomberger Brown 1999b; Wardrop & Ydenberg 2003; Dawson 2008).

Then, to determine if nestling survival was related to insect abundance, I used a generalized linear model with a binomial distribution that included the proportion of surviving young at day 12 for each nest, and a complementary log-log link function for each species. For all three species, I identified two groups of models. These groups of models started with two base models containing either mean insect abundance during the nestling period (IA_M) or hatching date (HD). Hatching date provides a proxy for other seasonal factors, like weather, parasitism and pressure to migrate (reviewed in Verhulst & Nilsson 2008) that could affect nestling survival. I did not include IA_M and HD in the same models because they were related for Cliff and Tree Swallows (see Tables 2 and 3). For Cliff and Tree Swallows, I added all possible combinations of brood size, site and year as possible covariates to my two base models (i.e., IA_M and HD) for a total of 14 models. The small number of Barn Swallow nests (n = 2 of 29; Figure 1) that experienced the loss of at least one nestling during my study affected my ability to add additional covariates to my base models. My 3rd (Barn) or 17th (Cliff and Tree) model was a null model that did not include covariates. I excluded four Tree Swallow nests from this analysis because nestling mortality was due to factors unrelated to insect abundance (i.e., predation [2], nest box knocked over by high winds [1] and a tractor [1]).

Finally, to determine the relationship between the mean mass of all nestlings in a brood (as an indicator of post-fledgling survival) and mean insect abundance, I used a general linear mixed model for each species. Since extremely low mean nestling masses (often due to several "runt" offspring that die in the nest) are not predictive of post-fledgling survival (Wardrop & Ydenberg 2003), I excluded one Barn, three Cliff and two Tree Swallow nests with a mean nestling mass more than two standard deviations below the mean for all nests. Previous work on Tree Swallows indicates that while nestling mass is influenced by insect abundance throughout the nestling period, it is most strongly affected by insect abundance during the period of rapid growth that occurs shortly before young are banded (McCarty & Winkler 1999a). Therefore, I selected two measures of insect abundance: 1) mean insect abundance during nestling rearing up to and including banding day (IA_{MB}: Barn: day 1-9; Cliff: day 1-10; and Tree: day 1-12); and 2) mean insect abundance on and one day prior to banding day (IA_{B1}: Barn: day 8-9; Cliff: day 9-10; and Tree: day 11-12).

Similar to my analysis on nestling survival, I identified three groups of models. For all three species, I started with three base models containing IA_{MB}, IA_{B1} or hatching date (HD). Then, for Cliff and Tree Swallows, I added all possible combinations of brood size, site and year as possible covariates to my three base models (i.e., IA_{MB}, IA_{B1} and HD) for a total of 21 models. My 4th (Barn) and 22nd (Cliff and Tree) model was a null model that did not include fixed effects. All of these models included a random variable for nest ID.

I determined the best-fit model for hatching date, nestling survival and mean mass by comparing the Akaike's Information Criterion with the small sample size correction (AIC*c*) and the weight (w_i) given to each model (Burnham & Anderson 2002). If two or more models had a $\Delta AICc < 2.0$, then I averaged the models to determine my parameter estimates and the relative importance of each variable. I was interested in the variables that had the greatest effect on my response, therefore I used the zero method for model averaging (Nakagawa & Freckleton 2011). Any variables included in my best-fit or averaged models with unconditional confidence intervals that included zero, were deemed to have little support. I centered and scaled all continuous variables (i.e., IA_M, IA_{MB}, IA_{B1} and HD) in my models (Grueber et al. 2011). All analyses were performed in R version 3.3.1 (R Core Team 2016) using the packages bblme version 1.0.18, lme4 (Bates et al. 2015), MuMln version 1.15.6 (Barton 2016) and plyr version 1.8.4

(Wickham 2011). Mean values are presented with the standard error (± SE), and the variation in my variables is presented in Table A1, Appendix 1.

RESULTS

Hatching date

For Barn Swallows, my best-fit model examining the relationship between hatching date and mean insect abundance during nestling rearing was the null model (Table 2), indicating that insect abundance during nestling rearing was not related to hatching date, site or year.

For Cliff and Tree Swallows, my best-fit models included hatching date (Table 2). Cliff and Tree Swallow nests that hatched earlier experienced higher insect abundance during nestling rearing than nests that hatched later (Table 3). For Cliff Swallows, insect abundance during nestling rearing was also higher in 2014 compared to 2015.

Nestling survival

During my study, nestling survival was high for Barn and Tree Swallows (96.8% and 90.7% surviving from hatch to day 12, respectively), but lower for Cliff Swallows (65.5%) (Figure 1, Table A1, Appendix 1).

For Barn Swallows, my top two models ($\Delta AICc \leq 2.0$) for predicting nestling survival included IA_M and the null model (Table 3). However, model averaged confidence intervals for IA_M included zero, indicating little evidence that this variable affected nestling survival (Table 5).

For Cliff Swallows, my top four best fitting models ($\Delta AICc \leq 2.0$) for nestling survival included hatch date, year and various combinations of brood size and site (Table

3). Model averaged parameter estimates showed that hatching date and year were the most important predictors of nestling survival (Table 5). Nestling survival was higher in earlier hatching nests, and in 2015 compared to 2014. Model averaged confidence intervals for brood size and site included zero, indicating little evidence that these variables affected nestling survival.

For Tree Swallows, my top five best fitting models (ΔAIC*c* ≤ 2.0) for nestling survival included IA_M or HD, and various combinations of brood size, site and year (Table 3). Model averaged parameter estimates showed that site and year were the most important predictors of nestling survival (Table 5). Nestling survival was higher at BEFV than JO but similar to WE (Table A1, Appendix 1), and in 2014 compared to 2015. Again, model averaged confidence intervals for IA_M, HD and brood size included zero, indicating little evidence that these variables affected nestling survival.

Nestling mass

For Barn Swallows, my top two best-fit models (ΔAIC*c* ≤ 2.0) for nestling mass included insect abundance on and one day prior to banding (IA_{B1}) and mean insect abundance from hatch to banding day (IA_{MB}) (Table 6). Model averaged confidence intervals for IA_{B1} and IA_{MB} included zero, indicating little evidence that insect abundance affected nestling mass (Table 7).

For Cliff Swallows, my top four best-fit models (ΔAIC*c* ≤ 2.0) for nestling mass included IA_{B1} (one model), IA_{MB} (one model) or hatching date (two models) (Table 6). Site and year were included in all four models, and brood size was included in one model. Model averaged parameter estimates showed that site and year were the most important predictors of nestling mass (Table 7) and nestling mass was higher at JO than WE (Table

A1, Appendix 1), and in 2015 compared to 2014. Model averaged confidence intervals for IA_{B1}, IA_{MB}, hatching date and brood size included zero, indicating little evidence that these variables affected nestling mass.

For Tree Swallows, my top two best-fit models ($\Delta AICc \leq 2.0$) for nestling mass included hatching date and the null model (Table 6). Again, model averaged confidence intervals for hatching date included zero, indicating little evidence that this variable affected nestling mass (Table 7).

DISCUSSION

The goal of my study was to examine the relationships between insect abundance and breeding success for three declining aerial insectivores. In doing so, I determined if low insect abundance (as a potential cause of population declines) was associated with lower reproductive success, and if all three species were similarly affected by low insect abundance suggesting a common driver of declines. At my sites, late breeding was associated with lower insect abundance during nestling rearing for Cliff and Tree Swallows. This suggested a potential cost for late-breeding birds, but low insect abundance was not related to decreased nestling survival and mass for the species studied. These results are consistent with Nooker et al. (2005), but differ from the results of several previous studies showing that periods of low insect abundance are associated with reduced nestling survival and body condition in Tree Swallows (Quinney et al. 1986; McCarty & Winkler 1999a; Winkler et al. 2013), and reduced post-fledgling survival in Barn Swallows (Grüebler & Naef-Daenzer 2008). I suggest four possible explanations for my results.

First, it is possible that my samples did not reflect the food provided to nestlings (but see Quinney & Ankney 1985). My nets were, however, placed in suitable foraging habitat for all three species (McCarty & Winkler 1999b; Ambrosini et al. 2002; Evans et al. 2007; Hussell 2012; Brown et al. 2017), and all three species were observed foraging near the nets (pers. obs.). The placement (both distance from nesting sites and height) of my nets was also within the typical foraging range of breeding Barn and Tree Swallows (distance: up to 400 or 200 m, respectively; height: < 10 or 12 m, respectively; Brown & Brown 1999b; McCarty & Winkler 1999b; Ambrosini et al. 2002). Less is known about the foraging ecology of Cliff Swallows, but this species forages within 1 km of its nesting site and from 0.5-30 m or higher above ground (Brown & Bomberger Brown 1996). Finally, my sampling was likely sufficient because the samples contained a large proportion of insects (86.5%) that are common food items for all three species (summarized in Brown & Bomberger Brown 1995, 1999b; Winkler et al. 2011).

Second, other measures of insect abundance, like nutritional quality, may be more important than total abundance for nestling survival and mass (de Ayala et al. 2006; Twining et al. 2016). All three of my sites were, however, located near wetlands and/or waterbodies that would presumably provide large numbers of high-quality insects for these species (Twining et al. 2016).

Third, it is also possible that although I observed periods of low insect abundance these levels were not low enough to affect nestling survival or mass. Years with low nestling survival as a result of low insect abundance are infrequent for Tree Swallows at other sites (Winkler et al. 2013). In these cases, low nestling survival is the result of prolonged periods of cold temperatures (Winkler et al. 2013). Similarly, low food availability, partly as a result of lower temperatures, can also affect mass gain in Tree Swallow nestlings (Quinney et al. 1986; McCarty & Winkler 1999a, but see Nooker et al. 2005). Prolonged periods of cold temperatures were not observed during my study, and Barn and Tree Swallow nestling survival rates were >90% in both years. Therefore, it is possible that my study occurred during two years with plentiful food.

Finally, it is possible that periods of low insect abundance were offset by increased foraging effort by adult swallows, which would buffer nestlings from the effects of low insect abundance. Adults may buffer nestlings from periods of low insect abundance through 1) decreased foraging effort in poor conditions, but substantially increased foraging effort in good conditions resulting in large nestling fat stores (Schifferli et al. 2014), or 2) providing stable food provisioning rates across varying degrees of insect abundance through increased foraging effort (Hussell 1988; McCarty & Winkler 1999a; Bortolotti et al. 2011). Both strategies would reduce the potential effect of low insect abundance on nestling mortality and mass, but at a potential cost to adult survival (Saino et al. 1999; Ardia 2005). The role of the latter three possible explanations on Barn, Cliff and Tree Swallows may differ between species, and they are not mutually exclusive.

My results indicate that insect abundance (within the range of abundances I sampled) did not affect nestling survival or mass of Barn, Cliff and Tree Swallow at my sites. It is difficult to conclude based on the restricted geographic range of my study and the limited duration of the work that insect abundance does not affect breeding success. However, other research demonstrating relationships between insect abundance and breeding success was also carried out at sites with a similarly restricted range (Quinney et al. 1986; McCarty & Winkler 1999a; Winkler et al. 2013) and during a similar time-frame as my study (i.e., two years; Quinney et al. 1986).

My results also indicate that while insect abundance was unrelated to breeding success for all three species, nestling survival for Cliff Swallows was lower (65.5% surviving to day 12) than Barn and Tree Swallows (>90%). Reduced nestling survival for Cliff Swallows may be explained by high levels of ectoparasites (Brown & Bomberger Brown 1999b), or high nest temperatures as a result of nesting under metal roofs (D. Nickerson, T.L.I. and A.G. Horn unpubl. data), both of which are correlated with hatching date and could have a greater effect on nestling survival and mass than insect abundance.

Conclusions

Insect availability has been suggested as a possible explanation for declines in aerial insectivores, including swallows, across North America (Nebel et al. 2010; Shutler et al. 2012). The concept of a common driver for aerial insectivore declines, in this case, insect abundance, is appealing for conservation efforts, as, presumably, if the driver was addressed it would benefit multiple species. However, despite sampling in an area where population declines for all three species are particularly steep (Nebel et al. 2010; Shutler et al. 2012; Michel et al. 2016), insect abundance did not affect swallow breeding success. The effect of insect abundance on aerial insectivore breeding success may be constrained to areas experiencing land use changes (e.g., loss of livestock and agricultural intensification), which, in addition to weather conditions, may also reduce insect abundance (Møller 2001; Ambrosini et al. 2002; Ghilain & Bélisle 2008). Broad-scale, multi-species research is needed to address the complex effects of potential drivers of population declines on aerial insectivores.

Table 2. Best-fit models for insect abundance during nestling rearing for Barn, Cliff and Tree Swallows. Of the eight possible models for each species, only models with a $w_i \geq 0.05$ are included.

Species	Model[1]	K[2]	ΔAICc[3]	w_i	Deviance
Barn	null	1	0.0	0.74	0.58
	year	3	3.9	0.11	0.55
Cliff	HD + year	4	0.0	0.70	0.50
	HD + site + year	7	2.5	0.21	0.50
	HD	2	4.7	0.07	0.58
Tree	HD	2	0.0	0.64	1.56
	HD + year	4	2.4	0.20	1.56
	HD + site	5	3.3	0.13	1.54

[1] Abbreviation: HD = hatching date.

[2] Number of parameters

[3] AIC*c* values for top model: Barn -28.8; Cliff -82.2; Tree -198.7.

Table 3. Model coefficients with SE and confidence intervals (CI) from the best-fit models for the relationship between insect abundance during nestling rearing and hatching date for Cliff and Tree Swallows. The best-fit model for Barn Swallows was the null model and is not included in the table.

Species	Coefficients[1]	Estimate	SE	Lower 95% CI	Upper 95% CI
Cliff	intercept	0.21	0.15	-0.09	0.51
	HD	-0.01	0.00	-0.02	-0.01
	year 2015	-0.08	0.03	-0.14	-0.02
Tree	intercept	-0.36	0.01	-0.38	-0.34
	HD	-0.20	0.02	-0.24	-0.16

[1] Abbreviation: HD = hatching date.

Table 4. Best-fit models for Barn, Cliff and Tree Swallow nestling survival. Of the three (Barn) or 17 (Cliff and Tree) possible models, only models with a $w_i \geq 0.05$ are listed. Models with a ΔAICc ≤ 2.0 were averaged to determine parameter estimates.

Species	Model[1]	K[2]	ΔAICc[3]	w_i	Deviance
Barn	IA_M	1	0.0	0.53	30.84
	null	1	0.9	0.34	27.65
	HD	1	2.7	0.14	30.35
Cliff	HD + year	3	0.0	0.36	129.54
	HD + brood size + year	4	0.7	0.25	127.90
	HD + site + year	5	1.0	0.22	128.12
	HD + brood size + site + year	6	1.6	0.16	126.23
Tree	IA_M + site + year	6	0.0	0.26	242.56
	HD + site + year	6	0.8	0.18	243.31
	IA_M + year	3	1.0	0.16	247.85
	HD + year	3	1.3	0.14	248.11
	IA_M + brood size + site + year	7	2.0	0.09	242.38
	HD + brood size + site + year	7	2.6	0.07	242.93
	IA_M + brood size + year	4	3.1	0.06	247.78
	HD + brood size + year	4	3.2	0.05	247.96

[1] Abbreviations: IA_M = mean insect abundance up to and including day 12; and HD = hatching date

[2] Number of parameters

[3] AICc values for top model: Barn 33.8; Cliff 149.5; Tree 283.4

Table 5. Averaged model coefficients with adjusted SE and confidence intervals (CI) from the best-fit models for Barn, Cliff and Tree Swallow nestling survival.

Species	Coefficients[1]	Estimate	SE	Lower 95% CI	Upper 95% CI	Relative importance (S^2)
Barn	intercept	1.29	0.17	0.95	1.64	-
	IA_M	-0.35	0.37	-1.20	0.05	0.61 (1)
Cliff	intercept	-0.41	0.21	-0.84	0.01	-
	HD	-1.82	0.43	-2.69	-0.95	1.00 (4)
	brood size	0.15	0.26	-0.20	0.95	0.42 (2)
	site WE	-0.14	0.24	-0.88	0.17	0.39 (2)
	year 2015	1.02	0.30	0.41	1.63	1.00 (4)
Tree	intercept	1.41	0.16	1.09	1.73	-
	IA_M	-0.08	0.11	-0.36	0.10	0.63 (3)
	HD	0.03	0.09	-0.14	0.32	0.38 (2)
	brood size	0.00	0.02	-0.09	0.14	0.11 (1)
	site JO	-0.20	0.19	-0.60	-0.02	0.64 (3)
	site WE	-0.12	0.15	-0.47	0.09	0.64 (3)
	year 2015	-0.62	0.13	-0.87	-0.37	1.00 (5)

[1] Abbreviations: IA_M = mean insect abundance up to and including day 12; and HD = hatching date.

[2] Number of averaged models.

Table 6. Best-fit models for Barn, Cliff and Tree Swallow nestling mass. Of the four (Barn) and 25 (Cliff and Tree) possible models for each species, only models with a $w_i \geq 0.05$ are included. Models with a $\Delta AICc \leq 2.0$ were averaged to determine parameter estimates.

Species	Model[1]	K^2	$\Delta AICc^3$	w_i	Deviance
Barn	IA_{B1}	1	0.0	0.59	1419.86
	IA_{MB}	1	1.8	0.24	1421.67
	HD	1	2.6	0.16	1422.43
Cliff	HD + brood size + site + year	6	0.0	0.27	649.19
	HD + site + year	5	0.1	0.26	651.48
	IA_{B1} + site + year	5	0.8	0.18	652.25
	IA_{MB} + site + year	5	1.6	0.12	653.05
	IA_{B1} + brood size + site + year	6	2.4	0.08	651.59
	IA_{MB} + brood size+ site + year	6	2.9	0.06	652.08
Tree	null	1	0.0	0.27	2331.79
	HD	1	0.7	0.19	2330.42
	IA_{MB}	1	2.2	0.09	2332.01
	HD + site	4	2.3	0.09	2327.94
	IA_{B1}	1	2.3	0.08	2332.09
	HD + year	3	2.8	0.07	2330.50

[1] Abbreviations: IA_{B1} = mean insect abundance on and one day prior to banding day; IA_{MB} = mean insect abundance up to and including banding day; and HD = hatching date

[2] Number of parameters

[3] AICc values for top model: Barn 1428.2; Cliff 664.1; Tree 2337.8.

Table 8. Averaged model coefficients with adjusted SE and confidence intervals (CI) from the best-fit models for Barn, Cliff and Tree Swallow nestling mass.

Species	Coefficients[1]	Estimate	SE	Lower 95% CI	Upper 95% CI	Relative importance (S[2])
Barn	intercept	282.51	11.35	260.05	304.97	-
	IA_{B1}	27.01	25.62	-6.60	82.52	0.71 (1)
	IA_{MB}	6.38	16.26	-25.11	69.33	0.29 (1)
Cliff	intercept	-5141.00	1569.00	-8244.76	-2036.75	-
	IA_{B1}	-0.16	0.44	-2.11	0.66	0.21 (1)
	IA_{MB}	0.00	0.31	-1.63	1.57	0.14 (1)
	HD	-0.75	0.83	-2.69	0.34	0.64 (2)
	brood size	-0.23	0.46	-1.81	0.39	0.33 (1)
	site WE	-2.35	0.76	-3.85	-0.85	1.00 (4)
	year 2015	2.56	0.78	1.02	4.10	1.00 (4)
Tree	intercept	22.25	0.14	21.98	22.52	-
	HD	0.17	0.26	-0.14	0.93	0.42 (1)

[1] Abbreviations: IA_M = mean insect abundance up to and including day 12; and HD = hatching date.

[2] Number of averaged models.

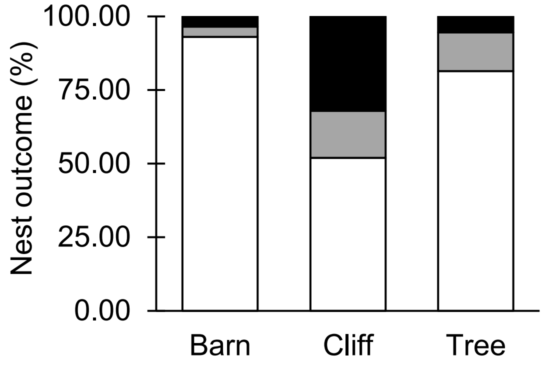

Figure 1. Proportion of Barn, Cliff and Tree Swallow nests that experienced no (white), some (grey) or complete (black) nestling mortality. Number of nests: Barn 29; Cliff 50; Tree 129.

Chapter 3. Breeding Phenology and Performance for Four Swallows over 57 Years: Relationships with Temperature and Precipitation

INTRODUCTION

Climate change has altered weather patterns across the planet, from gradual warming trends (Hayhoe et al. 2007; Hartmann et al. 2013) to temperature and precipitation extremes that result in worsening droughts, heavier rainfall, reduced snow cover, and more frequent and intense storms (Easterling et al. 2000; Hayhoe et al. 2007; Levinson & Bromirski 2007; Hartmann et al. 2013). Changes to weather patterns have wide-reaching impacts on the population dynamics and persistence of many taxa. These effects can include changes in species distributions, predator-prey interactions, demography and phenology (McCarty 2001b; Walther et al. 2002; Crick 2004; Parmesan 2006; Selwood et al. 2015).

One well-documented effect of warmer spring temperatures is a change in avian breeding phenology (i.e., the timing of breeding). Birds of a variety of species are arriving on the breeding grounds and nesting earlier than in the past (Dunn & Winkler 1999; Butler 2003; Sanz 2003; Donnelly et al. 2009; Townsend et al. 2013), which in turn, can affect breeding performance (Dunn & Møller 2014). For some species, early breeding results in more young fledged (Møller 2008; Vatka et al. 2011), higher nestling mass (Vatka et al. 2011) and increased rates of double-brooding (i.e., raising two or more broods each year, Townsend et al. 2013). In most species, however, early breeding results in poor nestling body condition, lower nestling survival and reduced rates of double-brooding (Visser et al. 2006; Both et al. 2009; Husby et al. 2009). The effects of early breeding are often mediated through a shift in food availability, especially for species that largely exploit a single prey item during breeding (Visser et al. 2006; Both et al. 2009; Husby et al. 2009; Vatka et al. 2011). Specifically, reduced food supply during breeding, from a mis-match between peak food abundance and peak food demand or an overall reduction in food abundance, results in lower breeding performance, and in turn drives population declines and increased risk of extinction (Both et al. 2006; Møller et al. 2008).

Aerial insectivores, including swallows (Hirundidae), swifts (Apodidae), nightjars (Caprimulgidae) and tyrant flycatchers (Tyrannidae), experienced severe and widespread population declines beginning in the mid-1980’s in North America, particularly in the northeast (Nebel et al. 2010; Shutler et al. 2012; Smith et al. 2015; but see Michel et al. 2016). Although the causes of the declines are unknown, like many other species, aerial insectivores face a variety of shared threats, including habitat loss, pesticides, pollution, road mortality and climate change (Nebel et al. 2010). Climate change, and its associated effects on local weather patterns, is a likely driver of these declines, because the rapid warming trend in North America (e.g., mid-1970’s) began in close proximity to population declines (Hansen et al. 2006; National Research Council 2007). Given their common food source, one way that climate change might drive declines for aerial insectivores is through an earlier emergence or lower abundance of aerial insects (Shutler et al. 2012).

Warmer temperatures are linked to both earlier first emergence and timing of peak abundance for a variety of insects (Visser et al. 2006; Bartomeus et al. 2011; Brooks et al. 2014; Kharouba et al. 2014). In addition, changes in winter temperature and precipitation also affect the annual abundance and diversity of insects (Finn & Poff 2008; Templer et al. 2012). In turn, reductions in insect availability during breeding have been repeatedly associated with lower breeding performance in the Tree Swallow, as measured by decreased clutch sizes, fewer fledglings and reduced nestling body condition (Quinney et al. 1986; Hussell & Quinney 1987; McCarty & Winkler 1999a; Nooker et al. 2005).

Although decreased breeding performance can contribute to population declines in aerial insectivores (Ambrosini et al. 2011), there is little information on whether breeding performance has declined during the period of population declines. While earlier breeding appears related to warmer spring temperatures (Dunn & Winkler 1999; Butler 2003; Sparks & Tryjanowski 2007; Møller 2008, 2011, but see Hussell 2003), it is not clear if early breeding could negatively affect performance. It is also unclear whether these patterns are consistent across species, suggesting a common driver of decline. Thus, research investigating changes in breeding performance before and after the onset of steep population declines is needed to determine if the declines result from reduced breeding performance, and if so, whether changes in breeding phenology and climatic conditions could contribute to changes in performance.

Here, I take a comparative, multi-species approach to determine if changes in breeding phenology and performance (i.e., clutch size, brood size and nestling survival) over time could account for declines in Bank, Barn, Cliff and Tree Swallows in the Maritime provinces of Canada, an area where aerial insectivores have experienced steep declines (Sauer et al. 2014). The climate in this region has changed since the mid-1900s, with increases in annual temperature (particularly during the winter) and rainfall, and decreases in snowfall and snow depth (Mekis & Vincent 2011; Vincent et al. 2012, 2015), and thus could be implicated in the observed population declines. To determine if there have been changes in breeding phenology and performance over time, I used historical data to compare each before (1962-1972) and after (2006-2016) the onset of steep population declines (i.e., during the mid-1980's, Nebel et al. 2010; Smith et al. 2015). Although the population trends during the before period are unknown, it is clear that populations of all four species were larger during the before period than during the after period (Sauer et al. 2014; A.C. Smith, pers. comm.). To help inform my understanding of the potential effect of climate change on population declines, I also related temperature and precipitation levels, two variables known to affect performance in aerial insectivores (McCarty & Winkler 1999a; Ambrosini et al. 2011; Winkler et al. 2013), on the breeding grounds to breeding phenology and performance from 1960-2016 in Barn and Tree Swallows, the two species with adequate data. My comparative, multi-species approach can be used to determine if there is a common pattern across species, which could help to explain declines in aerial insectivores as a larger group.

METHODS

I compiled most of the Bank, Barn, Cliff and Tree Swallow nest-monitoring information from historical nest monitoring data (1960-2013) found in the Maritime Nest Records Scheme (MNRS). MNRS volunteers in New Brunswick and Nova Scotia recorded data on the number of eggs and nestlings in the nests of all four species during one or more nest checks over the breeding season. I also included nest-monitoring data for Tree Swallows from two long-term study sites on Kent Island, New Brunswick (1987-2006) (Wheelwright & Schultz 1994) and near Wolfville, Nova Scotia (1988-1990, 1994-2013) (Leonard & Horn 1996), and for all four species from several sites around

Sackville, New Brunswick (2014-2016) (Saldanha 2016; Imlay et al. 2017b). At these latter sites, nests were typically checked every 1-3 days during the breeding season.

From the monitoring data, I tallied two variables that relate to breeding phenology (clutch initiation and hatching dates) and five variables that represent different components of breeding performance (clutch size, brood size, hatching success [whether or not at least one egg hatched], nestling survival [the number of surviving nestlings] and nest success [whether or not at least one young survived]). I applied several decision rules to ensure that these variables were included using consistent criteria (see Appendix 2 for details). Ultimately, I had at least one phenology or performance variable for 689 Bank, 2177 Barn, 687 Cliff and 4515 Tree Swallow breeding records. See Figure 2 for the spatial and temporal distribution of breeding records.

Changes in breeding phenology and performance

I compared breeding phenology and performance for the four species between two time periods: 1962-1972 and 2006-2016. These comparisons were between two periods rather than continuous because the data for Bank and Cliff Swallows were concentrated in the earlier and later years (Figure 2). I used linear regressions to compare clutch initiation dates (up to and including the median clutch initiation date for each year; see Appendix 2) to compare phenology for all four species from 1962-1972 to 2006-2016. I also used generalized linear models with a zero-truncated poisson distribution (for clutch size, brood size and nestling survival in successful nests) or binomial distribution (for hatching and nest success) to compare performance for all four species from 1962-1972 to 2006-2016.

Effects of climate on Barn and Tree Swallow phenology and performance

I examined the effect of climatic variables on Barn and Tree Swallow breeding phenology and performance over the 57-year time-span. Comparable data for Bank and Cliff Swallows were not available and so these species are excluded from the following analyses.

First, using ArcGIS version 10.3.1, I identified the closest weather station within an arbitrarily selected distance of 50 km (19.1 km ± 0.15 [SE]) of each breeding record with temperature and precipitation data. I retrieved temperature and precipitation data from Environment and Climate Change Canada: http://climate.weather.gc.ca/index_e.html (accessed 20 October 2016). When temperature and precipitation data were not available from the same weather station (314 of 6692 breeding records), I used data from the two closest stations within 50 km. I excluded 320 nest records from my analyses because temperature (86) and precipitation (234) data were not available.

Although many studies examine the relationship between spring temperatures and breeding phenology (e.g., Dunn & Winkler 1999; Hussell 2003), recent work has also demonstrated that winter temperature on the breeding grounds can affect breeding phenology and performance of insectivorous birds (Williams et al. 2015). This is likely due to the effects of temperature and/or precipitation on over-winter insect survival and development (Irwin & Lee 2000; Musolin & Saulich 2012; Templer et al. 2012). My exploratory data analysis suggested that minimum temperature and/or median precipitation over short periods of time throughout the winter was most predictive of breeding phenology for Barn and Tree Swallows. Therefore, I determined minimum temperature and median precipitation across six consecutive, 14 day windows (e.g., 1-14 January, 15-28 January, etc.) from 1 January to 25 March for all breeding records from 1960-2016 with weather data, resulting in 12 weather variables. Then, to reduce the number of weather variables, I conducted a principal components analysis with the centered and scaled weather variables. I identified four principal components with eigenvalues ≥ 1.0 (Table 7) to include in my models below (Norman & Streiner 1994). In general, loadings for these principal components indicated that the first (PC1) was related to temperature, with higher values indicating colder temperatures, and the remaining three (PC2, PC3 and PC4) were related to precipitation at different times during the winter, with higher values indicating less precipitation.

Next, to determine the best-fitting models to explain the potential effects of winter temperature and precipitation on Barn and Tree Swallow breeding phenology and performance, I used a linear regression (clutch initiation date) or generalized linear model with a poisson distribution (clutch size, brood size and nestling survival). My full models included all four principal components identified above, plus year, latitude and longitude, and, for models with different measures of breeding performance as the response variable (clutch size, brood size and nestling survival), I included clutch initiation date to account for seasonal declines in breeding performance (Møller 1994; Wardrop & Ydenberg 2003; Dawson 2008). Finally, I included an interaction between data source (a categorical variable that identified the data as from the MNRS or a long-term study) and year to account for changes in breeding performance that could be attributed to the different sources of data. This interaction was only included in my initial models for Barn Swallow brood size and nestling survival (Tables A2, A3). Graphical inspection of the results suggested that the inclusion of this term was due to smaller broods and lower nestling survival in one year (2016) of the three-year period when long-term data were available (Figure A1, Appendix 2). Since this result contrasted with my comparisons of the long-term data from 1962-1972 and 2006-2016 (Table 9) and appeared to be driven by a single year, my results for these two response variables below only include data from the Maritime Nest Records Scheme.

Finally, I centered and scaled all continuous explanatory variables (i.e., year, latitude, longitude and clutch initiation date) in my models (Grueber et al. 2011), and then modeled all possible combinations of the variables included in the full model, as well as a null model without covariates. The best-fitting model was determined using Akaike's Information Criterion with the small sample size correction, AIC*c*, and by examining the AIC*c* weight, w_i (Burnham & Anderson 2002). Since many of the top models ($\Delta AICc \leq 2.0$) were similar, I averaged all models with a $\Delta AICc \leq 2.0$ to determine my parameter estimates and the relative importance of each variable. I was interested in the variables that had the greatest effect on my response, therefore I used the zero method for model averaging (Nakagawa & Freckleton 2011). I restrict my interpretation of these models to explanatory variables with a significant effect on the response (i.e., those variables with 95% confidence intervals that do not span zero). All analyses were performed in R version 3.4.2 (R Core Team 2017) using MuMIn version 1.40.0.

RESULTS

Changes in breeding phenology and performance

Bank Swallows initiated clutches at similar times in 2006-2016 compared to 1962-1972, whereas Barn, Cliff and Tree Swallows initiated clutches 9.9, 8.1 and 10.4 days earlier in 2006-2016, respectively (Table 9).

Breeding performance was lower for Bank Swallows and higher for Barn and Tree Swallows in 2006-2016 compared to 1962-1972, and largely unchanged for Cliff Swallows (Table 9). These results are detailed below by each component of breeding performance.

Clutch sizes for Bank and Tree Swallows differed significantly between 1962-1972 and 2006-2016, with a decrease of 0.5 eggs/clutch for Bank Swallows and an increase of 0.5 eggs/clutch for Tree Swallows in the more recent period compared to the earlier period. Clutch sizes did not differ significantly for Barn and Cliff Swallows between these time periods.

Hatching success for all species differed between 1962-1972 and 2006-2016, with decreases in hatching success in the later period for Bank (26.1%), Barn (12.3%), Cliff (26.6%) and Tree Swallows (7.1%) compared to the earlier period. For successful nests, brood size also differed significantly between 1962-1972 and 2006-2016, with a decrease of 1.1 nestlings/clutch for Bank Swallows and an increase of 0.6 nestlings/clutch for Tree Swallows in the later period compared to the earlier period. Broods sizes did not differ significantly for Barn and Cliff Swallows between periods.

Nest success also differed significantly between the two periods for Bank and Barn Swallows, with an 18.9% decrease in nests that had at least one surviving young for

Bank Swallows and a 12.4% increase in nests with at least one surviving young for Barn Swallows in 2006-2016 compared to the earlier time period. Nest success did not differ significantly for the remaining species between these periods. Finally, for successful nests, nestling survival differed between 1962-1972 and 2006-2016, with a decrease of 1.2 nestlings/clutch for Bank Swallows and an increase of 0.6 nestlings/clutch for Tree Swallows in the later period compared to the earlier period. Survival did not differ significantly for Barn Swallows between these periods, and I was unable to analyze the data for Cliff Swallows due to the small sample size in 1962-1972 (n = 9).

Effects of climate on Barn and Tree Swallow phenology and performance

All of my top models for Barn and Tree Swallow breeding phenology included precipitation for both species, and, for Tree Swallows, temperature (Tables 10, 11). Model-average coefficients indicate that both species bred earlier after winters with less precipitation, and, for Tree Swallows, after warmer winters (Tables 12, 13).

Although temperature and precipitation were included in several top models for Barn and Tree Swallows breeding performance (Tables 10, 11), neither clutch size or brood size for either species, nor nestling survival for Barn Swallows were affected by temperature or precipitation (Tables 12, 13). However, for Tree Swallows, model-averaged coefficients indicate that nestling survival was higher after colder winters. Also, Tree Swallow nestling survival was both positively and negatively related to precipitation during different periods of the winter.

In addition to the relationships with weather, I also found a negative relationship between clutch initiation date and year for both swallows (Tables 12, 13), with birds breeding earlier in recent years. Also, for Barn Swallows, there was a positive relationship between nestling survival and year, indicating an increase in nestling survival from 1960 to 2016. This corroborates my previous analysis comparing changes in clutch initiation dates for both species and nest success for Barn Swallows between 1962-1972 and 2006-2016. Clutch initiation dates were negatively related to clutch size for both species, and, for Tree Swallows, brood size and nestling survival, indicating higher performance with earlier breeding.

DISCUSSION

The goal of my study was to determine if changes in breeding performance over time, potentially as a result of changes in breeding phenology and climate change, could explain population declines for four swallow species. I found changes in at least one measure of breeding performance for all species, and all species had lower hatching success. However, only Bank Swallows had consistently lower breeding performance in all components. Of those, fewer nests fledgling young and lower nestling survival, in particularly that could contribute to population declines. I also found that there was no change in the timing of Bank Swallow breeding in 2006-2016 compared to 1962-1972. In contrast, Barn, Cliff and Tree Swallows were breeding 8-10 days earlier. Finally, for Barn and Tree Swallows, earlier breeding phenology was related to warmer winter temperatures, and, for Tree Swallows, higher nestling survival was associated with colder winter temperatures and changes in winter precipitation. Therefore, not all species experienced similar changes in breeding phenology and performance, nor showed similar responses to weather.

Only the Bank Swallow showed a consistent decrease in breeding performance across all five measures between 1962-1972 and 2006-2016. I estimated that this decline in reproductive performance would result in an estimated 46% reduction in fledglings/pair. While I do not know the mechanism behind this reduction in breeding performance, the Bank Swallow was the only species that did not advance clutch initiation dates in recent years. Therefore, like other migratory birds that exhibit little or no change in spring phenology, it is possible that a mis-match between food supply and breeding phenology is driving population declines (Møller et al. 2008). Another possible explanation for the reductions in breeding performance is carry-over effects from winter to breeding (Chapter 4). Carry-over effects from poor wintering conditions to breeding have also been linked to population declines for some migratory birds (Finch et al. 2014), but other studies have found that breeding conditions have a greater effect on populations than carry-over effects from non-breeding conditions (Ockendon et al. 2013; Rushing et al. 2016).

Aside from decreased hatching success, I did not find a consistent decline in breeding performance over time for the remaining three species. Breeding performance either increased (Barn and Tree Swallows) or there was no change (Cliff Swallows), possibly due to advances in breeding phenology over time. These results are consistent with studies on a European population of Barn Swallows and the Willow Tit *Poecile montanus* that had higher breeding performance with earlier breeding phenology (Møller 2008; Vatka et al. 2011). Although I did not directly measure food availability across this time period, it is possible that by breeding earlier, swallows in my study may have aligned breeding with periods of abundant food (Møller et al. 2008, but see Dunn et al.

2011). In addition, recent research in this region indicates that food availability does not limit breeding success for Barn, Cliff and Tree Swallows, suggesting that insect abundance is high throughout the breeding season (Imlay et al. 2017a; Chapter 2).

Another possible explanation for my results is changes in the survival of different age classes of Bank, Barn and Tree Swallows. In general, swallows with previous breeding experience breed earlier and have higher performance than younger swallows (Hussell & Quinney 1987; Wardrop & Ydenberg 2003); although senescence may reduce performance for very old individuals (Møller & de Lope 1999). Therefore, lower survival rates for older Bank Swallows and younger Barn and Tree Swallows could explain the changes I observed (i.e., lower performance for Bank Swallows and higher performance for Barn and Tree Swallows, respectively). However, without long-term data on age class structure in populations prior to the onset of population declines, I am unable to examine this possibility.

In the Maritimes, climate change has resulted in warmer winter temperatures (especially minimum temperatures) and reductions in snowfall and snow depth (Mekis & Vincent 2011; Vincent et al. 2012, 2015), which are related to advances in breeding phenology for Barn and Tree Swallows. Similar results between temperature and breeding phenology have been reported for a variety of other migratory birds (Sanz 2003; Townsend et al. 2013), including North American populations of Tree Swallows (Dunn & Winkler 1999). To my knowledge, however, mine is the first study to demonstrate the importance of winter precipitation on breeding phenology. Winter temperature and precipitation were not related to clutch size and brood size for Barn and Tree Swallows, nor nestling survival for Barn Swallows, suggesting that conditions during breeding, like cold snaps and breeding habitat, likely have a stronger effect on performance than winter weather (Ambrosini et al. 2002; Ghilain & Bélisle 2008; Winkler et al. 2013). However, for Tree Swallows, nestling survival was lower after warmer winters, less precipitation during early January and March, and more precipitation during late February.

Since neither species is present on the breeding grounds during the winter, it seems likely that winter temperature and precipitation is affecting Barn and Tree Swallow breeding phenology and performance through insect availability (Williams et al. 2015). Snow pack is an important factor affecting overwinter insect survival (Templer et al. 2012). Reductions in snow pack, associated with warmer temperatures and/or reduced precipitation (Mekis & Vincent 2011; Vincent et al. 2012, 2015), may result in earlier, but less abundant and diverse insect populations (Finn & Poff 2008). While I am uncertain about the cause of contrasting trends for precipitation during different times of the winter, I speculate that it may be driven by the effects of winter precipitation on the survival and/or development of different types of insects during periods when they are most vulnerable (Todd 1996; Irwin & Lee 2000; Musolin & Saulich 2012). Ultimately, regardless of the annual variation in temperature and precipitation and associated effects on annual breeding performance, for Barn and Tree Swallows breeding performance was higher in 2006-2016, compared to 1962-1972, indicating that at this time, climate change is not negatively affecting breeding performance across a broader time period.

It is possible that the relationships I observed between winter weather on the breeding grounds and breeding phenology and performance, are due to similar conditions in breeding and non-breeding locations. If so, the effects on breeding phenology and performance are the result of carry-over effects from winter to breeding. This explanation is supported more strongly for Maritime breeding Tree Swallows that winter in southern Florida and Cuba (Burke 2014) and are potentially within a short enough distance for weather between these locations to be correlated. Maritime breeding Barn Swallows, however, winter in central and southern South America (Hobson et al. 2015; Hobson & Kardynal 2016; Chapter 6); the large distance between wintering and breeding locations for this species offers less support for this explanation.

Conclusions

The cause of broad-scale population declines for aerial insectivores in North America is currently unknown. Breeding performance declined substantially for Bank Swallows and is likely contributing to population declines, however, for the other three swallow species, performance is higher or unchanged. Interestingly, the only species experiencing lower breeding performance (Bank Swallow) did not advance its breeding phenology, whereas the other species did, by 8-10 days, likely in response to warmer temperatures (Dunn & Winkler 1999; Sanz 2003; Townsend et al. 2013) and/or less precipitation. An inability to advance breeding phenology for Bank Swallows might contribute to their lower breeding performance. Declines in aerial insectivores have been attributed to a broad-scale common driver affecting multiple species (Nebel et al. 2010; Smith et al. 2015; but see Michel et al. 2015). However, my results suggest that population declines for these three species cannot be explained by reductions in breeding performance. Furthermore, for Barn and Tree Swallows, climate change does not appear to be driving population declines through reduced breeding performance at this time. Together, this suggests that future work should consider the potential effects of conditions during migration and winter on population declines through their effects on swallow survival. For example, adult survival in Afro-Palearctic populations of Bank and Barn Swallows is closely related to precipitation during the winter (Cowley & Siriwardena 2005; Robinson et al. 2008; Norman & Peach 2013).

Citizen scientist data from programs like the MNRS present valuable opportunities for examining trends in breeding phenology and performance for a variety of species and over longer periods of time than most research projects. For my study, the MNRS data spanned a period of 57 years, both before and after these species began experiencing steep declines (e.g., mid-1980's, Nebel et al. 2010; Smith et al. 2015). I recommend that data from the MNRS and other related programs be used in similar projects aimed at understanding changes in breeding phenology, performance and population trends.

Table 7. Results of a principal components analysis for temperature and precipitation variables. The first four principal components (PC1-4) had eigenvalues > 1.0 and were used to model the relationships between Barn and Tree Swallow breeding phenology and performance. Bolded values indicate the highest loading for each variable.

Variables[1]	PC1	PC2	PC3	PC4
T1	-0.38	0.20	-0.02	0.06
T2	-0.42	0.12	-0.01	-0.17
T3	-0.42	-0.08	0.10	-0.01
T4	-0.39	0.12	-0.10	-0.06
T5	-0.38	-0.23	0.09	0.07
T6	-0.40	0.11	0.11	-0.09
P1	-0.17	-0.54	-0.16	0.21
P2	-0.08	-0.19	-0.62	0.07
P3	-0.05	0.15	-0.53	0.46
P4	0.03	0.05	-0.44	-0.80
P5	-0.02	-0.66	0.17	-0.22
P6	-0.09	0.28	0.18	-0.01
Eigenvalue	3.77	1.35	1.15	1.04
Variance	0.31	0.11	0.10	0.09
Cumulative variance	0.31	0.43	0.52	0.61

[1] Abbreviations for variables: T1 = 1 to 14 January, T2 = 15 to 28 January, T3 = 29 January to 11 February, T4 = 12 to 25 February, T5 = 26 February to 11 March, T6 = 12 to 25 March.

Table 8. Comparisons of the breeding phenology and performance of Bank, Barn, Cliff and Tree Swallows between two time periods, 1962-1972 and 2006-2016 using linear and generalized linear models. Mean values are presented with SD and sample size in brackets below. Asterisks were used to indicate significant differences between time periods (* = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$).

Species	Time period	Clutch initiation date[1]	Clutch size	Brood size[2]	Nestling survival[2]	Hatching success	Nest success
Bank	1962-1972	39.0 ± 7.3 (25)	4.7 ± 0.7* (107)	4.4 ± 0.8*** (117)	4.1 ± 1.0*** (81)	95.6%*** (275)	78.8%*** (137)
	2006-2016	40.6 ± 2.9 (143)	4.2 ± 1.0 (291)	3.3 ± 1.0 (215)	2.9 ± 1.0 (165)	69.5% (325)	59.9% (284)
Barn	1962-1972	38.7 ± 6.6*** (88)	4.6 ± 1.0 (350)	4.4 ± 0.9 (270)	4.2 ± 1.1 (86)	91.7%*** (630)	60.3%** (156)
	2006-2016	28.8 ± 4.2 (190)	4.6 ± 1.0 (427)	4.3 ± 1.1 (304)	4.1 ± 1.1 (274)	79.4% (467)	72.7% (395)
Cliff	1962-1972	40.9 ± 3.2*** (28)	3.7 ± 0.9 (114)	3.1 ± 1.0 (47)	–	89.4%*** (180)	44.4% (45)
	2006-2016	32.8 ± 4.3 (133)	3.5 ± 0.9 (294)	3.1 ± 1.0 (132)		62.8% (290)	41.2% (221)
Tree	1962-1972	30.4 ± 6.0*** (68)	5.0 ± 1.2** (186)	4.6 ± 1.1** (160)	4.3 ± 1.4* (64)	93.4%** (286)	77.9% (95)
	2006-2016	20.0 ± 4.9 (449)	5.5 ± 1.0 (973)	5.2 ± 1.1 (777)	4.9 ± 1.2 (531)	86.3% (955)	74.6% (721)

[1] May 1 = day 1.

[2] Only data from successful nests are included in calculations of brood size and nestling survival.

Table 9. Model selection table for the best-fitting models for the relationships between temperature and Barn Swallow breeding phenology and performance. Only models within ΔAICc ≤ 2.0 of the top model are displayed.

Response	Model[1,2]	df	AICc	ΔAICc	w_i	Log Likelihood
Clutch initiation date	Latitude + Longitude + PC2 + Year	6	1906.81	0.00	0.09	-947.27
	Latitude + Longitude + PC1 + PC2 + Year	7	1907.50	0.69	0.06	-946.56
	Latitude + PC2 + Year	5	1907.64	0.83	0.06	-948.72
	PC1 + PC2 + Year	5	1907.89	1.08	0.05	-948.85
	Latitude + PC1 + PC2 + Year	6	1908.36	1.55	0.04	-948.04
	Longitude + PC1 + PC2 + Year	6	1908.40	1.59	0.04	-948.06
	Latitude + Longitude + PC2 + PC4 + Year	7	1908.68	1.87	0.04	-947.16
Clutch size	CID	2	1811.05	0.00	0.04	-903.51
	CID + Longitude	3	1812.16	1.11	0.02	-903.05
	CID + PC4	3	1812.40	1.35	0.02	-903.18
	CID + Source	3	1812.51	1.46	0.02	-903.23
	CID + PC4 + Source	4	1812.58	1.52	0.02	-902.25
	CID + Latitude	3	1812.72	1.67	0.02	-903.34
	CID + PC3	3	1812.93	1.88	0.01	-903.44
	CID + PC1	3	1813.04	1.99	0.01	-903.50
Brood size	Latitude	2	1223.55	0.00	0.04	-609.75
	Latitude + Year	3	1224.02	0.47	0.03	-608.97
	Latitude + PC1 + Year	4	1224.68	1.13	0.02	-608.27
	null	1	1224.85	1.30	0.02	-611.42
	CID + Latitude	3	1224.95	1.40	0.02	-609.43
	Latitude + PC3	3	1225.07	1.52	0.02	-609.49
	Latitude + PC3 + Year	4	1225.24	1.69	0.02	-608.55
	Latitude + PC4	3	1225.50	1.95	0.02	-609.71
	Latitude + PC1	3	1225.53	1.99	0.02	-609.73
Nestling survival	PC3 + Year	3	948.58	0.00	0.04	-471.23
	Year	2	948.62	0.04	0.04	-472.28
	PC2 + PC3 + Year	4	949.41	0.83	0.03	-470.61
	PC2 + Year	3	949.60	1.02	0.03	-471.74
	Latitude + PC1 + PC3 + Year	5	949.74	1.16	0.02	-469.73
	Latitude + PC1 + PC2 + PC3 + Year	6	949.85	1.27	0.02	-468.72

Response	Model[1,2]	df	AICc	ΔAICc	w_i	Log Likelihood
	Latitude + PC3 + Year	4	949.96	1.38	0.02	-470.88
	Latitude + PC1 + Year	4	950.18	1.60	0.02	-470.99
	Latitude + Year	3	950.18	1.60	0.02	-472.03
	PC4 + Year	3	950.30	1.72	0.02	-472.09
	PC3 + PC4 + Year	4	950.40	1.82	0.02	-471.10
	Longitude + PC3 + Year	4	950.40	1.83	0.02	-471.11
	PC1 + Year	3	950.57	1.99	0.02	-472.23
	PC1 + PC3 + Year	4	950.57	1.99	0.02	-471.19

[1] PC1-4 represents principal components 1-4 identified in Table 2.

[2] Source was a categorical variable representing data that was collected as part of the Maritime Nest Records Scheme or long-term monitoring projects.

Table 10. Model selection table for the best-fitting models for the relationships between temperature and Tree Swallow breeding phenology and performance. Only models within ΔAICc ≤ 2.0 of the top model are displayed.

Response variable	Model[1,2]	df	AICc	ΔAICc	w_i	Log Likelihood
Clutch initiation date	PC1 + PC3 + Source + Year	6	6653.77	0.00	0.08	-3320.85
	Latitude + PC1 + PC3 + Source + Source:Year + Year	8	6654.15	0.38	0.06	-3319.01
	PC1 + PC3 + Source + Source:Year + Year	7	6654.31	0.54	0.06	-3320.10
	PC1 + PC3 + PC4 + Source + Year	7	6654.46	0.69	0.05	-3320.18
	Latitude + Source + PC1 + PC3 + Year	7	6654.46	0.69	0.05	-3320.18
	PC1 + PC3 + PC4 + Source + Source:Year + Year	8	6654.68	0.91	0.05	-3319.28
	Longitude + PC1 + PC3 + Source + Year	7	6655.01	1.23	0.04	-3320.45
	Latitude + PC1 + PC3 + PC4 + Source + Source:Year + Year	9	6655.08	1.31	0.04	-3318.46
	Latitude + PC1 + PC3 + PC4 + Source + Year	8	6655.57	1.80	0.03	-3319.72
	Longitude + PC1 + PC3 + PC4 + Source + Year	8	6655.71	1.94	0.03	-3319.79
	Latitude + Longitude + PC1 + PC3 + Source + Year	8	6655.73	1.95	0.03	-3319.80
Clutch size	CID	2	7026.48	0.00	0.07	-3511.24
	CID + PC2	3	7028.21	1.73	0.03	-3511.10
	CID + Source	3	7028.26	1.78	0.03	-3511.12
	CID + PC1	3	7028.28	1.80	0.03	-3511.13
	CID + Year	3	7028.28	1.80	0.03	-3511.13
	CID + Longitude	3	7028.31	1.83	0.03	-3511.15
	CID + PC4	3	7028.33	1.86	0.03	-3511.16
	CID + Latitude	3	7028.35	1.87	0.03	-3511.17
Brood size	CID + Source + PC1 + PC2	5	7682.25	0.00	0.04	-3836.11
	CID + Source + PC2	4	7683.00	0.75	0.02	-3837.49
	CID + Source + PC2 + PC4	5	7683.07	0.82	0.02	-3836.52
	CID + Source + PC1 + PC2 + PC4	6	7683.22	0.98	0.02	-3835.59

Response variable	Model[1,2]	df	AICc	ΔAICc	w_i	Log Likelihood
	CID + Longitude + Source + PC2	5	7683.55	1.30	0.02	-3836.76
	CID + Longitude + Source + PC1 + PC2	6	7683.66	1.41	0.02	-3835.81
	CID + Longitude + Source + PC2 + PC4	6	7683.85	1.60	0.02	-3835.90
	CID + Source + PC4	4	7683.90	1.65	0.02	-3837.94
	CID + Source	3	7684.02	1.77	0.01	-3839.00
	CID + Latitude + Source + PC1 + PC2	6	7684.09	1.85	0.01	-3836.02
	CID + Source + PC1 + PC2 + Year	6	7684.20	1.96	0.01	-3836.08
	CID + Source + PC1 + PC2 + PC3	6	7684.23	1.98	0.01	-3836.09
Nestling survival	CID + Source + PC1 + PC2	7	6522.74	0.00	0.09	-3254.33
	CID + Source + PC2	6	6522.78	0.05	0.09	-3255.36
	CID + Source + PC2 + PC4	7	6524.27	1.53	0.04	-3255.09
	CID + Source + PC1 + PC2 + PC4	5	6524.30	1.56	0.04	-3257.13
	CID + Longitude + Source + PC2	7	6524.41	1.68	0.04	-3255.17
	CID + Longitude + Source + PC1 + PC2	8	6524.49	1.76	0.04	-3254.20
	CID + Longitude + Source + PC2 + PC4	6	6524.52	1.78	0.04	-3256.23
	CID + Source + PC4	8	6524.69	1.95	0.03	-3254.29
	CID + Source	9	6524.71	1.98	0.03	-3253.29

[1] PC1-4 represents principal components 1-4 identified in Table 2.

[2] Source was a categorical variable representing data that was collected as part of the Maritime Nest Records Scheme or long-term monitoring projects.

Table 11. Model coefficients, SE and 95% confidence intervals (CI) for the best-fitting models explaining the relationships between temperature, precipitation and breeding phenology or performance for Barn Swallows. Bolded explanatory values indicated those with an effect on the response.

Response[1]	Explanatory variable[2,3]	Estimate	SE	Lower 95% CI	Upper 95% CI	Relative importance (N[4])
Clutch initiation date	(Intercept)	363.24	48.46	267.97	458.52	
	Latitude	**0.89**	**0.69**	**0.12**	**2.23**	**0.76 (5)**
	Longitude	0.29	0.34	-0.12	1.10	0.60 (4)
	PC1	0.23	0.29	-0.09	0.96	0.52 (4)
	PC2	**-1.54**	**0.30**	**-2.14**	**-0.94**	**1.00 (7)**
	PC4	-0.01	0.11	-0.79	0.49	0.09 (1)
	Year	**-0.18**	**0.02**	**-0.22**	**-0.14**	**1.00 (7)**
Clutch size	(Intercept)	1.45	0.69	0.10	2.81	
	CID	**-0.00**	**0.00**	**-0.01**	**-0.00**	**1.00 (8)**
	Latitude	0.00	0.01	-0.04	0.07	0.10 (1)
	Longitude	0.00	0.01	-0.05	0.02	0.14 (1)
	PC1	0.00	0.00	-0.02	0.03	0.09 (1)
	PC3	0.00	0.01	-0.03	0.05	0.09 (1)
	PC4	-0.01	0.02	-0.08	0.02	0.23 (2)
	Source[3]	0.01	0.04	-0.06	0.17	0.22 (2)
Nestling survival	(Intercept)	-12.38	4.69	-21.62	-3.15	
	Latitude	-0.03	0.07	-0.28	0.07	0.32 (5)
	Longitude	0.00	0.01	-0.05	0.09	0.05 (1)
	PC1	0.01	0.03	-0.04	0.14	0.30 (5)
	PC2	0.01	0.03	-0.03	0.12	0.23 (3)
	PC3	0.04	0.04	-0.02	0.14	0.57 (8)
	PC4	0.00	0.02	-0.07	0.12	0.11 (2)
	Year	**0.01**	**0.00**	**0.00**	**0.01**	**1.00 (14)**

[1] Model coefficients for Barn Swallow brood size are not provided because 95% confidence intervals for all explanatory variables spanned zero.

[2] PC1-4 represents principal components 1-4 identified in Table 2.

[3] Source was a categorical variable representing data that was collected as part of the Maritime Nest Records Scheme or long-term monitoring projects.

[4] Number of averaged models.

Table 14. Model coefficients, SE and 95% confidence intervals (CI) for the best-fitting models explaining the relationships between temperature, precipitation and breeding phenology or performance for Tree Swallows. Bolded explanatory values indicated those with an effect on the response.

Response	Explanatory variables^{1,2}	Estimate	SE	Lower 95% CI	Upper 95% CI	Relative importance (N^{3})
Clutch initiation date	(Intercept)	314.58	36.85	242.29	386.87	
	Latitude	-0.23	0.40	-1.45	0.34	1.00 (11)
	Longitude	0.04	0.13	-0.25	0.67	1.00 (11)
	PC1	**1.33**	**0.14**	**1.05**	**1.62**	**0.41 (5)**
	PC3	**-0.43**	**0.16**	**-0.75**	**-0.11**	**0.40 (4)**
	PC4	-0.06	0.12	-0.44	0.12	0.39 (5)
	Source	38.35	61.74	-82.72	159.43	1.00 (11)
	Source:Year	-0.02	0.03	-0.11	0.02	1.00 (11)
	Year	**-0.14**	**0.02**	**-0.17**	**-0.11**	**0.19 (3)**
Clutch size	(Intercept)	1.81	0.70	0.44	3.17	
	CID	**-0.01**	**0.00**	**-0.01**	**-0.01**	**1.00 (8)**
	Latitude	0.00	0.01	-0.03	0.04	0.11 (1)
	Longitude	0.00	0.00	-0.02	0.03	0.11 (1)
	PC1	0.00	0.00	-0.01	0.02	0.11 (1)
	PC2	0.00	0.00	-0.01	0.02	0.10 (1)
	PC4	0.00	0.00	-0.02	0.02	0.10 (1)
	Source	0.00	0.01	-0.06	0.04	0.11 (1)
	Year	**0.00**	**0.00**	**0.00**	**0.00**	**0.10 (1)**
Brood size	(Intercept)	1.92	0.98	0.00	3.83	
	CID	**-0.01**	**0.00**	**-0.01**	**-0.01**	**1.00 (12)**
	Latitude	0.00	0.01	-0.05	0.07	1.00 (12)
	Longitude	0.00	0.01	-0.01	0.05	0.51 (6)
	PC1	-0.01	0.01	-0.03	0.00	0.34 (4)
	PC2	0.02	0.01	-0.00	0.04	0.23 (3)
	PC3	0.00	0.00	-0.02	0.03	0.06 (1)
	PC4	0.00	0.01	-0.01	0.04	0.06 (1)
	Source	**0.08**	**0.03**	**0.01**	**0.14**	**0.87 (10)**
	Year	0.00	0.00	-0.00	0.00	0.06 (1)
Nestling survival	(Intercept)	4.80	2.72	-0.53	10.13	
	CID	**-0.01**	**0.00**	**-0.02**	**-0.01**	**1.00 (9)**
	Latitude	-0.07	0.05	-0.16	0.00	0.82 (7)

Response	Explanatory variables[1,2]	Estimate	SE	Lower 95% CI	Upper 95% CI	Relative importance (N[3])
	Longitude	0.00	0.01	-0.04	0.05	0.52 (5)
	PC1	**0.04**	**0.02**	**0.01**	**0.08**	**1.00 (9)**
	PC2	**-0.04**	**0.01**	**-0.07**	**-0.02**	**0.17 (2)**
	PC3	0.00	0.01	-0.02	0.04	0.16 (2)
	PC4	**0.04**	**0.01**	**0.01**	**0.07**	**0.08 (1)**
	Source	-0.77	3.19	-9.89	6.94	1.00 (9)
	Source:Year	0.00	0.00	-0.00	0.01	1.00 (9)
	Year	-0.00	0.00	-0.00	0.00	0.08 (1)

[1] PC1-4 represents principal components 1-4 identified in Table 2.

[2] Source was a categorical variable representing data that was collected as part of the Maritime Nest Records Scheme or long-term monitoring projects.

[3] Number of averaged models.

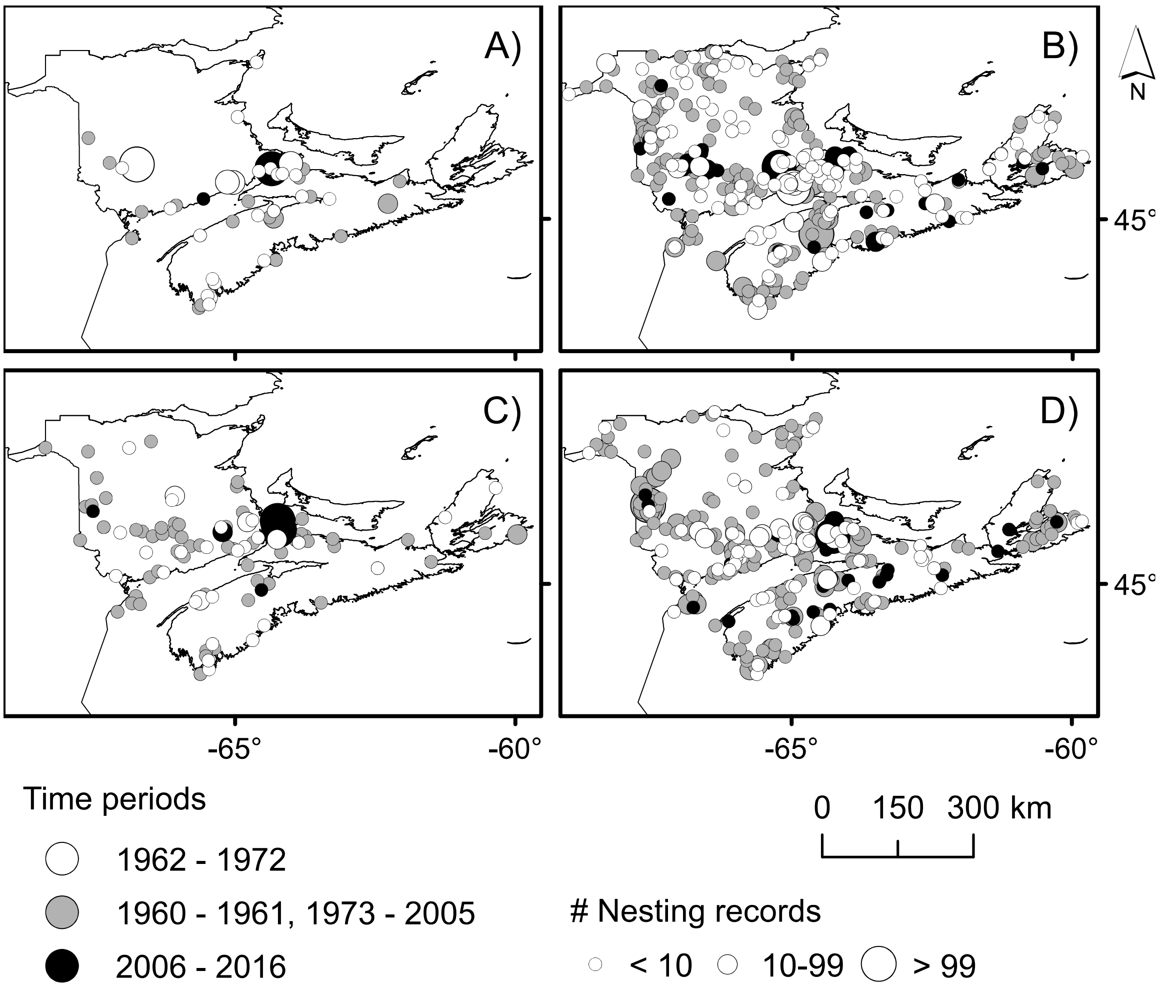

Figure 2. Temporal and spatial distribution of nest records for A) Bank, B) Barn, C) Cliff and D) Tree Swallows where at least one variable of breeding phenology and breeding performance could be identified. Breeding records within 5 km and during the same period of time are represented by a single point on this map.

Chapter 4. Intrinsic Markers Identify Carry-Over Effects from Non-Breeding to Breeding for Three Declining Aerial Insectivores

INTRODUCTION

Throughout the annual cycle, environmental conditions, like weather and habitat quality, affect animal survival and fecundity. These conditions have important implications for species evolution, ecology and conservation through their effects on fitness and population dynamics (Sherry & Holmes 1995; Wingfield 2008). For migratory species that move large distances over the course of their annual cycle, environmental conditions that affect survival and/or fecundity during one stage may be different than the conditions at another (Sherry & Holmes 1995; Rushing et al. 2016). Furthermore, the effects of ecological conditions at each stage are not independent, and these conditions may affect survival and fecundity at a later period (Webster & Marra 2005; Harrison et al. 2011; O'Connor et al. 2014). When this occurs at the individual level, these are known as carry-over effects.

Carry-over effects have been investigated extensively in migratory birds, with much of the work focusing on how environmental conditions during the non-breeding period affect subsequent migration and breeding. For many species, poor non-breeding conditions, especially those associated with reduced food availability, can result in higher stress levels, lower survival rates and poor body condition, which delays the timing of migration departure or arrival on the breeding grounds, and ultimately results in reduced breeding performance (Norris 2005; Harrison et al. 2011; Rockwell et al. 2012; Goodenough et al. 2017). These effects may vary with the age and sex of an individual

(Saino et al. 2004, 2017; Drake et al. 2013; López-Calderón et al. 2017b). For one well-studied species, the American Redstart *Setophaga ruticilla*, individuals that wintered in areas with low food availability had higher levels of stress (Marra & Holberton 1998; Angelier et al. 2013) and lower body condition (Johnson et al. 2006; Angelier et al. 2011) than those that wintered in areas with high food availability. During the subsequent breeding season, the former individuals also arrived on the breeding grounds later, bred later and raised fewer offspring (Norris et al. 2004). For some species or under specific circumstances, carry-over effects from the non-breeding period may have a stronger influence on breeding performance than conditions during the breeding period (Finch et al. 2014), thus highlighting the importance of understanding the effects of environmental conditions throughout the annual cycle.

Despite the importance of this work, it is often difficult to track individuals across the vast distances covered through their annual cycle and collect information on winter conditions and potential carry-over effects (Marra et al. 2015). Many recent studies have used intrinsic markers from a variety of tissues to gather information on habitat conditions, stress and environmental constraints during the non-breeding period. In keratinous tissues, like nails and feathers, intrinsic markers provide an indicator of conditions during the period of tissue growth. One commonly used marker for evaluating non-breeding habitat conditions is stable isotopes. Ratios of stable isotopes vary across the landscape in a predicable manner in relation to factors such as precipitation and evaporation (Bortolotti et al. 2013), plant and fungal communities (Briones et al. 2001; Craine et al. 2009; Powell et al. 2012), and anthropogenic sources of nitrogen (Hebert & Wassenaar 2001; Drake et al. 2013; but see Pardo & Nadelhoffer 2010). Since isotopes reflect different types of landscapes, they can be used to infer the characteristics of habitat used during the non-breeding period (Wassenaar & Hobson 2000; Norris et al. 2004; Evans et al. 2012). For example, areas with higher rainfall have lower δ^2H (Bortolotti et al. 2013), and areas with higher agricultural intensity may have higher δ^{13}C, due to the presence of C_4 plants like maize, (Cerling et al. 1997) and higher δ^{15}N, due to fertilizer and/or other agricultural practices (Hebert & Wassenaar 2001; Drake et al. 2013).

Another common intrinsic marker is corticosterone; a stress hormone that is released through activation of the hypothalamic-pituitary-adrenal axis in response to environmental conditions (Romero 2004; Landys et al. 2006; Wingfield 2013). Levels of corticosterone vary according to the energetic status of individuals (Lynn et al. 2010; Angelier et al. 2015; Krause et al. 2017) and elevated corticosterone levels are often associated with poor environmental conditions (Dickens & Romero 2013), like low food availability (Marra & Holberton 1998; Fairhurst et al. 2013).

Another approach is to measure changes in telomere length between sampling periods (referred to as telomere dynamics). Telomeres are well conserved sequences of non-coding DNA that protect coding DNA during replication (Blackburn 2005). Increased rates of telomere shortening are associated with oxidative stress, an imbalance between the production of reactive oxygen species and antioxidant defences (Reichert & Stier 2017), and poor environmental conditions (Angelier et al. 2018), like poor habitat quality (Angelier et al. 2013; Young et al. 2013). Unlike stable isotopes and corticosterone measured in keratinous tissues, this method can provide an indicator of environmental constraints across a longer period of time (Haussmann et al. 2012; Monaghan 2014).

Avian aerial insectivores are experiencing steep population declines in North America, particularly in the northeast (Nebel et al. 2010; Shutler et al. 2012). The cause of the declines is unknown, however two observations suggest that conditions during the non-breeding period are contributing to population declines. Firstly, within this guild, declines are steeper for long-distance migrants (those that winter in South America) than short-distance migrants (those that winter in the southern USA or Central America), suggesting that conditions during the non-breeding period are contributing to the declines through lower survival and/or carry-over effects from non-breeding to breeding (Nebel et al. 2010). Secondly, for one member of this guild, the Tree Swallow, a long-term decline in adult mass, measured during the breeding season, is thought to be driven by poor non-breeding conditions (Rioux Paquette et al. 2014). Despite these observations and the considerable research linking non-breeding conditions to subsequent reproductive success for Afro-Palearctic populations of aerial insectivores (e.g., Saino et al. 2004, 2017; López-Calderón et al. 2017), these relationships have not been examined for aerial insectivores breeding in North America.

The goal of this chapter was to determine if poor non-breeding conditions result in carry-over effects from non-breeding to breeding for three declining species of swallows (Bank, Barn and Cliff Swallow) in North America. Maritime breeding populations of these three species likely winter in areas of southern Brazil, Bolivia, Paraguay, Uruguay and northern Argentina, although this varies by species, and, for Barn Swallows, year (Chapter 6). I used a multi-species approach to determine if carry-over effects were similar across species. If so, this would support the idea that there is a common driver of population declines for aerial insectivores as a group (Nebel et al. 2010; Smith et al. 2015). However, it is also possible that given the variability in population trends (Michel et al. 2016), that these species are affected by similar non-breeding conditions in different ways.

To determine if there were carry-over effects, I analysed stable isotopes (δ^2H, δ^{13}C and δ^{15}N) and corticosterone (CORT$_f$) in winter-molted feathers (Pyle 1997; Imlay et al. 2017a) to determine the condition of non-breeding habitat and stress levels during this period, respectively. I also measured changes in telomere length from blood samples between years to determine stress-related aging, simply referred to as stress throughout this chapter, across the non-breeding period; this measurement also incorporated stress during the previous breeding season. I expected that poor non-breeding habitats (e.g., those with low food availability) would be related to higher stress levels (as indicated by high CORT$_f$ and greater rates of telomere shortening). In turn, either poor non-breeding conditions and/or high stress would result in carry-over effects, like lower spring mass, later breeding and lower breeding performance.

METHODS

Field methods

From May to August 2014 to 2016, I monitored the nests of Bank, Barn and Cliff swallows at several sites in New Brunswick, Canada. These sites included three Bank Swallow colonies along the Tantramar River (45.90º, -64.34º), and three Barn and Cliff Swallows colonies within 50 km of Moncton (46.09º, -64.78º). Using the methods outlined in Chapter 2 (Imlay et al. 2017b), I used frequent nest checks, typically every 2-3 days, except when severe rainfall prevented nest monitoring at Bank Swallow colonies, to identify clutch initiation dates, clutch size and nestling survival until day 12.

During this study, I also captured adult swallows to determine nest ownership and collect feather and blood samples. For Bank Swallows, I used tube traps to determine nest ownership. For Barn and Cliff swallows, I applied a small amount of different coloured LA-CO® All-weather® Paintstiks® to the rim or entrance of nests, which then transferred to the feet, breast, belly and/or tail feathers of the adults. Once captured in mist-nets, I could assign nest ownership based on paint colors and, for Barn Swallow, determine which individuals double-brooded (i.e., successfully raised or attempted to raise two broods) in a single year. To determine stable isotopes and $\mathrm{CORT_f}$, I collected 2-3 contour feathers from the flanks of all three species. I assumed these feathers were molted during the non-breeding period (Pyle 1997; Imlay et al. 2017a) and would therefore reflect stable isotope and corticosterone levels during this time. To determine changes in telomere length, I collected a small blood sample (<70 uL) from the brachial vein of all three species, and stored the blood samples on Whatman® FTA® classic cards (Smith & Burgoyne 2004). I also banded all adults with a Canadian Wildlife Service aluminum band and measured their mass.

Stable isotope analysis

I prepared all feather samples for stable isotope analysis by soaking samples in a 2:1 chloroform:methanol solution for 24 hours and then air drying at room temperature for 24 hours at Dalhousie University. Then, to determine stable isotope ratios in feathers, I sent samples to the Stable Isotopes in Nature Laboratory, University of New Brunswick

(SINLAB, δ^2H, δ^{13}C and δ^{15}N, 2013-2014), Stable Isotope Hydrology and Ecology Laboratory, Environment and Climate Change Canada (SIHEL, δ^2H, 2014-2017) and the Department of Soil Science Laboratory, University of Saskatchewan (DSSL, δ13C and δ^{15}N, 2014-2017).

Analysis of δ^2H followed the methods outlined by Wassenaar and Hobson (2003). At the SINLAB, samples were analyzed using a Thermo-Finnigan High Temperature Conversion Elemental Analyzer (TC/EA) and a Delta XP mass spectrometer. At SIHEL, samples were analyzed using a Eurovector elemental analyzer (Eurovector, Milan, Italy) with an Elementar Isoprime (Isoprime, Manchester, UK) continuous-flow isotope-ratio mass spectrometer. Results from both labs were calibrated with two keratin reference materials (e.g., caribou hoof keratin standard [-197.0 ‰] and kudu horn keratin standard [-54.1 ‰]).

Analysis of δ^{13}C and δ^{15}N was conducted at the SINLAB with a Carla Erba NC2500 of Costeck 4010 Elemental Analyzer with a Delta Plus or XP continuous flow isotope-ratio mass spectrometer (Thermo-Finnigan, Bremen, Germany) interfaced with a Conflow II or III, respectively. Results were calibrated with three reference materials: nicotinamide, bovine liver and smallmouth bass muscle. Similarly, at the DSSL, samples were analyzed using a Costech ECS4010 elemental analyzer (Costech Analytical Technologies, Valencia, California, USA) with a Delta V Advantage mass spectrometer with Conflo IV interface (Thermo Scientific, Bremen, Germany). Results were calibrated with two reference materials (BWB and egg albumen).

Stable isotope values are expressed in standard delta (δ) notation as parts per thousand (‰) deviation from the international standards: non-exchangeable hydrogen

(Vienna Standard Mean Ocean Water VSMOW), carbon (Vienna Pee Dee Belemnite VPDB) and nitrogen (atmospheric nitrogen AIR). Based on within-run replicates measurements of laboratory standards, the estimated measurement error is within ± 2.0 ‰ for δ^2H, ± 0.1 ‰ for δ^{13}C and ± 0.2 ‰ for δ^{15}N.

Corticosterone analysis

To determine CORT$_f$, I sent feather samples to the Toronto Zoo, Ontario where a corticosterone immunoassay (EIA) similar to Baxter-Gilbert et al. (2014) was used. Briefly, feathers were first washed with distilled water and air dried, and then sprayed with 100% methanol and air dried. Next, feathers were fully submerged in methanol for 24 hours in a 50ºC waterbath. The extract was then removed, evaporated under air for up to 48 hours, and stored at -20ºC until analyzed. Prior to conducting the EIA, the evaporated extracts were reconstituted with 0.15 mL of EIA buffer resulting in a 33.3x concentration of the sample. To obtain CORT$_f$ values, anti-corticosterone antibody (CJM006, C. Munro, University of California, Davis, CA, USA) and corticosterone-HRP label (C. Munro, University of California, Davis, CA, USA) were used. On each plate, corticosterone standards (Steraloids Q1550, 39 – 10,000 pg/ml), assay controls and reconstituted extracts diluted in EIA buffer were loaded in duplicate. Assay sensitivity was 107.1 pg/ml and inter- and intra-assays CV's were 19.2% and 4.4%, respectively. Parallelism between serially concentrated samples (neat, 5x, 10x, etc.) and the standard curve was obtained and the optimal concentration was selected for analysis of the experimental samples.

CORT$_f$ was standardized by the total length, from the start of the calamus to the tip of the feathers included in assay and expressed as pg/mm. For samples where the exact value of $\mathrm{CORT_f}$ could not be determined (< 0.01 pg/mm) due to the detection limits of the EIA, I set the numerical value of these samples to 0.009 pg/mm (Bank: n = 113/152 [74.3%], Barn: n = 45/157 [28.7%], Cliff: n = 18/125 [14.4%]). The standard error (± SE) in mass around the mean of feather samples for Bank, Barn and Cliff Swallows was small (1.7 ± 0.003, 1.6 ± 0.002 and 1.9 ± 0.005 mg, respectively), suggesting that differences in sample mass within species were unlikely to affect my results (Lattin et al. 2011).

Telomere analysis

To determine telomere length, I sent blood samples to the Centre d'Etudes Biologiques de Chizé, CNRS-Université de La Rochelle. Two mm² of the FTA card was cut, and DNA was extracted using a Mascherey-Nagel Nucleospin Tissue kit by following manufacturer protocol. DNA purity and quality was then assessed by using a Nanodrop spectrophotometer (Nussey et al. 2014). Telomere length was measured at the Centre d'Etudes Biologiques de Chizé by using the monochrome multiplex quantitative PCR method (MMqPCR) on a BioRad CFX 96 (BioRad). This MMqPCR method has been previously used to monitor telomere length in humans (Cawthon 2009) and wild birds (Parolini et al. 2015). The protocol previously used successfully for European Barn Swallows (Parolini et al. 2015) was followed with slight modifications. Briefly, this protocol used specific telomere primers that have previously been designed for MMqPCR (forward primer: 5'-ATCATTCAGGTTGAAGACCAGA-3', reverse primer: 5'-GTTATGATTTATTAGCTGTACAGCAGT-3') (Parolini et al. 2015) and a fragment of the CTCF gene as the reference gene. This gene is known as a single copy gene, which is well conserved among vertebrates. Then the CTCF primers previously described and validated for Barn Swallows (Forward primer: 5’-CCCGCGGCGGGCGGCGCGGGCTGGGCGGCTCCCAATGGAGACCTCAC-3’; Reverse primer: 5’-CGCCGCGGCCCGCCGCGCCCGTCCCGCCCATCACCGGTCCATCATGC-3’) (Parolini et al. 2015) were used in a MMqPCR with 1 ng of DNA per reaction. Both telomere primers were used at a concentration of 800nM and both single copy gene primers were used at a concentration of 500nM. These concentrations were optimized to allow both telomere and CTCF amplifications without creating primer-dimers. Optimized telomere PCR conditions were the same as those established by Parolini et al. (2015): 15 min at 95°C; 2 cycles of 15s at 94°C, 15s at 49°C; and 35 cycles of 15s at 94°C, 10s at 62°C, 15s at 74°C with signal acquisition, 10s at 84°C, 15s at 88°C with signal acquisition. Each MMqPCR was conducted using a total reaction volume of 10 µl including 8 µl of Master Mix (iQ SYBRGreen, Bio Rad). All samples were run in triplicates. For each species, a standard curve, which consisted of a serial dilution of a pooled DNA of five individuals, was included. For all three species, the efficiencies of all amplifications (telomere and CTCF) were within the acceptable range (88-102%) and the coefficient of variation in relative telomere length among plates was below 6.0%.

To determine telomere length for individuals captured in at least two subsequent years, I subtracted telomere length in the first year the individual was captured from the telomere length in the second year the individual was captured. Negative values indicated telomeres that shortened between years and positive values indicated telomeres that elongated. Since adults were first captured about one year apart from the previous year’s capture (Bank: 357.8 ± 1.4 [SE], Barn: 360.9 ± 1.9, Cliff: 360.6 ± 1.6 days), I did not standardize telomere length by the time between captures.

Statistical analysis

To determine the relationships between non-breeding habitat, stress, and potential carry-over effects, I used a type of piecewise structural equation modeling (piecewise SEM) known as confirmatory path analysis (Lefcheck 2016). This approach allows for multiple explanatory and response variables in a causal network, but does not include latent (i.e., unmeasured) variables (Shipley 1997). This method is appropriate for smaller numbers of observations, assuming that the sample size is sufficient for each piece of the model (Lefcheck 2016). This analysis is detailed below through a four-step process that includes first identifying variables, identifying relationships among variables, modeling these relationships, and finally testing for missing relationships.

First, I identified five levels of variables for the path analysis: 1) non-breeding habitat (variables: δ^{2}H, δ^{13}C and δ^{15}N), 2) non-breeding stress (variables: $CORT_f$ or telomere dynamics), 3) body condition (variable: spring mass), 4) breeding phenology (variable: clutch initiation date), and 5) breeding performance (variables: clutch size [female $CORT_f$ analyses only], only/first brood nestling survival, and whether or not the individual double-brooded [Barn Swallow analyses only]. The last three levels of variables were all considered potential carry-over effects. For Barn Swallows, I included the incidence of double-brooding as this may be a better metric for annual reproductive success than first brood nestling survival (Møller 1990).

Then, using these five levels of variables, I identified potential causal relationships between variables for my path analysis (Figure 3A). I selected the relationships to examine *a priori* based on the available literature for migratory birds, including my study species (see below), and my specific research question. Non-breeding habitat had potential effects on non-breeding stress, condition and breeding phenology (Marra & Holberton 1998; Angelier et al. 2013; López-Calderón et al. 2017b; Saino et al. 2017). Non-breeding stress had potential effects on condition, breeding phenology and performance (Marra & Holberton 1998; Harms et al. 2015), and condition had potential effects on breeding phenology and performance (Harms et al. 2015; López-Calderón et al. 2017b). Breeding phenology had potential effects on breeding performance (Brown & Bomberger Brown 1999b; Saino et al. 2004, 2017), and, for females, within breeding performance, clutch size had a potential effect on nestling survival. It was not possible to include CORT_f and telomere dynamics in the same path analysis as I needed an individual to be recaptured in at least two consecutive years to measure telomere dynamics. This resulted in considerably fewer individuals for analyses on telomere dynamics than CORT_f, so these indicators of stress were modeled in separate path analyses, referred to as either the CORT_f or telomere dynamics analysis.

For each species, I used these causal relationships (Figure 3A) in two analyses where I modeled the response for females and males separately and included CORT_f as my indicator of stress. For Barn Swallows, I also used these causal relationships (Figure 3A) in a path analyses for both sexes where I included telomere dynamics as my indicator of stress. For Bank and Cliff Swallows, my sample size was insufficient for a similar analysis with telomere dynamics as my indicator of stress. Therefore, for these two species, I used a less complex path analysis where non-breeding habitat had potential effects on non-breeding stress and condition, and non-breeding stress had a potential effect on condition (Figure 3B).

Next, for each dependent variable in the analyses above, the relationships were modeled to determine which explanatory variables had a significant effect on the dependent variables. For most dependent variables, I used linear mixed models with individual ID as a random effect to account for the capture of the same individual across several years. However, there were a few exceptions to the use of linear mixed models. For two dependent variables, I used generalized linear mixed model with a poisson (nestling survival) or binomial (double-brood) distribution with individual ID as a random effect. I also used a linear regression for all dependent variables in the Cliff Swallow telomere analysis as all individuals were only included once. For my analyses, all explanatory variables were scaled by subtracting the mean and dividing by the standard deviation. Prior to performing the path analyses, I calculated variance inflation factors (VIFs) for all explanatory variables to determine if there was collinearity among my predictors (Petraitis et al. 1996); all VIFs were ≤ 1.6, indicating minimal collinearity.

After performing the analyses, I tested whether my models were missing relationships among unconnected variables for all complex models, using a directed separation test. Directed separation tests indicated that there were no missing relationships in any model ($p > 0.05$), except for the male Barn Swallow corticosterone analysis ($F = 159.07$, $df = 14$, $p < 0.001$). This test indicated that the potential effect of δ^2H on double-brooding was missing. Therefore, I also added this relationship to this analysis and present the results below.

All analyses were conducted in R version 3.4.3 (R Core Team 2017) with packages lme4 (Bates et al. 2015) and piecewiseSEM (Lefcheck 2016). Below, I restrict my interpretation of these analyses to explanatory variables with a significant ($p < 0.05$) effect on the response; this may result in some analyses not describing all levels of variables identified above.

RESULTS

The relationships between non-breeding habitat, stress and potential carry-over effects varied by species and sex. In general, for the three species, I observed carry-over effects from non-breeding habitat and/or stress on spring mass, breeding phenology and/or performance (Figures 4, 5 and 6). Below, I describe my results for each species in greater detail.

Bank Swallow

For female Bank Swallows in the corticosterone path analysis, there were no relationships between non-breeding habitat, $CORT_f$ and potential carry-over effects. Spring mass was, however, negatively related to nestling survival, with larger females having fewer young (Table 14, Figure 4A). Similarly, clutch initiation dates were negatively related to clutch size, with early nesting birds having larger clutches. In turn, clutch size was positively related to nestling survival with larger clutches having higher survival.

For male Bank Swallows in the corticosterone path analysis, $\delta^{13}C$ had a positive effect on mass, with males wintering in areas of higher $\delta^{13}C$ having a larger mass (Table 14, Figures 4B). In turn, mass was negatively related to clutch initiation date, with larger males nesting earlier. Clutch initiation dates were negatively associated with nestling survival, with early nesting birds having higher nestling survival.

Finally, for both sexes in the telomere path analysis, δ^2H had a positive effect on adult mass in the spring, with individuals wintering in areas with lower rainfall having a larger mass (Table 14, Figure 4C).

In summary, for Bank Swallows, there were carry-over effects from non-breeding habitat on mass for both sexes, and, for males, subsequent effects on breeding phenology and performance.

Barn Swallow

For female Barn Swallows in the corticosterone path analysis, there was a positive relationship between δ^2H and CORT$_f$, with females wintering in areas with lower δ^2H having lower CORT$_f$ (Table 15, Figures 5A and 7D). δ^2H also had a negative effect on clutch initiation dates, with females wintering in areas with lower δ^2H nesting later. In turn, clutch initiation date had a negative effect on clutch size, with early nesting birds having larger clutches, and clutch size was positively related to nestling survival, with larger clutches having higher survival. Clutch initiation date also had a negative effect on double-brooding, with early nesting birds having a higher incidence of double-brooding. δ^{15}N and mass were negatively related, with females wintering in areas of lower δ^{15}N having a larger mass. However, neither δ^{15}N nor mass had an effect on breeding phenology or performance.

For male Barn Swallows in the corticosterone path analysis, δ^2H had a positive effect on CORT$_f$, with males wintering in areas with lower δ^2H having lower CORT$_f$

(Table 15, Figures 5B and 7E). There was also a negative relationship between δ^2H and mass, with males wintering in areas with lower δ^2H having a larger mass.

Finally, for both sexes in the telomere path analysis, δ^2H had a negative effect on telomere dynamics, with individuals wintering in areas with less rainfall experiencing greater rates of telomere shortening (Table 15, Figures 5C and 7F).

In summary, for Barn Swallows, there were carry-over effects from non-breeding habitat on stress, mass, breeding phenology and/or performance for both sexes, and, for males, there were effects of stress on breeding performance.

Cliff Swallow

For female Bank Swallows in the corticosterone path analysis, I found a negative relationship between δ^2H and mass, with females wintering in areas with more rainfall having a higher mass (Table 16, Figure 6A). In turn, mass had a negative effect on clutch initiation date, with larger individuals earlier nesting, and clutch initiation date had a negative effect on clutch size and nestling survival, with early nesting birds laying larger clutches and having higher nestling survival. There was also a negative relationship between $CORT_f$ and clutch size, with females with lower $CORT_f$ having larger clutches. Clutch size was positively related to nestling survival, with larger clutches having higher survival.

For male Cliff Swallows in the corticosterone path analysis, I found a negative relationship between $CORT_f$ and mass, with lower $CORT_f$ for larger males (Table 16, Figure 6B). However, neither $CORT_f$ nor mass were associated with breeding phenology or performance. Clutch initiation dates were negatively associated with nestling survival, with early nesting birds having higher survival.

Finally, for both sexes in the telomere path analysis, I found a positive relationship between telomere dynamics and mass, with individuals that experienced greater rates of telomere shortening having a larger mass (Table 16, Figure 6C).

In summary, for Cliff Swallows, there were carry-over effects from non-breeding habitat and/or stress on mass for both sexes, and, for females, there were also effects on breeding phenology and performance.

DISCUSSION

I found that environmental conditions during the non-breeding period (as indicated with δ^2H, δ^{13}C, δ^{15}N, $CORT_f$ and telomere dynamics) resulted in carry-over effects during breeding for declining populations of Bank, Barn and Cliff Swallows, however, the particular effects differed with species and sex. Male Bank Swallows, and female Barn and Cliff Swallows had carry-over effects that ultimately resulted in lower annual reproductive success through reduced nestling survival (all species) and a lower incidence of double-brooding (Barn Swallows only). For female Bank Swallows, there was no support for carry-over effects from non-breeding to breeding, and, for male Barn and Cliff Swallows, non-breeding conditions solely affected mass.

In most cases, the relationships we observed were associated with varying values of δ^2H. Both sexes of Barn Swallows and female Cliff Swallows had higher stress after wintering in areas with higher δ^2H. For male Barn Swallows and female Cliff Swallows, higher δ^2H was also associated with lower spring mass, later breeding and/or lower breeding performance. Similar effects have also been observed in Afro-Palearctic swallows (Saino et al. 2004, 2017; López-Calderón et al. 2017b) and other migratory birds (Rockwell et al. 2012; Goodenough et al. 2017) wintering in areas with higher δ^2H. This is usually attributed to lower insect abundance in areas that receive less rainfall (i.e., have higher δ^2H values). In contrast, for Bank Swallows, lower δ^2H was associated with lower mass, and, for female Barn Swallows, despite the relationships between lower δ^2H and lower stress, lower δ^2H was also associated with later breeding and lower performance. If lower δ^2H is associated with higher rainfall in the wintering areas of these species, then this result is particularly surprising given that increased rainfall during this period is associated with higher survival for Afro-Palearctic populations of these species (Szép 1995a, 1995b; Cowley & Siriwardena 2005; Robinson et al. 2008; Norman & Peach 2013) and, increased rainfall is associated with higher body condition for other migratory birds (Strong & Sherry 2000; Angelier et al. 2011; Wunderle et al. 2014; López-Calderón et al. 2017b). It is possible that, like Black and White Warblers *Mniotilto varia*, Bank and female Barn Swallows wintered in higher quality habitats (i.e., lower δ^2H), initiated migration earlier, but due to poor environmental conditions during migration these species either arrived in poor condition or began breeding later and with lower performance (Paxton & Moore 2015).

I also observed carry-over effects associated with δ^{13}C and δ^{15}N. For male Bank Swallows, lower δ^{13}C were associated with lower mass, but this led to earlier breeding and higher performance, and for female Barn Swallows, lower δ^{15}N was associated with higher mass. Interpreting the landscape level factors that drive δ^{13}C and δ^{15}N values can be difficult as the values vary with a variety of factors, such as climate, land-use, vegetation and fungal communities, and/or nitrogen availability (Briones et al. 2001; Craine et al. 2009; Pardo & Nadelhoffer 2010; Powell et al. 2012). Furthermore, studies demonstrating carry-over effects as a result of these variables vary in their specific findings, even within a single species. For example, female House Martins *Delichon urbicum* wintering in areas with lower $\delta^{15}N$ bred earlier than those wintering in areas with high $\delta^{15}N$ ((López-Calderón et al. 2017b). However, male House Martins and female Yellow Warblers *Setophaga petechia* wintering in areas with lower $\delta^{15}N$ bred later and had poorer performance (Drake et al. 2013; López-Calderón et al. 2017b).

In addition to the carry-over effects I observed that could be attributed to winter habitat, female and male Cliff Swallows had carry-over effects solely driven by non-breeding stress levels (i.e., unrelated to $\delta^{2}H$, $\delta^{13}C$ and $\delta^{15}N$ values). This suggests that there are important non-breeding conditions not captured by the isotopes that result in higher levels of $CORT_f$ and greater rates of telomere shortening. More work to understand the landscape level factors that drive variation in the isotopes and stress-levels for these species would help to understand the specific conditions that drive carry-over effects and help to identify the threats potentially associated with population declines.

The relationships between intrinsic markers and carry-over effects varied across species. Part of this variation is likely due to biological differences between the three species I studied. For example, inter-specific differences in interstitial telomere length (Foote et al. 2013) could affect the relationships between telomere length and other variables. It is also possible that my approach explains the observed differences. First, for at least one species, the Bank Swallow, the lack of variation in $CORT_f$ (74.3% of samples had values of <0.01 pg/mm, compared to only 28.7% or 14.4% for Barn and Cliff Swallows, respectively) likely made it difficult to detect relationships. Secondly, stable isotopes and $CORT_f$ document non-breeding habitat and stress during a short period of time (i.e., the period of feather replacement), therefore, depending on the time of molt for each species, these intrinsic markers may not fully represent non-breeding conditions that resulted in carry-over effects.

It is also important to note that my measurement of telomere dynamics had several limitations that may have affected the results of my study. I measured telomere dynamics across a full year, potentially masking the effects of poor conditions during key times of the non-breeding period. Also, I relied on older birds (those in their second breeding season or older), which may winter in isotopically-distinct habitats from younger individuals (Chapter 6) and, thus, experience different than younger swallows (López-Calderón et al. 2017b). Furthermore, I was also unable to account for sex-related differences in telomere dynamics (Noguera et al. 2015).

Conclusions

This work adds to the growing body of literature demonstrating that poor non-breeding conditions can result in carry-over effects during breeding that affect reproductive success and may ultimately lead to population declines (Norris et al. 2004; Norris 2005; Finch et al. 2014). Here, I demonstrate that for at least three declining aerial insectivores, there are carry-over effects from wintering to breeding that result in reduced reproductive performance, although the exact relationships varied by species and sex. Like with Afro-Palearctic migratory birds (Vickery et al. 2014), non-breeding conditions in South America potentially linked with precipitation levels and agricultural intensity may be important drivers of population declines for many species, including for Barn and Cliff Swallows. However, migration strategy (Paxton & Moore 2015) may also play a role in how non-breeding conditions result in carry-over effects. More research is needed to understand the potential effects of the timing of migration, conditions during migration and the specific habitats used by Bank and female Barn Swallows during the winter to fully understand the effects of non-breeding conditions and carry-over effects.

To the best of my knowledge, only one other study has examined the relationships between stable isotopes ($\delta^{15}N$ only), $CORT_f$, telomere dynamics and carry-over effects (Young et al. 2017). Irrespective of differences in the findings between these studies, it is clear that using multiple intrinsic markers, such as stable isotopes, $CORT_f$ and telomere dynamics, in an integrated fashion can provide a more complete understanding of the relationships between conditions during one stage of the annual cycle and carry-over effects in subsequent stages. Furthermore, through multi-species comparisons we can better understand the non-breeding factors that result in carry-over effects for a broader group of species.

Table 12. Estimates of standardized path coefficients from confirmatory path analyses for Bank Swallows. The conditional R^2 includes both the effects of fixed and random effects. Bolded effects were significant ($p < 0.05$).

Model	Response	Explanatory	Estimate	SE	P	R^2	n
Corticosterone: females	$CORT_f$	δ^2H	-0.05	0.12	0.68	0.75	89
		$\delta^{13}C$	-0.22	0.12	0.10		
		$\delta^{15}N$	0.12	0.11	0.27		
	mass	δ^2H	0.03	0.10	0.77	0.92	
		$\delta^{13}C$	-0.11	0.10	0.35		
		$\delta^{15}N$	-0.17	0.10	0.13		
		$CORT_f$	0.06	0.11	0.57		
	clutch initiation date	δ^2H	0.01	0.13	0.94	0.51	
		$\delta^{13}C$	0.09	0.14	0.54		
		$\delta^{15}N$	-0.07	0.12	0.56		
		mass	-0.05	0.11	0.65		
		$CORT_f$	0.00	0.11	0.99		
	clutch size	$CORT_f$	-0.12	0.09	0.18	0.40	
		mass	-0.09	0.09	0.30		
		clutch initiation date	**-0.55**	**0.09**	**<0.001**		
	nestling survival	$CORT_f$	-0.11	0.09	0.23	0.17	
		mass	**-0.14**	**0.07**	**0.04**		
		clutch initiation date	0.00	0.08	0.97		
		clutch size	**0.17**	**0.09**	**0.05**		
Corticosterone: males	$CORT_f$	δ^2H	-0.17	0.13	0.24	0.99	63
		$\delta^{13}C$	0.08	0.10	0.79		
		$\delta^{15}N$	-0.03	0.04	0.78		
	mass	δ^2H	-0.04	0.13	0.79	0.09	
		$\delta^{13}C$	**0.31**	**0.15**	**0.04**		
		$\delta^{15}N$	-0.16	0.14	0.29		
		$CORT_f$	-0.21	0.13	0.11		
	clutch initiation date	δ^2H	-0.17	0.13	0.21	0.74	
		$\delta^{13}C$	0.08	0.15	0.59		
		$\delta^{15}N$	-0.04	0.13	0.79		
		$CORT_f$	0.11	0.13	0.40		
		mass	**-0.34**	**0.13**	**0.01**		
	nestling survival	**clutch initiation date**	**-0.22**	**0.09**	**0.02**	0.11	
		$CORT_f$	0.00	0.09	0.99		
		mass	-0.06	0.09	0.49		

Model	Response	Explanatory	Estimate	SE	P	R^2	n
Telomere dynamics	telomere dynamics	δ^2H	0.00	0.01	0.95	0.42	46
		$\delta^{13}C$	-0.02	0.01	0.21		
		$\delta^{15}N$	0.02	0.01	0.09		
	mass	**δ^2H**	**0.50**	**0.18**	**0.02**	0.87	
		$\delta^{13}C$	0.14	0.15	0.43		
		$\delta^{15}N$	0.22	0.16	0.25		
		telomere dynamics	-1.76	2.13	0.48		

Table 13. Estimates of standardized path coefficients from confirmatory path analyses for Barn Swallows. The conditional R^2 includes both the effects of fixed and random effects. Bolded effects were significant ($p < 0.05$).

Model	Response	Explanatory	Estimate	SE	P	R^2	n
Corticosterone: females	CORT$_f$	**δ^{2}H**	**0.33**	**0.11**	**0.004**	0.72	87
		δ^{13}C	0.02	0.13	0.88		
		δ^{15}N	-0.06	0.12	0.63		
	mass	δ^{2}H	0.10	0.12	0.44	0.19	
		δ^{13}C	0.14	0.12	0.26		
		δ^{15}N	**-0.32**	**0.12**	**0.01**		
		CORT$_f$	0.03	0.11	0.79		
	clutch initiation date	δ^{2}H	-0.30	0.12	0.02	0.16	
		δ^{13}C	-0.11	0.11	0.37		
		δ^{15}N	-0.02	0.12	0.90		
		CORT$_f$	0.14	0.11	0.20		
		mass	-0.03	0.11	0.81		
	clutch size	CORT$_f$	0.01	0.10	0.92	0.36	
		mass	-0.09	0.10	0.39		
		clutch initiation date	**-0.34**	**0.10**	**0.002**		
	nestling survival	CORT$_f$	-0.07	0.08	0.32	0.44	
		mass	-0.05	0.07	0.46		
		clutch initiation date	-0.01	0.08	0.86		
		clutch size	**0.40**	**0.09**	**<0.001**		
	double-brood	CORT$_f$	-0.67	0.38	0.08	0.61	
		mass	0.04	0.25	0.87		
		clutch initiation date	**-2.11**	**0.59**	**<0.001**		
Corticosterone: males	CORT$_f$	**δ^{2}H**	**0.35**	**0.12**	**0.01**	0.37	71
		δ^{13}C	-0.19	0.14	0.17		
		δ^{15}N	0.24	0.13	0.09		
	mass	**δ^{2}H**	**-0.27**	**0.12**	**0.04**	0.50	
		δ^{13}C	-0.16	0.14	0.28		
		δ^{15}N	-0.01	0.14	0.92		
		CORT$_f$	-0.19	0.12	0.13		
	clutch initiation date	δ^{2}H	0.24	0.13	0.08	0.09	
		δ^{13}C	0.25	0.14	0.08		
		δ^{15}N	-0.07	0.14	0.65		
		CORT$_f$	0.05	0.13	0.69		
		mass	0.08	0.13	0.53		

Model	Response	Explanatory	Estimate	SE	P	R2	n
	nestling survival	CORT_f	-0.02	0.08	0.81	0.22	
		mass	0.08	0.08	0.31		
		clutch initiation date	-0.03	0.08	0.70		
	double-brood	**$\delta^{2}H$**	**-1.21**	**1.33**	**0.37**	0.00	
		CORT_f	**-1.05**	**2.33**	**0.65**		
		mass	**-0.09**	**1.51**	**0.95**		
		clutch initiation date	-5.72	3.96	0.15		
Telomere dynamics	telomere dynamics	**$\delta^{2}H$**	**-0.30**	**0.13**	**0.04**	0.12	54
		$\delta^{13}C$	0.15	0.14	0.29		
		$\delta^{15}N$	0.02	0.13	0.89		
	mass	$\delta^{2}H$	-0.19	0.14	0.22	0.71	
		$\delta^{13}C$	-0.01	0.15	0.97		
		$\delta^{15}N$	-0.25	0.14	0.09		
		telomere dynamics	0.09	0.13	0.53		
	clutch initiation date	$\delta^{2}H$	0.23	0.15	0.14	0.10	
		$\delta^{13}C$	0.04	0.14	0.81		
		$\delta^{15}N$	0.16	0.14	0.30		
		telomere dynamics	0.13	0.15	0.38		
		mass	-0.04	0.14	0.80		
	nestling survival	telomere dynamics	-0.17	0.12	0.16	0.54	
		mass	-0.04	0.12	0.76		
		clutch initiation date	0.00	0.11	0.97		
	double-brood	telomere dynamics	-0.10	0.33	0.77	0.31	
		mass	-0.13	0.31	0.69		
		clutch initiation date	**-1.06**	**0.53**	**0.05**		

Table 14. Estimates of standardized path coefficients from confirmatory path analyses for Cliff Swallows. The conditional R^2 includes both the effects of fixed and random effects. Bolded effects were significant ($p < 0.05$).

Model	Response	Explanatory	Estimate	SE	P	R^2	n
Corticosterone: females	CORT$_{f}$	$\delta^{2}H$	0.08	0.13	0.56	0.07	58
		$\delta^{13}C$	0.27	0.14	0.08		
		$\delta^{15}N$	0.11	0.15	0.47		
	mass	**$\delta^{2}H$**	**-0.35**	**0.13**	**0.01**	0.21	
		$\delta^{13}C$	0.11	0.14	0.47		
		$\delta^{15}N$	-0.09	0.14	0.51		
		CORT$_{f}$	-0.17	0.13	0.22		
	clutch initiation date	$\delta^{2}H$	-0.04	0.13	0.75	0.95	
		$\delta^{13}C$	-0.17	0.14	0.25		
		$\delta^{15}N$	0.04	0.13	0.76		
		CORT$_{f}$	-0.06	0.07	0.45		
		mass	**-0.29**	**0.10**	**0.02**		
	clutch size	**CORT$_{f}$**	**-0.31**	**0.12**	**0.03**	0.23	
		mass	-0.22	0.12	0.10		
		clutch initiation date	**-0.45**	**0.12**	**0.001**		
	nestling survival	CORT$_{f}$	-0.10	0.13	0.47	0.37	
		mass	0.14	0.11	0.21		
		clutch initiation date	**-0.27**	**0.11**	**0.02**		
		clutch size	**0.38**	**0.13**	**0.003**		
Corticosterone: males	CORT$_{f}$	$\delta^{2}H$	-0.01	0.14	0.95	0.00	67
		$\delta^{13}C$	-0.06	0.13	0.62		
		$\delta^{15}N$	-0.02	0.14	0.88		
	mass	$\delta^{2}H$	0.03	0.13	0.82	0.10	
		$\delta^{13}C$	-0.04	0.12	0.74		
		$\delta^{15}N$	-0.16	0.13	0.24		
		CORT$_{f}$	**-0.29**	**0.12**	**0.02**		
	clutch initiation date	$\delta^{2}H$	0.11	0.12	0.44	0.71	
		$\delta^{13}C$	0.04	0.13	0.77		
		$\delta^{15}N$	-0.01	0.13	0.93		
		CORT$_{f}$	-0.03	0.13	0.81		
		mass	0.00	0.13	0.98		
	nestling survival	CORT$_{f}$	-0.19	0.15	0.21	0.51	
		mass	0.16	0.13	0.21		
		clutch initiation date	**-0.45**	**0.13**	**0.001**		

Model	Response	Explanatory	Estimate	SE	P	R^2	n
Telomere dynamics	telomere dynamics	δ^2H	0.00	0.00	0.16	0.16[1]	24
		δ^{15}N	-0.04	0.04	0.37		
		δ^{13}C	-0.00	0.01	0.70		
	mass	δ^2H	0.02	0.04	0.59	0.29[1]	
		δ^{13}C	0.07	0.21	0.74		
		δ^{15}N	0.15	0.85	0.86		
		telomere dynamics	**12.18**	**4.44**	**0.01**		

[1] No random effects were included in these models.

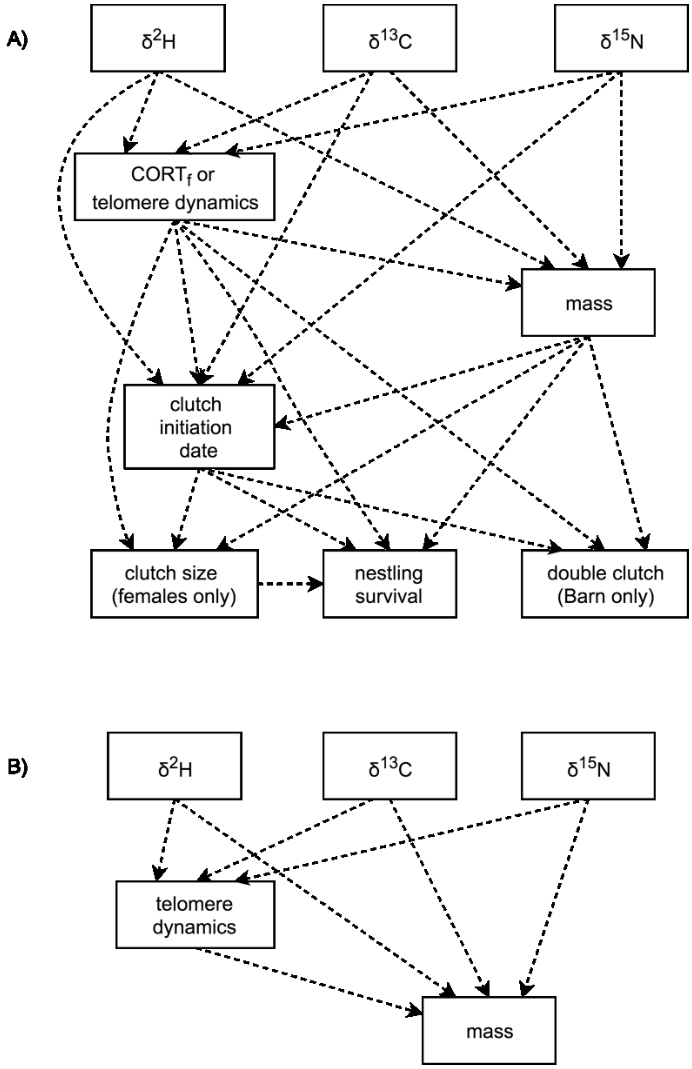

Figure 3. Full possible path diagrams for Bank, Barn and Cliff Swallows, showing the complex (A) and simple (B) paths. The complex path was used for all corticosterone path analyses and Barn Swallow telomere dynamics path analysis. The simple path was used for Bank and Cliff Swallow telomere dynamics path analysis.

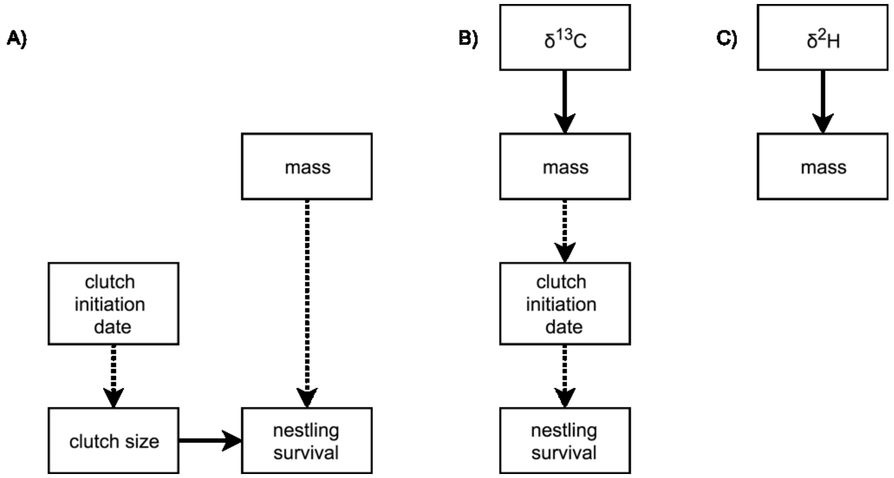

Figure 4. Path diagrams for Bank Swallows showing potential carry-over effects for A) females with $\mathrm{CORT_f}$ as an indicator of stress, B) males with $\mathrm{CORT_f}$ as an indicator of stress, and C) both sexes with telomere dynamics as an indicator of stress. Significant positive and negative relationships are indicated with solid and dashed arrows, respectively, and the width of the arrow indicates the magnitude of the effect; non-significant paths are not displayed.

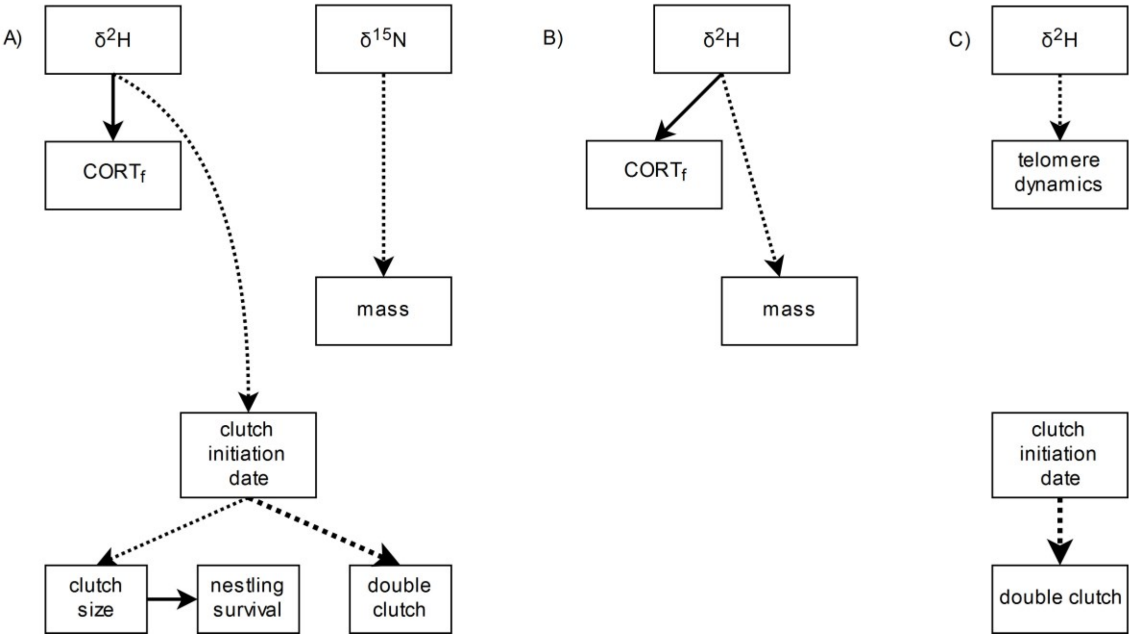

Figure 5. Path diagrams for Barn Swallows showing potential carry-over effects for A) females with CORT$_f$ as an indicator of stress, B) males with CORT$_f$ as an indicator of stress, and C) both sexes with telomere dynamics as an indicator of stress. Significant positive and negative relationships are indicated with solid and dashed arrows, respectively, and the width of the arrow indicates the magnitude of the effect; non-significant paths are not displayed.

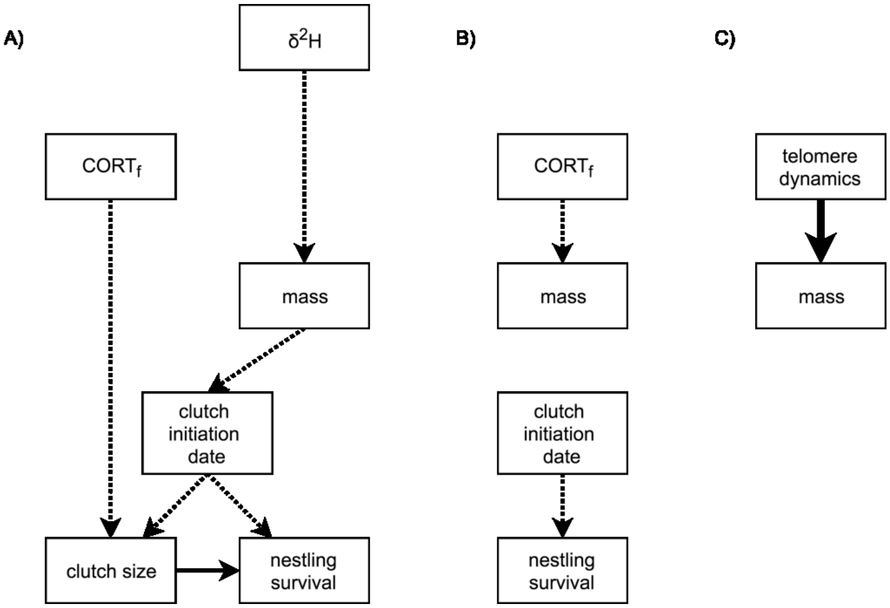

Figure 6. Path diagrams for Cliff Swallows showing potential carry-over effects for A) females with CORT$_f$ as an indicator of stress, B) males with CORT$_f$ as an indicator of stress, and C) both sexes with telomere dynamics as an indicator of stress. Significant positive and negative relationships are indicated with solid and dashed arrows, respectively, and the width of the arrow indicates the magnitude of the effect; non-significant paths are not displayed.

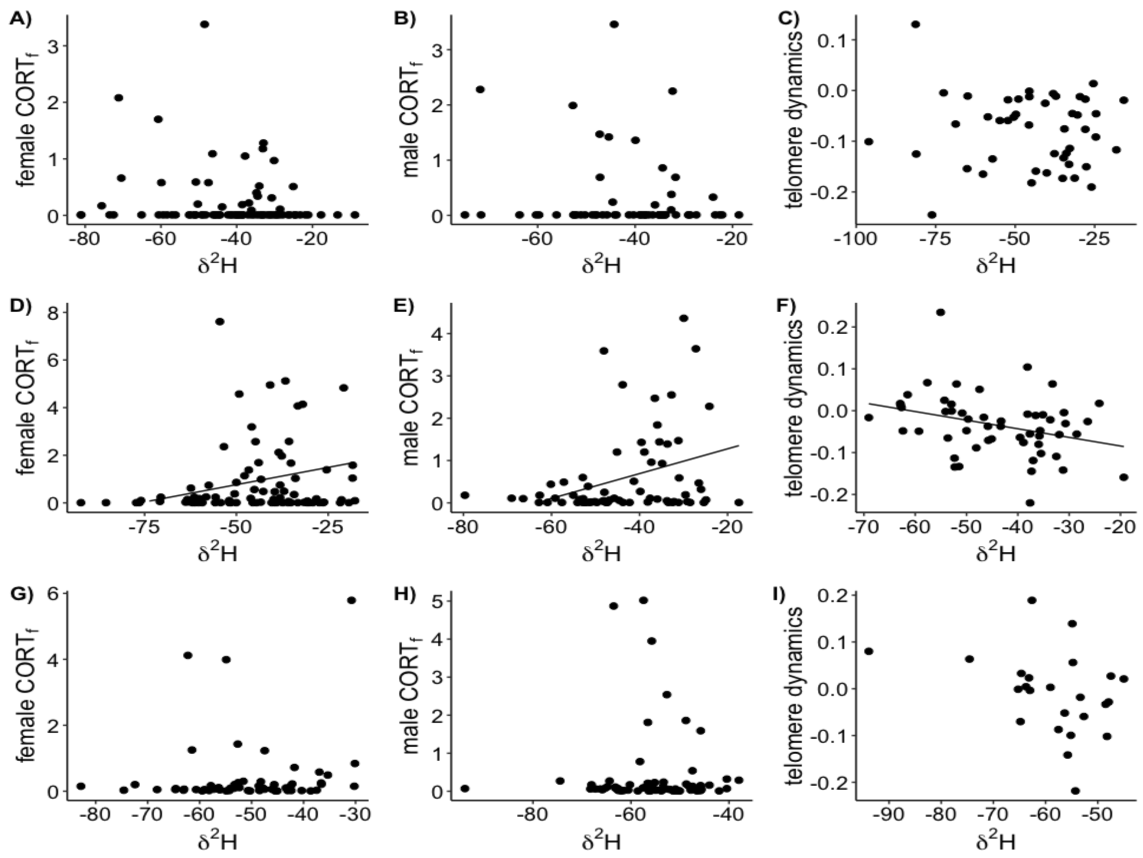

Figure 7. Relationships between δ^2H and two different indicators of stress ($CORT_f$ and telomere dynamics) for female and/or male Bank (A-C), Barn (D-F) and Cliff Swallows (G-I).

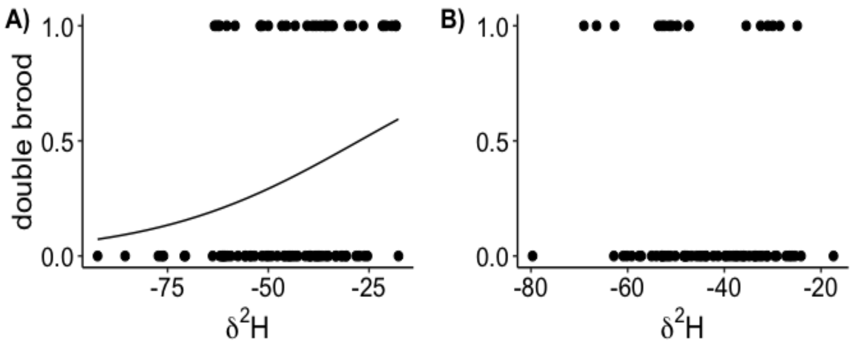

Figure 8. Relationships between δ^2H and the likelihood of double brooding for female (A) and male (B) Barn Swallows.

Chapter 5. Winter Locations, Migratory Connectivity and Fidelity of Three Declining Nearctic-Neotropical Migrant Swallows

INTRODUCTION

Throughout the annual cycle, migratory animals travel among different habitats where they are exposed to different factors affecting survival (Egevang et al. 2010; Schofield et al. 2010; Cherry et al. 2016). Within populations, distance travelled and habitats used may vary according to several factors, such as age, sex or year (e.g., Bunnefeld et al. 2011; Mellone et al. 2013; Müller et al. 2014). Understanding causes of population declines of migratory species is challenging and requires identifying the full range of habitats used during the annual cycle, annual variation in habitat use, and associated threats in those habitats (reviewed in Webster & Marra 2005, Wilcove & Wikelski 2008).

In addition to determining the habitats used during the annual cycle, it is also important to understand aspects of a species ecology that can affect conservation planning. Two important ecological concepts affecting the population dynamics of migratory birds include migratory connectivity among and fidelity to various sites during different stages of their annual cycle. Migratory connectivity describes population-level connections between two or more locations during the annual cycle and fidelity is defined as an individual's propensity to return to the same location annually (reviewed in Webster et al. 2002; Wilcove & Wikelski 2008). Both migratory connectivity and fidelity may affect the susceptibility of populations to adverse conditions throughout their annual cycle. For example, populations with strong migratory connectivity, where individuals from the same population breed and winter together and are thus concentrated in the same area at both times of year, are more susceptible to adverse conditions, than populations with low migratory connectivity (Rubenstein et al. 2002; Webster et al. 2002; Taylor & Norris 2010). Similarly, populations with high fidelity, where individuals return to the same location annually, may be at greater risk than those with low fidelity, as individuals may be less likely to change locations when conditions are poor or be less able to adapt to unfamiliar habitats (Wilcove & Wikelski 2008; van Wijk et al. 2016). While high fidelity is needed for populations to exhibit strong migratory connectivity (Hjernquist et al. 2009), the reverse is not necessarily true, and populations where individuals exhibit either high or low fidelity may have weak connectivity. Therefore, to understand the effect of environmental conditions on populations throughout all stages of the annual cycle, it is first necessary to determine the strength of migratory connectivity and fidelity to breeding and wintering areas. The long-distances travelled by migrants throughout the annual cycle can, however, make it difficult to track individuals.

For small migratory birds, typically two methods have been used to identify wintering locations, migratory connectivity and fidelity. The first is to attach archival light-weight electronic tracking units, like geolocators (Stutchbury et al. 2009b; English et al. 2017; Szép et al. 2017) or GPS tags (Hallworth & Marra 2015; Fraser et al. 2017), to migrating birds. These tracking units provide critical information on winter locations and connectivity that can inform conservation decisions (Renfrew et al. 2013; Finch et al. 2015; Cooper et al. 2017). These devices, however, have several limitations, including the need to recapture the tagged bird to retrieve the data, and the potential for increased mortality and decreased reproductive performance in tagged individuals (Costantini &

Møller 2013; Gómez et al. 2014; Scandolara et al. 2014; Morganti et al. 2018). Further, small sample sizes associated with these limitations can make it difficult to generalize results across a population. An alternative method is to use intrinsic markers, like stable isotopes, to compare values obtained from sampled tissues reflecting underlying patterns across landscapes (isoscapes) and infer likely locations where the tissue was grown (Hobson 1999; Rubenstein & Hobson 2004; Inger & Bearhop 2008). While intrinsic markers do not yield the same quantity of information about movements, nor the same level of precision as electronic tracking units, they have been reliably used approximate locations where tissues were grown (Haché et al. 2012; Garcia-Perez & Hobson 2014; Hobson et al. 2014). Intrinsic markers also allow for sampling of large numbers of birds to generalize population-level movements, migratory connectivity and fidelity. The combination of intrinsic and extrinsic markers represents a powerful tool to decipher animal movements (Hobson 2011).

Populations of avian aerial insectivores, including swallows, are in steep decline and while trends among species vary considerably (Michel et al. 2016), these declines are particularly severe in the northeast (Nebel et al. 2010; Shutler et al. 2012; Smith et al. 2015). While many cause(s) of decline are unknown, two key factors suggest that conditions on the wintering grounds or during migration are contributing to population declines. First, there is a higher rate of decline for long-distance migrants (birds that migrate to South America) compared to short-distance migrants (those that migrate to the southern USA and Central America) (Nebel et al. 2010). Secondly, only one of the three long-distance migrants examined, the Bank Swallow, has shown lower breeding success in recent years suggesting that conditions outside the breeding season are driving population declines (Imlay et al. 2018; Chapter 3). Understanding how these conditions could affect populations, requires that wintering locations be identified and aspects of wintering ecology, like migratory connectivity and winter fidelity be determined.

Therefore, the goal of my study was to describe the winter locations of Bank, Barn and Cliff Swallows using geolocators and stable isotope measurements of winter-grown feathers. I also examined migratory connectivity on a local scale between breeding colonies within the Maritimes and winter locations, and the winter site fidelity of adults captured in multiple years. While both aspects of a species' ecology are important for conservation, migratory connectivity has received far greater attention than fidelity in the scientific literature. This work will help target conservation efforts to wintering areas used by these declining populations (Sauer et al. 2014), and will provide insight into how aspects of wintering ecology can contribute to population declines.

METHODS

From June to August 2013 to 2017, I captured adult Bank, Barn and Cliff Swallows at several sites in New Brunswick and Nova Scotia, Canada. Bank Swallows were captured at colonies along the Tantramar River, NB (45.90°, -64.34°), Barn and Cliff Swallows were captured at three colonies within 50 km of Moncton, NB (46.09°, -64.78°), and Barn Swallows were also captured on McNabs Island, NS (44.60°, -63.52°). The average (± SD) distance between colonies was 0.6 ± 0.2 km, 89.7 ± 61.1 km and 76.5 ± 59.4 km for Bank, Barn and Cliff Swallows, respectively.

To determine wintering locations and migration routes, in 2013 I deployed geolocators (eight month, stalkless ML6540, Biotrack Limited) on Bank (n = 8 individuals, 1 colony) and Cliff Swallows (n = 21 individuals, 3 colonies), using a leg-loop harness (Rappole & Tipton 1991) (Table 18); these individuals were also banded with a Canadian Wildlife Service aluminum band. In addition, to determine if the geolocators affected survival, I banded a control group of Bank (n = 110) and Cliff Swallows (n = 8) that did not receive a geolocator. I retrieved the geolocators in 2014 and 2015 and documented the return rates of geolocator and control birds. In general, the first individuals captured at each colony received a geolocator and the remaining birds were part of the control group. The maximum number of days between captures of tagged and control birds was three days, so I consider it unlikely that there are differences between the groups in, for example, condition that would affect return rates in subsequent years.

I assumed that feathers used to determine stable isotope composition (i.e., ratios of $^{2}H/^{1}H$ [$\delta^{2}H$], $^{13}C/^{12}C$ [$\delta^{13}C$] and $^{15}N/^{14}N$ [$\delta^{15}N$]), were molted during the winter (Pyle 1997) and therefore contained an isotopic signature of the region where they were molted. I collected either one inner rectrix (2013; 67 Bank and 40 Cliff Swallow samples) or 2-3 contour (flank) feathers (2014-2016; 335 Bank, 216 Barn and 183 Cliff Swallow samples) from adults. In 2014, I added feather corticosterone analyses to another aspect of my study (Chapter 3), which required a change from sampling rectrix to contour feathers. Although rectrix feathers are molted during the winter, I later learned that contour feathers could be molted during breeding, migration or winter (Imlay et al. 2017a). Therefore, to determine if rectrix and contour feather were molted at the same locations and therefore give comparable information on winter locations, I compared isotope values for an inner rectrix and two contour feathers from a sample of 15 adults from all three species sampled in 2017 (see Appendix 2). My results suggest that contour feathers from all three species were molted during the winter based on their isotopic signatures, however, for Bank and Cliff Swallows, these feathers may not have been molted at the same locations as the rectrices (Figure A2, Appendix 3). Therefore, in my analyses below, I examine winter locations for each feather type, and solely use the contour feathers in my analysis of migratory connectivity and fidelity for each species.

Geolocator data analysis

Of the 29 geolocators that were deployed, six were retrieved, and four contained over a year (402.5 ± 12.2 [SE] days) of data; the remaining two geolocators failed after 13 and 31 days, respectively. We used a Fisher's exact test to determine if return rates were different between birds equipped with a geolocator and those in the control group.

Using the downloaded data from the four individuals with a full year of information (one Bank Swallow and three Cliff Swallows), we determined the likely winter locations for each individual. First we identified twilights using a light threshold value of 1.5 in the TwGeos version 0.0-1 (Wotherspoon et al. 2016). Twilights were edited or deleted using the twilightEdit function in TwGeos. A twilight time was defined as an outlier if it was different from the four neighbouring twilight times by 45 minutes or more. Once identified, twilights were either deleted, if they differed by 25 minutes or more from the two adjacent twilights, or adjusted, if they differed by less than 25 minutes from the two adjacent twilights.

Then, the data was calibrated when each individual was stationary at the breeding colony (i.e., 20-32 days after geolocators were deployed). Calibration involves using the deployment coordinates to correct for any light interferences that could affect the light data recorded by the geolocator. This analysis method uses a distribution of zenith angles for calibration (Cooper et al. 2017). The zenith angle is defined as the angle between the 90º vertical axis between the sun and earth at the time that the light threshold is crossed (Cooper et al. 2017). At the known deployment location the error distribution is also calculated by fitting a log-normal distribution to the difference between estimated and known twilight times. Both the twilights defined by the threshold method and the median zenith angle were used to calculate raw coordinates in the Solar/Satellite Geolocation for Animal Tracking (SGAT) version 0.1.3 package (Sumner et al. 2009); these coordinates served as a prior in the model.

Next, to calculate the final inferred positions, we used an Estelle model in SGAT. In this model we included: 1) the initial position of the individual when the tag was deployed; 2) a prior with raw coordinates derived from twilights identified using the threshold method (described above); 3) a model describing the error in twilight times (described above); 4) a range of zenith angles (described above); 5) the distribution of probable flight speeds (up to ~60 km/h with faster speeds possible but improbable) with a high frequency of short movements and low frequency of long-distance movements; and 6) a spatial probability mask of North and South America from 60°N to 60°S and 30°W to 140°W where stationary positions over water were not possible. We used 150,000 samples (i.e., a set of estimated positions) from three independent chains in a Markov Chain Monte Carlo simulations for burn-in and tuning the model. Then we use another set of 15,000 samples to determine the posterior distribution of the final positions.

Finally, because we were interested in the locations of these individuals during the winter period, we used the GeoLight version 2.0 package (Lisovski & Hahn 2012) to identify periods of five or more days when the individual was stationary. We identified all stationary positions of at least two weeks from 14 October 2013 to 27 February 2013; this period was selected as it occurred three weeks after and before the fall and spring equinoxes, respectively, and during the period when most individuals are likely to be wintering (Garrison 1999; Brown et al. 2017). Then, using the final positions from the posterior distributions, we mapped the mean position for each twilight period, along with the outermost cardinal positions for the 95% credible intervals during each of the stationary periods (1-3 periods/individual) in ArcMap 10.5 (ESRI, Redlands, California). We plotted an ellipse of each individual's stationary positions during the winter using both the mean position and the cardinal positions for the 95% credible intervals.

Stable isotope laboratory analysis

A description of the laboratory methods used to determine stable isotope ratios ($\delta^{2}H$, $\delta^{13}C$ and $\delta^{15}N$) in feather samples is provided in Chapter 4.

Stable isotope data analysis

In this study, I rely on stable isotope analyses to determine winter locations, which are based on the isotopic values of molted feathers. For simplicity, throughout this chapter I refer to winter molt locations as winter locations. One limitation of this approach is that these isotope values reflect where the feather was molted, and not necessarily all locations where the individual wintered. Similarly, I can only describe migratory connectivity and fidelity in relation to isotopically similar habitats, which may or may not be the same location, and is not on the same scale of precision as research using tracking devices instead of stable isotopes. With these limitations in mind, I conducted three analyses for each species to determine: 1) likely wintering locations using rectrix and contour feathers; 2) migratory connectivity between breeding colonies and winter locations using contour feathers; and, 3) annual fidelity to winter locations using contour feathers. These analyses are described in more detail in the following paragraphs.

I assigned feathers from Bank, Barn and Cliff Swallows to likely wintering locations using the δ^2H and δ^{13}C values obtained above. This was a multi-step process. First, I used isotopic discrimination factors (Hobson et al. 2012; Garcia-Perez & Hobson 2014) to calibrate South American δ^2H and δ^{13}C isoscapes (Bowen et al. 2005; Powell et al. 2012) for feather samples across the wintering range of each species in South America. For Bank Swallows, I used their wintering range map determined by Ridgely et al. (2003), and, for Barn Swallows, I used the eastern North American breeding population wintering range map described by Hobson and Kardynal (2016). For Cliff Swallows, my geolocator results indicated that these individuals wintered in eastern Brazil (Figure 7) outside of their known wintering range (Ridgely et al. 2003). Therefore, I expanded the wintering range to include locations within the ellipses from the outermost cardinal positions for the 95% credible intervals from my geolocator analysis (Figure 7) using ArcMap. Then, I removed 22 Bank, nine Barn and one Cliff Swallow samples (range: 0.4-6.6% of samples/species) from my data set with δ^2H or δ^{13}C values that were either higher or lower than the minimum and maximum values for each isoscape for that species and therefore, unlikely to have been molted during the winter; these samples were also not included in subsequent analyses below. Next, using a process similar to previous work (Van Wilgenburg & Hobson 2011; Garcia-Perez & Hobson 2014), I determined the probability that each feather sample was molted in each cell of the δ^2H and δ^{13}C isoscapes. Finally, to determine likely molt locations across all samples for each species in each year, I used a 2:1 odds ratio to reclassify the probability of each cell, so that the upper two-thirds of the estimated probability of origin was considered likely and the remaining one-third was considered unlikely. I summed the spatially explicit probabilities for each sample and mapped the most probable wintering locations of all Bank, Barn and Cliff Swallows based on rectrix (2013, Bank and Cliff) and contour (2014-2016, all species) feather samples.

To determine if the estimates of winter locations from geolocator and stable isotope data resulted in similar locations, I visually compared the results from both approaches for the two Cliff Swallows with both sets of data. For the winter locations derived from the stable isotope data, I only included areas in the upper two-thirds of the estimated probability of origin (i.e., the likely areas).

To determine migratory connectivity between breeding colonies and wintering locations, we conducted a Mantel test with 9999 replicates for each species (Ambrosini et al. 2009). Our matrices included the orthodromic (i.e., great circle) distance between individuals for each species during breeding, with a distance of 0 km for individuals at the same breeding colony, and the three-dimensional distance in δ^2H, $\delta^{13}C$ and $\delta^{15}N$ for each individual with smaller distances indicating more similar values of δ^2H, $\delta^{13}C$ or $\delta^{15}N$ and larger distances indicating less similar values. We defined strong connectivity as populations with an $r_M > 0.5$ (Finch et al. 2017), although recognize that connectivity varies along a strong-weak continuum (Webster et al. 2002).

To determine if individuals exhibited fidelity to the same winter location across years, I determined if individuals captured in at least two years from 2014-2016 had similar δ^2H, $\delta^{13}C$ and $\delta^{15}N$ values in each year they were captured using a linear mixed model for each species. Individuals captured in two years were included once in the model, and individuals captured in three years (Bank and Barn, only) were included three times to account for comparisons across all three years (i.e., 2014 and 2015, 2015 and 2016, and 2014 and 2016). Therefore, I included individual ID as a random effect in my Bank and Barn Swallow models. I arbitrarily considered that individuals had fidelity to isotopically similar locations across years if there was a significant relationship between all three isotopes (δ^2H, δ^{13}C and δ^{15}N) in earlier and later captures, and the slope of all these relationships was between 0.9 and 1.1.

Unless otherwise noted above, all analyses were conducted in R version 3.4.2 (R Core Team 2017) with the following packages: ade4, cluster, fpc, geosphere and lme4 (Bates et al. 2015). The stable isotope assignment was performed using scripts adapted from Van Wilgenburg and Hobson (2011).

RESULTS

Winter locations from geolocators

Return rates did not differ between Bank and Cliff Swallows equipped with geolocators and the control group (Bank: p = 0.52, Cliff: p = 0.51) (Table 17). The sole Bank Swallow had two stationary periods of 90 and 45 days. This individual wintered along the southern part of the Colombia-Venezuela border and northwestern Brazil, and moved in a southerly direction during the winter (Figure 10A). The three Cliff Swallows all wintered in southern Brazil (Figure 10B-D), with stationary periods that ranged from 25-129 days (after removing days within three weeks of the equinox). For the individuals that had three stationary periods during the winter, both moved in a southwesterly direction for the second stationary period before travelling either north (Figure 10B) or west (Figure 10D) for the third.

Winter locations from stable isotope assignment

In general, for Bank Swallows, most of the probable wintering locations were in the southern parts of the species putative winter range. Using rectrix feathers from 2013, the most probable winter locations were consistent with southern Brazil, Uruguay and north-eastern Argentina, with a few smaller areas in northern Venezuela and western Ecuador (Figure 11A). Using contour feathers from 2014-2016, the most probable winter locations included these areas, along with southeastern Bolivia and Paraguay (Figure 11B-D). Based on Figures 11B-D, there appears to be little annual variation in probable winter areas across these three years.

For Barn Swallows, using contour feathers from 2014-2016, the most probable winter locations were consistent with eastern and southern Brazil, eastern Bolivia, Paraguay, Uruguay and north-eastern Argentina (Figure 12). There was some annual variation in these wintering areas, especially during the winter of 2014-2015, when the likelihood of wintering in eastern Brazil was low.

For Cliff Swallows, the most probable wintering locations were consistent with the southern half of the species known winter range. Using rectrix feathers from 2013, the most probable winter locations corresponded with the western and southern parts of Brazil, northern Bolivia, southern Paraguay and northern Colombia (Figure 13A). Using contour feathers from 2014-2016, the most probable winter locations included these areas, along with northern Argentina, Uruguay and Venezuela (Figure 13B-D). Similarly to Bank Swallows, there was little annual variation in probable winter locations.

Winter locations from geolocators and stable isotope assignment

Although limited by sample size, I found overlap in the estimated winter locations derived from geolocators and stable isotopes for two Cliff Swallows (Figure 14), suggesting that both approaches will identify similar areas. However, the stable isotope assignment identified a broader probable wintering location than the geolocator.

Migratory connectivity and fidelity

For Bank Swallows, despite the significant relationship, there was weak migratory connectivity between breeding colonies and wintering areas (Mantel correlation coefficient, $r_M = 0.01$, $p = 0.04$). Also, for Barn and Cliff Swallows, there was weak migratory connectivity between breeding colonies and wintering areas and these relationships were not significant (Barn: $r_M = 0.04$, $p = 0.10$, Cliff: $r_M = 0.003$, $p = 0.43$).

There was no evidence that individual Bank, Barn and Cliff Swallows wintered in the same location across years, suggesting weak fidelity to winter locations. For individual Bank Swallows, there was a significant relationship between $\delta^{2}H$, $\delta^{13}C$ and $\delta^{15}N$ in contour feathers in at least two years ($p < 0.001$, $p < 0.001$ and $p = 0.002$, respectively), however, the slope of these relationships were all < 0.9 (i.e., 0.66, 0.68 and 0.37, respectively) (Figure 15A-C), indicating that individuals did not exhibit strong fidelity. Similarly, for individual Barn Swallows, there was a significant relationship between $\delta^{13}C$ and $\delta^{15}N$ ($p < 0.001$), but not $\delta^{2}H$ ($p = 0.29$), but the slope of these relationships was 0.80 and 0.66, respectively (Figure 15D-F). Finally, for Cliff Swallows, there was a significant relationship between $\delta^{13}C$ ($p < 0.001$), but not $\delta^{2}H$ or $\delta^{15}N$ ($p = 52$ and $p = 0.11$, respectively), but the slope of this relationship was 0.54 (Figure 15G-I).

DISCUSSION

For the first time, I describe the likely winter locations and examine migratory connectivity of Nearctic-Neotropical Bank and Cliff Swallows, and winter site fidelity for all three species. My results indicate that the most probable winter locations for Maritime populations of all three swallows are in the southern-most areas of each species' known wintering ranges. For Bank and Cliff Swallows, winter locations from geolocators and stable isotopes suggest that many swallows are not stationary throughout the winter, although there is little variability in the population-level winter locations across years. In contrast, for Barn Swallows, stable isotope results indicate that winter locations may vary annually. For all three species, my results also suggest weak migratory connectivity between Maritime breeding colonies and wintering locations, and weak fidelity to winter locations.

The long-distances travelled by Maritime populations of Bank, Barn and Cliff Swallows to reach their wintering areas may help explain the higher rates of declines for aerial insectivores (Nebel et al. 2010; Hobson et al. 2015). Survival during migration may be affected by various threats, such as lower quality stopover habitats (Baker et al. 2004; Woodworth et al. 2014) and storms during migration (Newton 2007; Wellicome et al. 2014), and longer distances may increase the likelihood that individuals encounter these threats. Irrespective of distance, southern parts of South America that overlap the most probable winter locations for these swallows, like the Cerrado and La Plata Basin, are experiencing high rates of land-use change involving deforestation (Lambin et al. 2003; Hansen et al. 2010), wetland loss (Davidson 2014) and conversion of natural savanna to increasingly intensive agricultural areas (Sano et al. 2010; Lee & Berbery 2012). These land cover changes in themselves or the additional effects of land cover change on weather patterns, such as increased temperatures, higher winds and altered precipitation regimes (Loarie et al. 2011; Lee & Berbery 2012; Luyssaert et al. 2014), may contribute to additional stress on wintering swallows.

Range-wide research on a variety of migratory birds has demonstrated broad-scale patterns of migratory connectivity across both longitudinal and latitudinal gradients (Kelly et al. 2002; Rubenstein et al. 2002; Hahn et al. 2013; Hallworth et al. 2015; English et al. 2017). To a lesser extent, strong migratory connectivity has also been demonstrated on a more localized scale (Moller & Hobson 2004; Hjernquist et al. 2009). For example, there was strong migratory connectivity for breeding populations of Collared Flycatchers *Ficedula albicollis* populations within 10-100 km of each other (Hjernquist et al. 2009). My results did not reveal patterns of migratory connectivity at my local scale, possibly due to the small distances between breeding colonies. Nearctic-Neotropical populations of Barn Swallows exhibit broad-scale patterns of migratory connectivity, with eastern population travelling to more southerly winter locations than western populations (Hobson et al. 2015). Although I have no information on other populations of Nearctic-Neotropical Bank and Cliff Swallows, it is possible that the long distances travelled by Maritime populations reflects similar connectivity as the Barn Swallows. Alternatively, consistent with other broadly distributed populations of migratory birds (Fraser et al. 2012; Renfrew et al. 2013; Trierweiler et al. 2014; Finch et al. 2017), it is also possible that the weak connectivity between breeding and wintering areas for Bank and Cliff Swallows during my study, reflects weak connectivity across their range.

While some passerines return to the same general winter location across years (Hasselquist et al. 2017; Wellbrock et al. 2017), I did not observe fidelity to winter locations for the three swallow species I studied. Like with Purple Martins (Fraser et al. 2017), my limited geolocator results suggest that some individuals undertake large-scale movements during the winter. In addition, winter locations varied with feather type for Bank and Cliff Swallows, suggesting that these feathers may have been molted at different locations. These movements and variation in the timing of molt across years could mask fidelity to specific areas, if the birds undertake similar movements annually. Alternatively, because older migratory birds may winter in different locations than younger birds (Szép et al. 2009; López-Calderón et al. 2017a), it is also possible that age-related shifts in winter locations could result in low fidelity. During my study, most individuals were first captured as adults of unknown age, therefore I could not examine the relationships between age and isotopes. However, like previous studies (Hjernquist et al. 2009; Goodenough et al. 2017), I did find a relationship for some isotopes among individuals recaptured one or two years after an earlier capture (i.e., δ^{13}C for all three species and δ^{15}N for Bank and Barn Swallows). This provides a comparison between older and younger individuals and suggests that as swallows age, they may winter in different areas and thus exhibit less fidelity. Since environmental conditions during the winter affect survival and subsequent breeding success for many species (Norris et al. 2004; Cowley & Siriwardena 2005; Saino et al. 2017), age-related changes in winter habitats could result in differential effects on fitness (Drake et al. 2013; López-Calderón et al. 2017b).

The accuracy of stable isotope assignments can be improved by incorporating data on the abundance of birds throughout their wintering range (i.e., areas with greater abundance have a higher probability of occurrence), mark-recapture and/or geolocator data on winter locations (Van Wilgenburg & Hobson 2011; Hallworth et al. 2013). These sources of information were limited, however, because eBird data for these species in South America (a potential source of information on abundance) was largely restricted to coastal areas and mark-recapture data were not available. Also, I only retrieved a few geolocators from Bank and Cliff Swallows, making it difficult to generalize these results to the full population. Although results for Cliff Swallows were consistent between the two approaches, they differed between the sole geolocator-derived estimate for a Bank Swallow and the population-level stable-isotope assignment. While there was no difference in return rates between tagged and control birds in my study, none of the 57 geolocators deployed on Bank Swallows elsewhere in North America during 2013 were retrieved (B. Whittam, pers. comm.) and these devices adversely affect the survival of other aerial insectivores (Costantini & Møller 2013; Gómez et al. 2014; Scandolara et al. 2014; Morganti et al. 2018). It is possible that the tag affected migratory behaviour, however with just a single individual it is hard to be conclusive. Therefore, I did not incorporate the geolocator data in my stable isotope assignment.

Conclusions

My findings suggest that Maritime populations of Bank, Barn and Cliff Swallows likely winter throughout large areas of central and southern South America, potentially in areas that are experiencing high rates of land use change. Despite weak migratory connectivity and low fidelity, which should make these populations less susceptible to adverse changes in wintering conditions (Rubenstein et al. 2002; Webster et al. 2002; van Wijk et al. 2016), these populations are in decline. Furthermore, conditions during this period are implicated in the declines (Nebel et al. 2010; Imlay et al. 2018), suggesting that, despite their mobility, these species are unable to avoid poor conditions during this time presumably because of broad-scale degradation of winter habitats (Gaston & Fuller 2008) and/or conditions during migration (Nebel et al. 2010; Hobson et al. 2015). Conservation efforts to address threats to broadly distributed, possibly nomadic, populations are challenging. More traditional approaches to conservation, such as habitat protection, may not be effective as this will only include a small proportion of the population, and, possibly, for only part of the winter (Gaston & Fuller 2008; Runge et al. 2014). Instead, conservation efforts will need to consider management of threats at a landscape level (Runge et al. 2014) through increasing the capacity of these habitats to support large swallow populations (Gaston & Fuller 2008). Since food availability is often the limiting factor for birds during the winter (Sherry et al. 2005), conservation efforts could focus on addressing the spatial and temporal abundance of food for swallows. This could include addressing intensive agricultural practices, such as landscape homogeneity and pesticide use, which are associated with lower insect abundance (Benton et al. 2002; Rioux Paquette et al. 2013; Morrissey et al. 2015; Pisa et al. 2015).

Table 15. Number of adult Bank and Cliff Swallows either equipped with a geolocator or in the control group in 2013, and their return rates across the next two years (2014 and 2015).

Species	Geolocators		Control	
	# deployed	# returned[1] (%)	# banded	# returned[1] (%)
Bank	8	1 (12.5)	107	23 (21.5)
Cliff	21	52 (23.8)	8	1 (12.5)

[1] Individuals recaptured in both 2014 and 2015 are only counted once.

[2] Two geolocators failed prematurely with only 13 and 31 days of data, respectively.

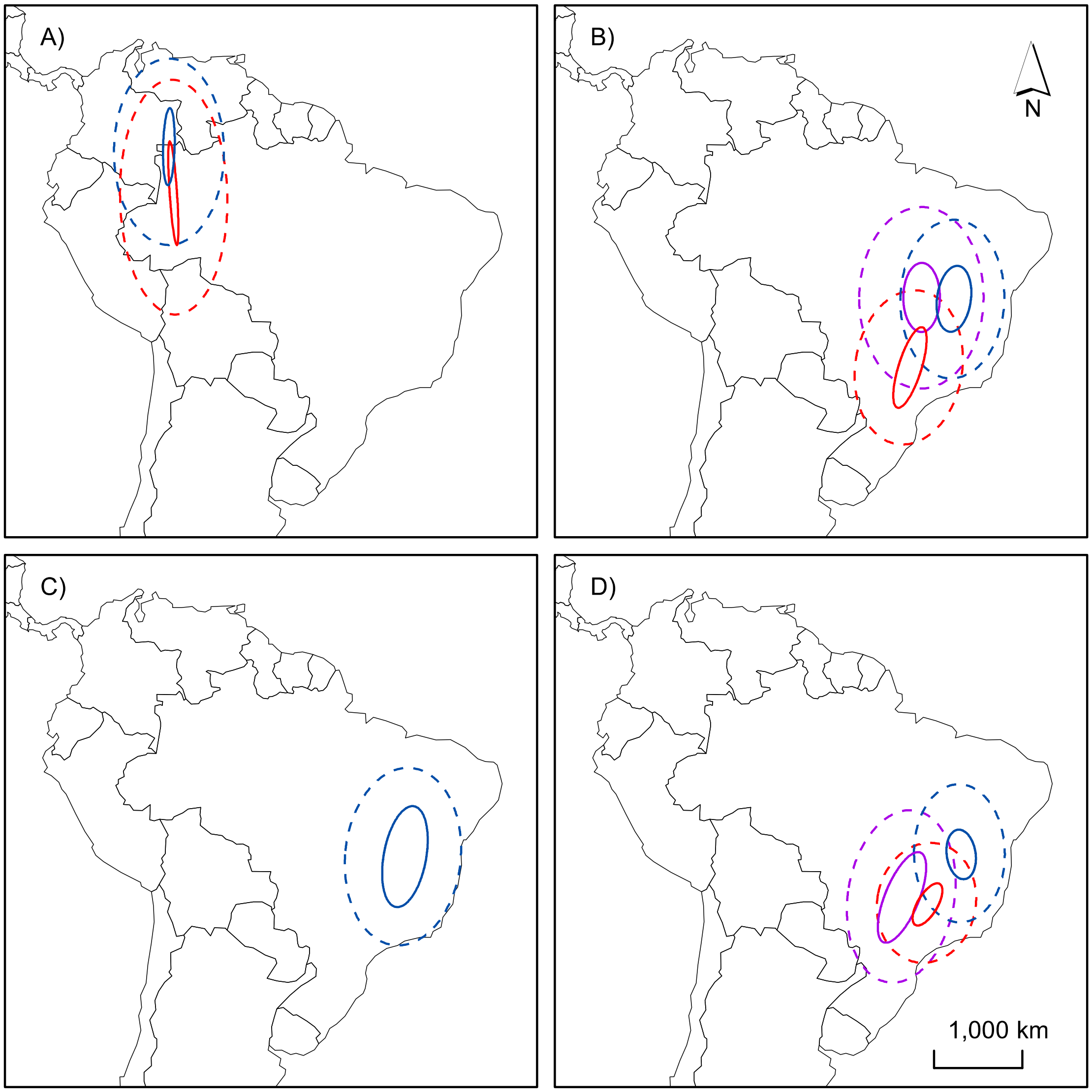

Figure 9. Winter locations during stationary periods from 14 October 2013 and 27 February 2014 for one Bank (A) and three Cliff Swallows (B-D) equipped with geolocators. Solid lines indicate most likely positions using mean latitude and longitude and dashed likes indicate most likely positions using the outermost cardinal locations using 95% credible intervals. Blue, red and purple lines indicate the first, second and/or third stationary periods, respectively, for each individual.

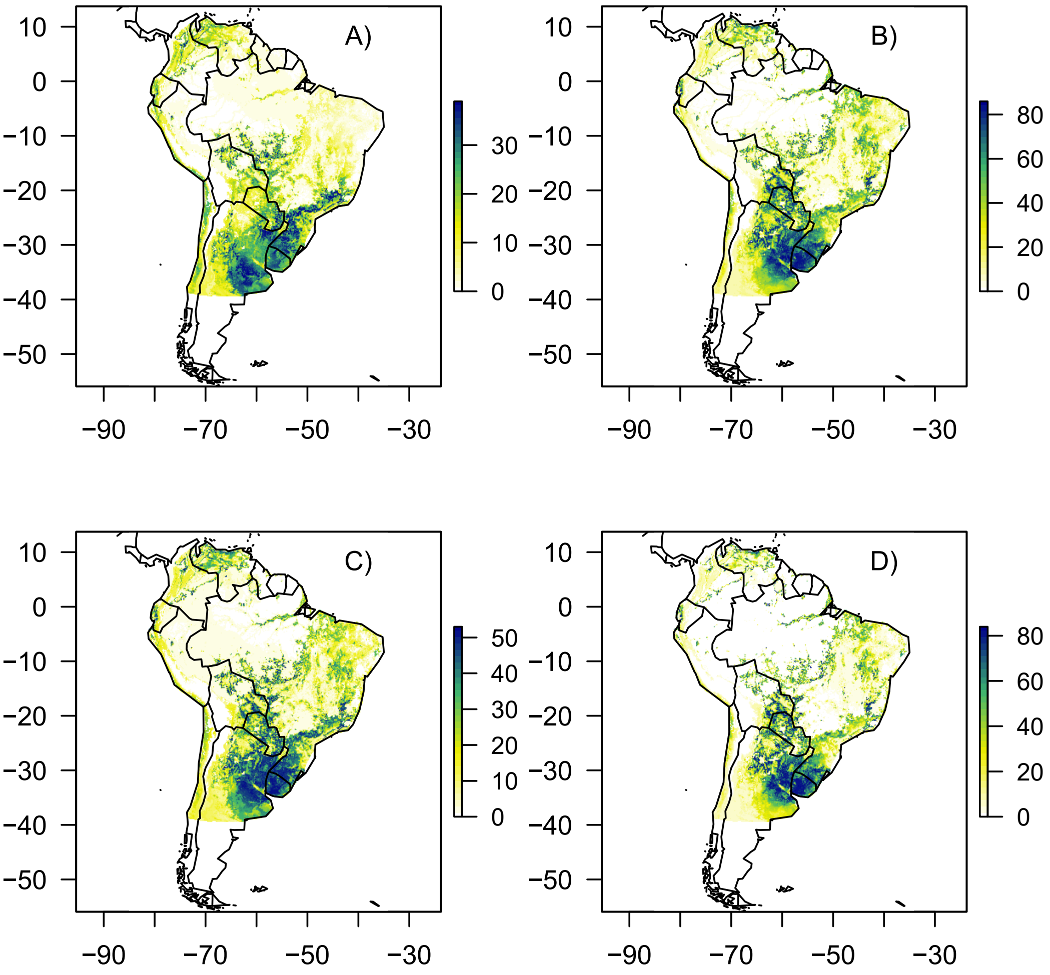

Figure 10. Most probable wintering locations based on δ^2H and $\delta^{13}C$ isotopes for Maritime populations of Bank Swallows using rectrix feathers collected in 2013 (A) and contour feathers collected in 2014 (B), 2015 (C) and 2016 (D). N = 52, 112, 72 and 113, respectively.

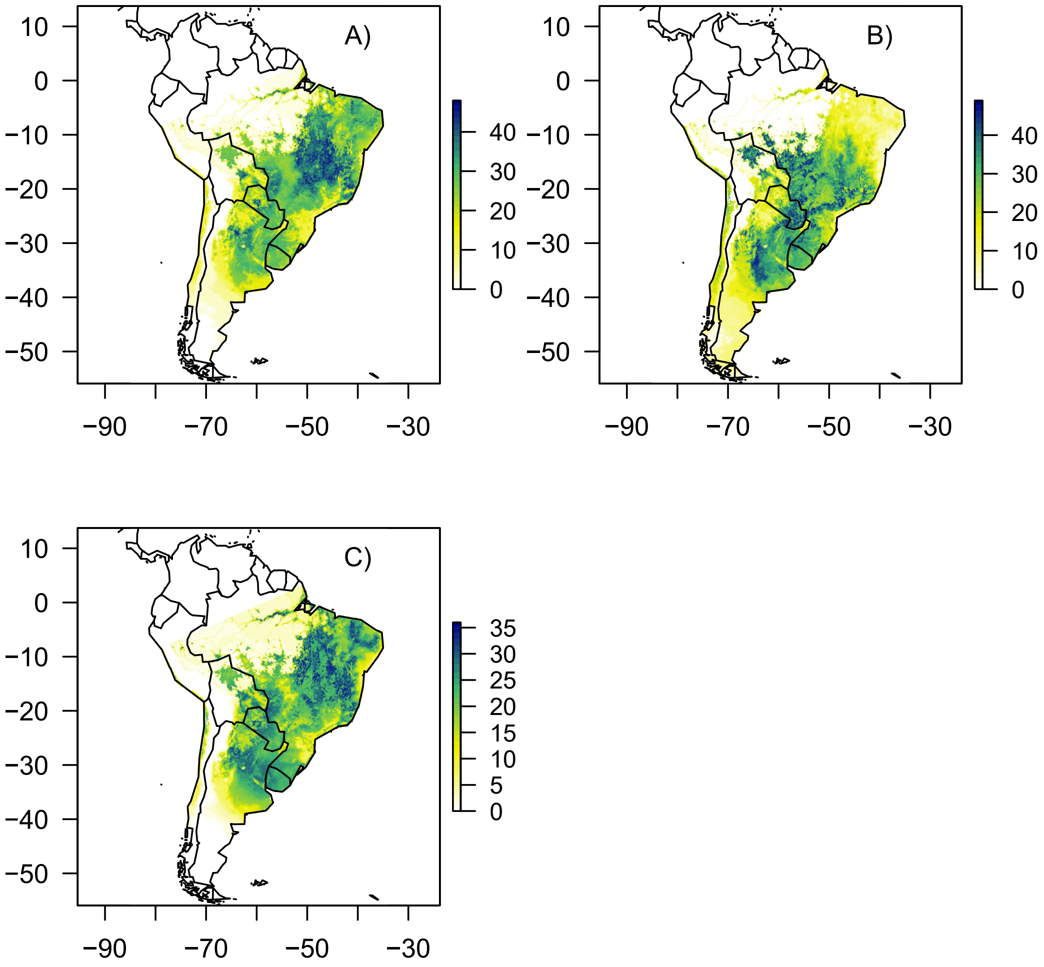

Figure 11. Most probable wintering locations based on δ^2H and δ^{13}C isotopes for Maritime populations of Barn Swallows using contour feathers collected in 2014 (A), 2015 (B) and 2016 (C). N = 68, 66 and 58, respectively.

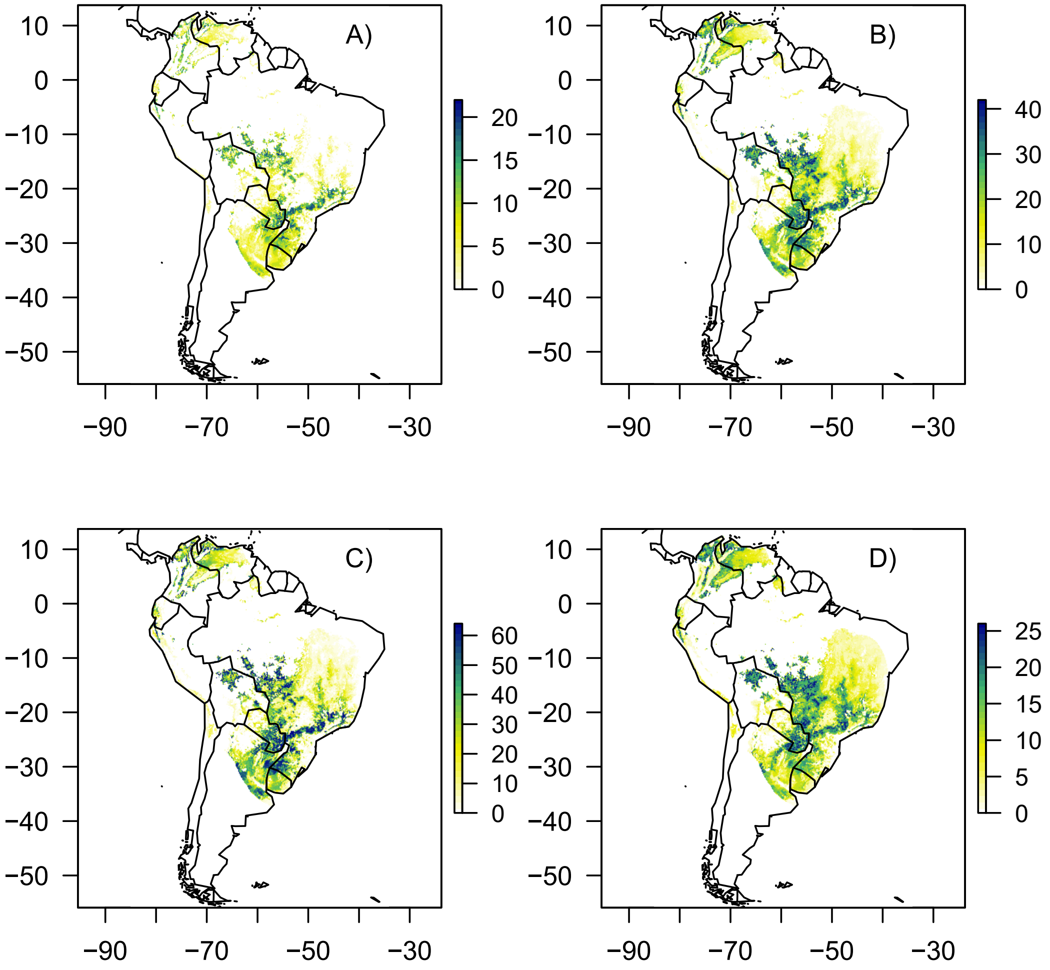

Figure 12. Most probable wintering locations based on δ^2H and δ^{13}C isotopes for Maritime populations of Cliff Swallows using rectrix feathers collected in 2013 (A) and contour feathers collected in 2014 (B), 2015 (C) and 2016 (D). N = 25, 54, 78 and 33, respectively.

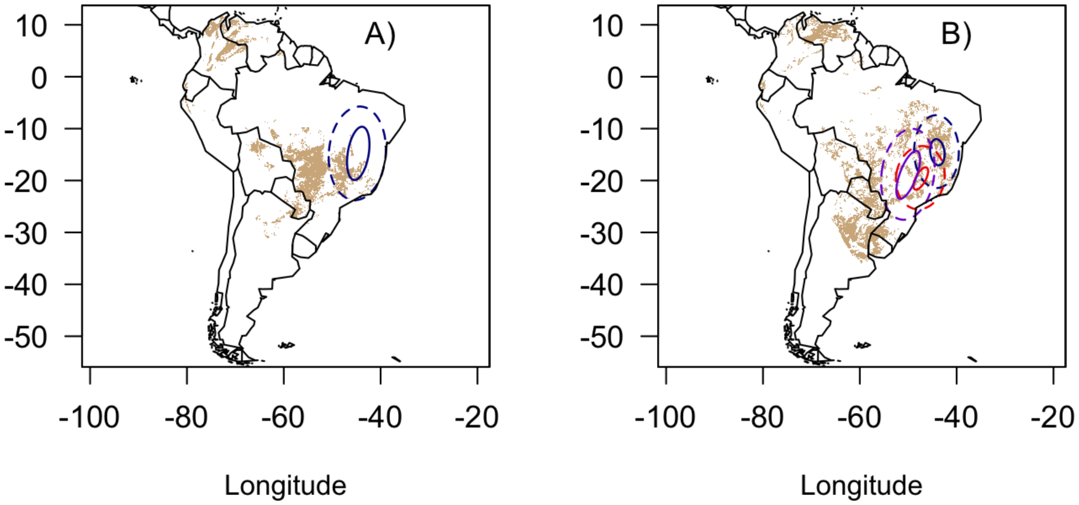

Figure 13. Winter locations during stationary periods from 14 October 2013 and 27 February 2014 for two Cliff Swallows equipped with geolocators, and their likely winter location based on δ^2H and $\delta^{13}C$ isotopes from contour feathers collected in 2014. Solid lines indicate most likely positions using mean latitude and longitude and dashed likes indicate most likely positions using the outermost cardinal locations using 95% credible intervals. Blue, red and purple lines indicate the first, second and/or third stationary periods, respectively, for each individual.

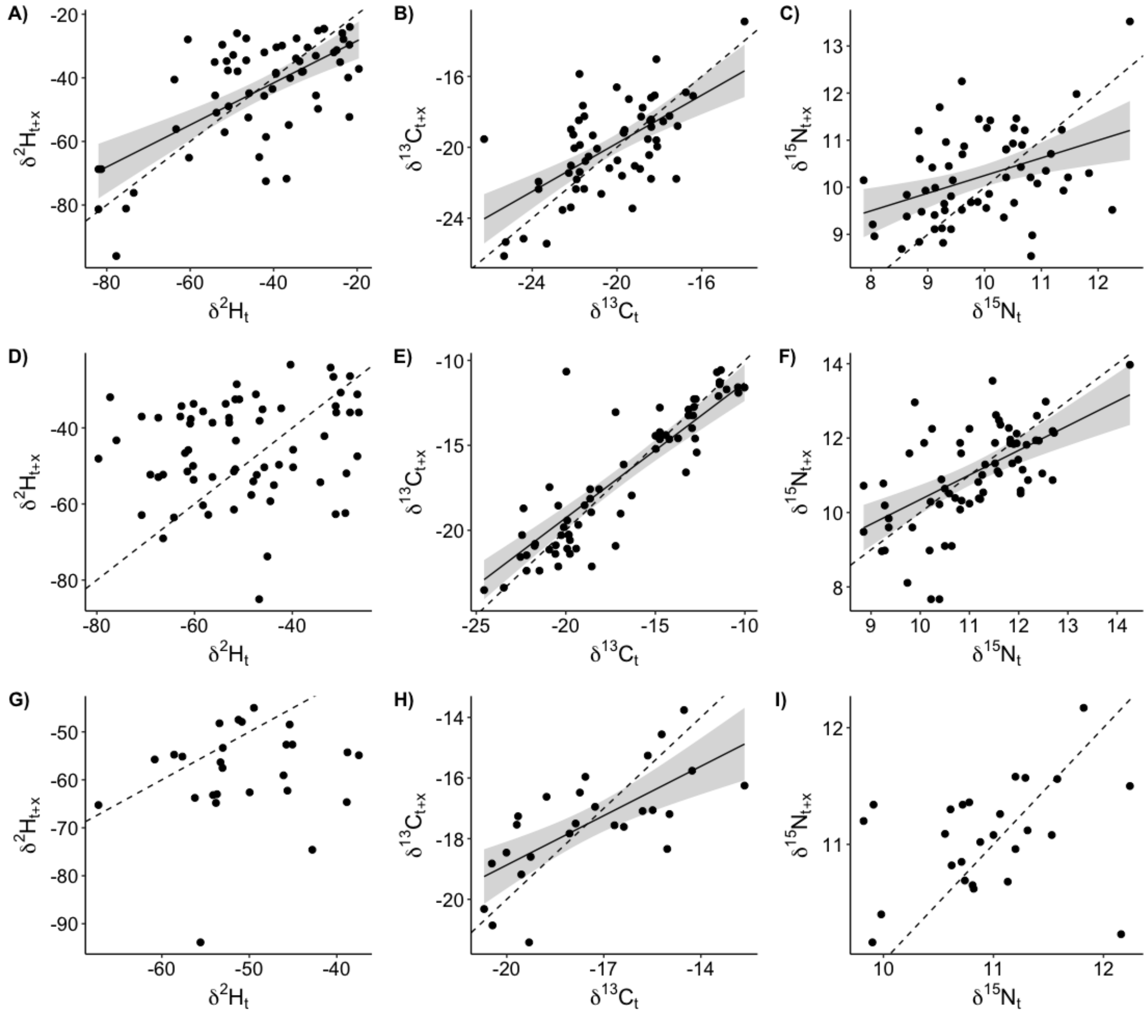

Figure 14. Relationships between stable isotopes (δ^2H, $\delta^{13}C$ and $\delta^{15}N$) from winter-molted contour feathers for individual Bank (A-C), Barn (D-F) and Cliff Swallows (G-I) captured in at least two years (t and t+x). Solid lines and grey areas indicate significant relationships ($p < 0.05$) and 95% confidence intervals between t and t+x (all slopes were ≤ 0.80), and dashed lines indicate the reference line with a slope = 1.0. N = 60, 67 and 26, respectively.

Chapter 6. A Review of the Threats to Adult Survival for Swallows

INTRODUCTION

Many species are facing increased risk of extinction from a diversity of threats (e.g., Dulvy et al. 2014; Purcell et al. 2014; Paleczny et al. 2015). In many cases the relationships amongst various threats are not clear, and so interactions between threats and ultimate cause(s) of population declines may not be obvious. Furthermore, efforts to identify and address threats, are hampered by the fact that studies are typically conducted on a single species, location and/or threat, making it difficult to generalize across a broader suite of species. These challenges make it difficult to identify and address the threats most likely to drive population declines. However, quantifying the relationship between threats and demographic processes, such as fecundity, recruitment and survival, may provide insights into how threats affect declines (Rappole & McDonald 1994; Selwood et al. 2015; Rushing et al. 2016), and focus conservation efforts on mitigating specific threats (Green 1999).

Life history theory predicts that population trends in species with a short life span and high reproductive output should be driven by breeding success (Sæther & Bakke 2000). However, there is compelling evidence that for many species of declining migratory passerines, a group of birds that typifies this pace of life, population trends are driven by reductions in adult survival (Baillie & Peach 1992; Murphy 2001; Fletcher et al. 2006; Buehler et al. 2008; Perlut et al. 2008; Ambrosini et al. 2011; Norman & Peach 2013). Indeed, in some species, such as the Cerulean Warbler *Setophaga cerulea*, conservation efforts aimed at increasing breeding success could not compensate for reductions in adult survival (Buehler et al. 2008). Despite the important influence of adult survival on population trends, research on declining bird populations is often focussed on the effects of threats and other limiting factors (collectively referred to as threats throughout this chapter) on fecundity.

Considerable research has examined the effects of various threats on fecundity for swallows (e.g., Fassbinder-Orth et al. 2013; Møller 2013; Winkler et al. 2013; Rioux Paquette et al. 2014). This is partly due to their colonial nature (either naturally, or with the placement of suitable nesting sites), makes it easy to obtain large samples. But also due to the steep population declines that these species are experiencing throughout much of their breeding range (Sanderson et al. 2006; Heldbjerg & Fox 2008; Sauer et al. 2014). In North America, long-term population trends for swallows and other aerial insectivores show a common negative change point during the 1980's (Nebel et al. 2010; Smith et al. 2015), suggesting that there may be common threat(s) driving population declines for this guild (Nebel et al. 2010; Smith et al. 2015). However, given the spatial variability in population trends within and among a few species, it is also possible that several factors are involved in aerial insectivore declines (Michel et al. 2016). Identifying common threats affecting population trends is useful for conservation efforts, as reducing these threats would benefit multiple species. However, despite a growing body of literature on aerial insectivore declines, the threats driving population declines, irrespective of whether they are common to all species, have yet to be determined. Furthermore, for some species, research suggests that declines for at least some populations are not being driven by reductions in fecundity (Imlay et al. 2018; Chapter 3).

Therefore, the goal of my study was to understand what was known about the threats to adult survival throughout the annual cycle five species of declining swallows: Bank, Barn, Cliff, and Tree Swallow, and Purple Martin. To that end, I conducted a literature review to determine and the relationships between threats and adult survival for these species. I also describe the hierarchical relationships among threats, so that conservation efforts can understand and address both the direct and indirect effect of threats. This multi-species comparison was also used to determine if there was evidence of common threats among species, and to identify key knowledge gaps that, if addressed, may inform population declines.

METHODS

Focal species

The five species of swallows in this chapter, Bank, Barn, Cliff and Tree Swallow, and Purple Martin, are all New World passerines; although Bank and Barn Swallows also have Old World populations. All seven species typically breed in their second year, and live for a maximum of 8-13 years, depending on the species and population (Brown & Bomberger Brown 1999a; Garrison 1999; Winkler et al. 2011; Brown & Tarof 2013; Brown et al. 2017). While most swallows usually raise one brood each year, Barn Swallows often raise two successful broods (Brown & Bomberger Brown 1999a).

Literature review of threats to adult survival

To determine the documented threats to adult survival in swallows, I searched Biological Abstracts (© Thomson Reuters) using keywords associated with the common and scientific names of the focal species (Bank Swallow, Sand Martin [an alternative name for Bank Swallow], Barn Swallow, Cliff Swallow, Tree Swallow, Purple Martin, *Riparia riparia*, *Hirundo rustica*, *Petrochelidon pyrrhonota*, *Tachycinta bicolor*, and *Progne subsis*), adult survival (survival, return rate, mortal*, fatal*, lethal*, and impact), and potential threats (habitat, loss, degradation, weather, climate, temperature, precipitation, wind, compet*, density-depend*, road, collision, aggregat*, quarr*, pit, pesticide*, pollut*, insect, food, diseas*, parasit*, predat*, harvest*, and human). The search included studies conducted throughout the species' geographic range between 1990 and 2017 (i.e., a period of time during which many populations were declining, Heldbjerg & Fox 2008; Sauer et al. 2014). This literature search was completed on 23 May 2017 and a full list of the references that compared adult survival for one or more species in relation to one or more threats is provided in Table 18.

RESULTS

Threats to adult survival

From the results of my literature search, I identified eight broad categories of threats – habitat change (which includes habitat creation, loss and degradation), weather, competition, incidental loss (i.e., accidental mortality due to human activities), contaminants, insect availability, disease and predation (including human harvest). I will use these broad categories of threats to summarize the information below. Within each category, I also considered whether the threat directly affected adult survival or if it had an indirect on adult survival through another threat. The relationships between threats and their indirect and direct effects on adult survival are illustrated in Figure 16.

Habitat change

Throughout their annual cycle, swallows are often associated with human infrastructure and working landscapes for breeding, foraging and roosting (Brown & Bomberger Brown 1999a; Garrison 1999; Winkler et al. 2011; Brown & Tarof 2013; Brown et al. 2017). These landscapes are experiencing high rates of broad-scale changes with human activities and changing weather patterns (Tilman et al. 2001; Hoekstra et al. 2005; Zedler & Kercher 2005; Mantyka-Pringle et al. 2012). While familiarity with habitats can confer higher survival for swallows (Brown et al. 2008), ultimately, habitat changes generally do not directly affect adult survival. Rather the effect of habitat changes on swallow survival is indirect (Figure 16) and will be described in more detail for five threats below.

Weather

Many studies have documented relationships between adult survival in swallows and weather. During breeding and migration, extended periods of cold temperatures and heavy rain or snowfall are associated with mass mortality events for several swallows (Brown & Bomberger Brown 1998; Hess et al. 2008; Møller 2011). Also during breeding, higher levels of precipitation are associated with lower survival for some populations of Bank Swallows (Cowley & Siriwardena 2005, but see Norman & Peach 2013), but not Barn Swallows (Robinson et al. 2008). During the winter, higher levels of rainfall are related to increased survival for Bank and Barn Swallows (Cowley & Siriwardena 2005; Robinson et al. 2008; Norman & Peach 2013). At a broader scale, there are mixed effects of larger climatic conditions on adult survival. While there was no relationship between the El Niño Southern Oscillation (ENSO) and Purple Martin survival in one region (Stutchbury et al. 2009a), Barn Swallow survival is often correlated with ENSO and/or the North Atlantic Oscillation (NAO) (Balbontín et al. 2009; García-Pérez et al. 2014). However, even within a species, the relationship between ENSO or NAO and survival varies (Balbontín et al. 2009; García-Pérez et al. 2014). For example, adult survival for Barn Swallows was related to ENSO and NAO in one population, but not in another population over 3,000 km away (García-Pérez et al. 2014). This variability (i.e. strength and direction) in these relationships may be due to the differences in the effect of these indices on weather at different breeding and wintering locations or during migration (Balbontín et al. 2009; García-Pérez et al. 2014) and/or low migratory connectivity between breeding and wintering populations (e.g., breeding populations wintering in a broad geographic area) (Stutchbury et al. 2009a; García-Pérez et al. 2014). Given the rapid increases in global temperatures (Hansen et al. 2006; National Research Council 2007) and associated effects on local weather patterns like temperature extremes, droughts, and more frequent and intense storms (Easterling et al. 2000; Hayhoe et al. 2007; Hartmann et al. 2013), the effect of weather on adult survival will likely increase in the future.

Competition

There is limited research on the effect of intraspecific competition on adult survival for swallows and none on interspecific competition. Density-dependence has an effect on adult survival for Bank and some Barn Swallow populations, likely through competition for food (Paradis et al. 2002; Norman & Peach 2013; Balbontín & Møller 2015). However, other factors, such as high predation pressure, may reduce the magnitude of this effect (Balbontín & Møller 2015).

Incidental loss

For swallows, potential sources of incidental loss include collisions with vehicles and infrastructure, aggregate extraction (i.e. removing sand or gravel from a pit or quarry), and rapid water level fluctuations associated with hydroelectric dams. The latter two solely affect Bank Swallows during breeding when they can be trapped in collapsed or flooded burrows. Swallows are frequently observed during road mortality surveys (reviewed in Erritzoe et al. 2003, Bishop & Brogan 2013), particularly on roads with tree belts or hedgerows as these areas, presumably, provide good foraging sites (Orlowski 2005; Grüebler et al. 2008). Unlike predation, road mortality is more likely to affect individuals in good condition (Bujoczek et al. 2011), resulting in the loss of high quality individuals. In Europe, it is estimated road mortality affects one million Barn Swallows annually, of which roughly one-third includes adult swallows (Orlowski 2005). In North America, however, selection on Cliff Swallow wing morphology has reduced road mortality (Brown & Bomberger Brown 2013). A study on the effect of wind turbines on Tree Swallows found it affects less than 0.01% of the population (Zimmerling et al. 2013), and I was unable to find estimates of mortality for either aggregate extraction and water fluctuations. Incidental loss will likely increase in the future with continued habitat change, like higher road density (Dulac 2013), further affecting adult survival.

Contaminants

Due to their use of agricultural areas and wetlands for foraging, roosting and/or nesting (Boutin et al. 1999; Winkler 2006; Laughlin et al. 2013), swallows are frequently exposed to a variety of contaminants, either directly from the environment or through their insect prey (Mora et al. 2002; Haroune et al. 2015). As a result, adult swallows often contain high levels of organophosphates, organochlorines (e.g., DDT/DDE), polychlorinated biphenyls (PCBs) and metals with potentially lethal or sub-lethal effects (Baron et al. 1999, Burgess et al. 1999, Mora et al. 2002, 2012, Custer et al. 2007, Hawley et al. 2009). Only two studies have examined effects on adult survival, with lower survival for female Tree Swallows nesting in areas with high levels of PCBs (Custer et al. 2007) and negligible differences in survival for Tree Swallows with high levels of mercury (Hallinger et al. 2011) compared to control groups. The future effects of this threat will likely increase as the prevalence of some contaminants is increasing with habitat change (Tilman et al. 2001; Bommarco et al. 2013) and warmer temperatures result in additional stress on birds with high contaminant loads (Hallinger & Cristol 2011). Swallows may, however, reduce contaminant load during molt which minimizes adverse effects of accumulated contaminants (Hallinger et al. 2011).

Insect availability

Apart from the consumption of some berries (e.g., bayberry and myrtle *Morella* spp.) by Tree Swallows (Piland & Winkler 2015), swallows solely forage on aerial insects throughout the annual cycle. Despite the importance of this food source and known declines in aerial insect populations (Hallmann et al. 2017), I was unable to find any research relating insect availability to adult survival. However, habitat change, contaminants, and weather can reduce insect availability for swallows (Figure 16). Habitat changes from low landscape-level homogeneity (often associated with low intensity agricultural land use, e.g., pastures and hayfields separated by hedgerows) to high landscape-level homogeneity (often associated with intensive agricultural practices, e.g., corn and soy production) reduces insect abundance (Benton et al. 2002; Grüebler et al. 2008; Rioux Paquette et al. 2013) and alters diet composition (Orłowski & Karg 2013). Intensive agricultural practices often entail increased pesticide use, which affects the abundance of aerial insects (Van Dijk et al. 2013; Morrissey et al. 2015; Pisa et al. 2015), and these practices are correlated with Barn Swallow population declines in the Netherlands (Hallmann et al. 2014) and altered diets of other aerial insectivores (Poulin et al. 2010; Nocera et al. 2012; English et al. 2018). While the effects of weather are often more short-term than habitat change and contaminants, reduced insect availability during breeding occurs during periods of cold temperatures, rainfall and high winds (Nooker et al. 2005; Møller 2013; Winkler et al. 2013).

Disease

Many studies have documented the presence of various bacteria, viruses and parasites (i.e. arthropods, flatworms, nematodes and protozoa) in adult swallows (Davidar & Morton 2006; Brown et al. 2007; Heneberg et al. 2011; Caron et al. 2014; Stenkat et al. 2014; Von Ronn et al. 2015). These infections have a wide range of effects on adult survival for swallows. Feather mites increase Cliff Swallow survival, presumably through the removal of old preening oil and/or removal or competition with other infectious agents on feathers (Brown et al. 2006), but have no effect on Barn Swallows (Pap et al. 2005). Neither the increased prevalence of West Nile Virus nor chronic infection with a protozoan *Haemoptroteus progenei* has an effect on Purple Martin survival (Davidar & Morton 1993; Stutchbury et al. 2009a); however, the initial protozoan infection may reduce survival (Davidar & Morton 1993). Infection with an unidentified filarial nematode is associated with lower survival in Purple Martins, and, although uncommon, most adults with both infections died (Davidar & Morton 2006).

Future rates of infection are predicted to increase with immunosuppression as a result of habitat and climate change (Martinez & Merino 2011 [review], Mason et al. 2013, but see Deviche et al. 2001). As a result of warmer temperatures associated with climate change, the prevalence of several common parasites in Barn Swallows has increased (Møller 2010). As rates of disease increase, the likelihood of multiple infections will also increase, resulting in even greater reductions in adult survival than a single infection (Davidar & Morton 2006; Ley et al. 2012). Furthermore, the sub-clinical effect of disease on decreased survival may be an important threat, particularly when declining species are under stress from other threats (Dunn et al. 2013).

Predation

Throughout their annual cycle, adult swallows face a wide variety of predators, including raptors, mammals and fish (Ash 1995; Bijlsma & van den Brink 2005; Stevens et al. 2009; O'Brien et al. 2014; Balbontín & Møller 2015). At breeding colonies, predation can result in large losses of adult swallows (e.g., 58%, Young 1994), and sex-biased mortality (Møller & Nielsen 1997) which further reduces fecundity and contributes to population declines. Given that high rates of predation are often localized to areas where predators learn to exploit an abundant food source (Young 1994; Rebecca 2004) and are unlikely to represent broader-scale population-level effects, it is difficult to determine the effect of predation on adult survival across the species' range. While domestic cat *Felis catus* predation affects a large number of birds in North America (Blancher 2013; Loss et al. 2013), aerial species, like swallows, experience a lower risk of predation than ground nesting and feeding birds (Blancher 2013; Balbontín & Møller 2015). In contrast, populations of several avian predators of swallows (e.g., Peregrine

Falcon *Falco peregrinus* and Merlin *F. columbarius*) are increasing across North America (Hoffman & Smith 2003; Farmer et al. 2008), potentially resulting in greater predation pressure.

DISCUSSION

I reviewed the direct and/or indirect effect of eight threats – habitat change, weather, competition, incidental loss, contaminants, insect availability, disease and predation – on adult survival for swallows. The effects of these threats are often intertwined, as several, particularly habitat change and weather, have multiple indirect effects on adult survival (Figure 16). Furthermore, I observed that the effects of many threats are likely to increase in the future.

While my conclusions are limited by several factors, like the lack of information for some threats, species and their geographic ranges (including a reliance on research for Old World populations of Bank and Barn Swallows), I found that weather had a common negative effect on adult survival for four of the five species examined. In particular, cold snaps during spring and fall, either during migration or just after arriving on the breeding grounds (Brown & Bomberger Brown 1996, 1998; Hess et al. 2008; Møller 2011), and reduced rainfall during the winter (Szép 1995a, 1995b; Cowley & Siriwardena 2005; Robinson et al. 2008; Norman & Peach 2013; García-Pérez et al. 2014) showed similar negative effects on survival; although the effects of the latter were likely indirect and associated with insect abundance.

I was unable to find any papers relating adult survival to habitat change or insect availability, and very little information on the effects of contaminants on adult survival.

All three of these threats have received extensive attention in the literature for their effects on fecundity in Barn and Tree Swallows (e.g., McCarty & Winkler 1999a; Bishop et al. 2000; Ambrosini et al. 2002; Nooker et al. 2005; Fredricks et al. 2012; Winkler et al. 2013; Rioux Paquette et al. 2014; Schifferli et al. 2014), but very little is known about survival. This lack is particularly glaring as reductions in insect availability (possibly as a result of habitat change, weather and/or contaminants) is considered to be the most likely driver of population declines for aerial insectivores (Nebel et al. 2010). Clearly, this represents a key knowledge gap for aerial insectivore declines as a whole. Since demands on food are highest during the breeding season and fall migration (Kelly et al. 2013), reductions in food availability during these times could have a disproportionate effect on populations.

I also found that for most threats, except weather, there was very little information on their effects during the non-breeding period. This also represents a key knowledge gap as non-breeding conditions are strongly related to population trends for several species (Ambrosini et al. 2011; Ockendon et al. 2014; Sicurella et al. 2016). Initial efforts to quantify and address threats during this period might focus on incidental loss (especially road mortality), contaminants and disease as these threats all effects on adult survival during breeding, and likely have similar effects during the non-breeding period. The lack of information on threats throughout this period may be partly due to the lack of information on non-breeding locations for specific populations of Nearctic-Neotropical swallows. However, this knowledge gap is quickly being addressed with tracking technologies (Fraser et al. 2012; Hobson et al. 2015; Knight et al. 2017) and stable isotope analysis (Garcia-Perez & Hobson 2014; Chapter 5), which provides opportunities to investigate these threats during this time.

Addressing the effects of threats on population declines is not without challenges. The foremost challenge is the need for cooperation among countries throughout the annual range of these species on the implementation of conservation efforts described below. The effects of weather, especially those driven by global climate change, are perhaps the most intractable for conservation efforts, particularly if the aim is to address these effects in the short-term. However, there are strong relationships between weather and demographic processes for many other taxa (Selwood et al. 2015), indicating that this threat plays an important role in global biodiversity declines and should be addressed for many species, including aerial insectivores. Conservation efforts to address this threat over the long-term may include habitat protection, management and planning for currently suitable habitats and those that may become suitable in the future; active species management, particularly efforts to address other threats; and changes to current laws and policies (reviewed in Heller & Zavaleta 2009, Mawdsley et al. 2009). Similarly to weather, addressing the effects of disease on adult survival for swallows may also be challenging. If decreased adult survival can be attributed to a few specific diseases (such as White-nose syndrome in North American bats, Foley et al. 2011), then conservation efforts could involve direct management of the disease(s) (e.g., treatment of infected individuals and vaccine development). However, from the research to date, reduced adult survival for swallows as a result of disease is largely attributed to greater rates of infection with multiple pathogens or parasites (Davidar & Morton 2006), which may be driven by changes to weather (Møller 2010). Therefore, conservation efforts to address disease will also need to consider the ultimate driver of increased rates of infection. Perhaps a more immediate and tractable threat for conservation efforts to address are the effects of contaminants on adult survival for swallows. Although the results of studies on Tree Swallows were mixed, for many species research has demonstrated severe, negative effects of some contaminants on populations (Gibbons et al. 2015; Pisa et al. 2015). Bans on specific contaminants have been successfully used to recover many declining species and can be implemented over a relatively short period of time. For example, following the ban of DDT throughout many western counties, raptor populations increased (e.g., Schmidt-Rothmund et al. 2014, Ambrose et al. 2016). For aerial insectivores, banning contaminants linked to reductions in adult survival may bolster populations by minimizing the direct effects on individuals (Custer et al. 2007), and indirectly through lower contaminants in their food (Haroune et al. 2015), and increasing food availability and/or quality (Nocera et al. 2012).

Conclusions

Developing effective conservation strategies requires understanding when and where species experience threats during the annual cycle and determining how these threats affect demographic processes. However, the variety and ubiquity of the direct and indirect effects of threats can make it difficult to assess threats and their interactions, especially across several species. Furthermore, most research on threats focuses on the breeding grounds (Faaborg et al. 2010; Marra et al. 2015), and on fecundity rather than adult survival. In doing so, conservation efforts may focus on addressing threats that only affect populations during one stage of the annual cycle. Furthermore, for migratory birds, this could result in conservation efforts that do not target the demographic processes that have the greatest effect on population trends.

Table 16. Research documenting the relationships between threats and adult survival rates for Bank, Barn, Cliff and Tree Swallows, and Purple Martins.

Threat	Species	Effect on survival^1		
		Positive	Negative	No effect
Weather	Bank Swallow		Szép 1995a, 1995b; Cowley & Siriwardena 2005; Robinson et al. 2008; Norman & Peach 2013	
	Barn Swallow		Robinson et al. 2008; Møller 2011; García-Pérez et al. 2014	
	Cliff Swallow		Brown & Bomberger Brown 1996, 1998	
	Purple Martin			Stutchbury et al. 2009a
	Tree Swallow		Hess et al. 2008	
Competition	Bank Swallow		Norman & Peach 2013	
	Barn Swallow		Balbontín & Møller 2015	Paradis et al. 2002
Incidental loss	Barn Swallow		Orlowski 2005	
	Cliff Swallow		Brown & Bomberger Brown 2013	
	Tree Swallow		Zimmerling et al. 2013	
Contaminants	Tree Swallow		Custer et al. 2007; Hallinger et al. 2011	
Disease	Barn Swallow			Pap et al. 2005
	Cliff Swallow	Brown et al. 2006		
	Purple Martin		Davidar & Morton 1993, 2006	Stutchbury et al. 2009a
Predation	Bank Swallow		Young 1994	
	Barn Swallow		Ash 1995; Bijlsma & van den Brink 2005; Balbontín & Møller 2015	

[1] Methods included to quantify changes in adult survival included: 1) numbers of mortalities compared to the total population size (9 of 26 studies or 34.6%), 2) number of mortalities compared to total population size while accounting for detectability (1 or 3.5%), 3) number of mortalities based on annual return rates (4 or 15.4%), and 4) mark-recapture models (12 or 46.2%)

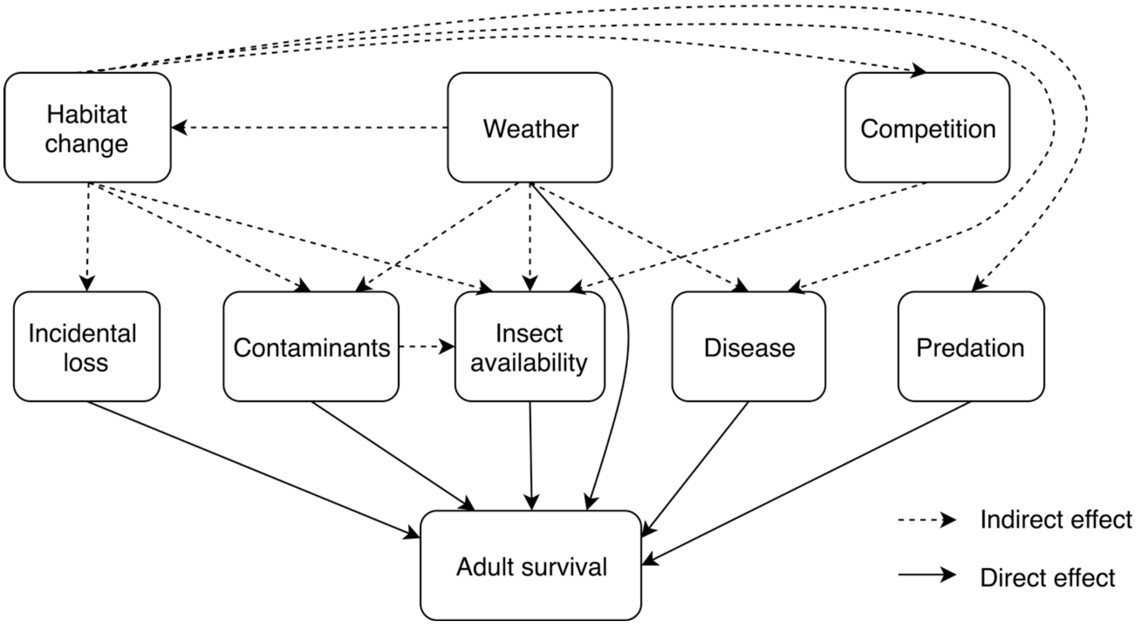

Figure 15. The relationships between threats and adult survival for seven declining swallows.

Chapter 7. Conclusion

AERIAL INSECTIVORE DECLINES

The overarching goal of my thesis was to determine the likely driver(s) of population declines for several species of swallows. Throughout most of this work I examined the effects that two likely drivers – insect availability on the breeding grounds and non-breeding conditions – have on breeding performance. I also take a comparative approach to examining the declines to determine if the drivers are similar for multiple species. Below I address these aspects of my research.

Likely drivers of population declines

In Chapters 2 and 3, I determined if changes in breeding performance, potentially as a result of lower insect availability, may be contributing to population declines. Through insect sampling, I found that, for Barn, Cliff and Tree Swallows, insect abundance was unrelated to breeding performance, at least during the years sampled and at my study sites (Chapter 2). Therefore, I examined long-term data on breeding performance to determine if there was a change between two time periods – before (1962-1972) and after (2006-2016) the initiation of steep population declines – for Bank, Barn, Cliff and Tree Swallows that could indicate a mis-timing between breeding and food-availability. My findings suggest that population declines for Barn, Cliff and Tree Swallows can not be attributed to reductions in breeding performance between these time periods (Chapter 3). However, for the Bank Swallow, I did find a reduction in breeding performance in recent years, potentially due to a mis-timing between breeding and insect abundance.

In Chapter 4, I determined if non-breeding conditions resulted in carry-over effects during breeding for Bank, Barn and Cliff Swallows. High $\delta^{2}H$ (potentially associated with less rainfall and lower insect abundance) was associated with lower mass, later breeding and lower success for male Barn and Cliff Swallows, but higher mass for Bank and female Barn Swallows. Also, high $\delta^{13}C$ and $\delta^{15}N$ were associated with higher mass, but later breeding and lower success for male Bank Swallows, and lower mass for female Barn Swallows. These results indicate that non-breeding conditions may contribute to population declines, especially since these species winter in areas of South America associated with land-use change, including increased agricultural intensity and changes in weather patterns (Chapter 5).

Common response among species

Throughout my research, I found many similarities in the demographic responses of swallows to their environment. For example, breeding performance for Barn, Cliff and Tree Swallows was unrelated to insect abundance on the breeding grounds (Chapter 2). Similarly, all three species advanced their breeding over time, with unchanged or higher performance than in the past (Chapter 3). Also, for male Barn and Cliff Swallows poor non-breeding conditions resulted in similar carry-over effects during breeding (Chapter 4). Finally, when sufficient information was available, adult survival was negatively affected by inclement weather four species of swallows (Chapter 5). Similar responses across several species suggest that conservation efforts aimed at addressing particular threats may have a beneficial effect on multiple species of aerial insectivores.

There was, however, one notable exception to these similarities. In many cases, the Bank Swallow showed responses that diverged from those of the other species.

Unlike the other species, Bank Swallows did not advance their breeding and have shown an estimated 46% decline in reproductive performance (Chapter 3). Also, while Bank Swallows experienced carry-over effects from non-breeding to breeding, the conditions that resulted in negative carry-over effects differed from male Barn and Cliff Swallows (Chapter 4).

The reasons for these differences are unknown, but there are several possible explanations. Bank Swallows are about half to two-thirds the size of the next largest species (Brown & Bomberger Brown 1999b; Garrison 1999), and thus may have different energetic requirements. Bank Swallows are the last species to arrive on the breeding grounds, and, nests two to three weeks later than the other species (which are relatively synchronous) (pers. obs.). Also, Bank Swallows typically nests in habitats that experience considerable annual change (i.e., river and coastal) (Garrison 1999). Population trends for Bank Swallows are considerably steeper than the other species, with an estimated 98% decline between 1970 and 2011 in Canada (COSEWIC 2013). It is possible that the life history characteristics described above have a disproportionate effect on the response of this species to different threats.

AERIAL INSECTIVORE FUTURE RESEARCH AND CONSERVATION

For populations of swallows in the Maritimes, a region where species are experiencing steep declines, it is clear that reductions in breeding performance can not explain population declines for all species (Chapter 3). Indeed, my work shows that conditions during the non-breeding period affect stress and subsequent breeding performance (Chapter 4). This work is consistent with other research indicating that non-breeding conditions also affect adult survival (Chapter 5). The results of my research suggest that, with the exception of the Bank Swallow, the main threats to these species, at least in the Maritime region of Canada, are not on the breeding grounds. Therefore, the next steps to address population declines for these species, should focus on threats during the non-breeding period and their effects on survival and subsequent breeding. Ideally, this would include work on populations experiencing different population trends (even if this is restricted to different rates of decline).

One major challenge for this work is tracking individuals that make long-distance movements to and from the wintering grounds, and possibly throughout their wintering grounds. However, new technologies, such as the Motus Wildlife Tracking Network (Taylor et al. 2017) and archival GPS tags (Hallworth & Marra 2015), may present opportunities to follow individuals throughout the non-breeding period and understand the threats encountered during this period. In addition, although limited to individuals that survive the non-breeding period, feather and blood samples collected on the breeding grounds may containing information on prevalence of different threats, such as contaminants and disease, during the non-breeding period. This, coupled with the high return rates to breeding colonies, presents opportunities to understand how different threats influence survival throughout the year.

Another avenue for future research is the relationship between double-clutching and population dynamics for Barn Swallows. About one-third of the pairs in the Maritimes raise two broods annually (pers. obs.). If the young from later broods contribute little to the population then carry-over effects from non-breeding to breeding will not play a large role in population declines for these species. However, if the young from later broods do contribute to the population, then the carry-over effects I observed could help explain population declines for this species.

There are many challenges associated with addressing population declines for broadly-distributed, abundant species, especially those that migrate throughout their annual cycle, like swallows. These challenges are often the result of the scale at which conservation efforts are considered. For example, variability in the main threats to the species across their range and the protection offered by different jurisdictions can make it difficult to identify appropriate actions to address these threats. Also, when species exhibit little fidelity to specific areas or undertake large movements during part of the year, it becomes increasingly important to protect or mitigate threats on larger tracts of suitable habitat. In these cases, some conservation efforts aimed at an extremely broad (i.e., the species' range) or small scale (i.e., a single breeding or roost site) will likely be insufficient. Instead, focusing on threats that are at a more regional scale may be most effective. This could include measures like protecting or restoring winter roost sites in areas where winter habitat loss is a primary concern. Although, some more broadly-aimed actions, such as banning pesticides, may be effective at a broader scale if combined with more regional measures. Since populations of common migratory birds are presently experiencing unprecedented rates of decline worldwide, this problem calls for a new approach to conservation with a focus on collaboration among jurisdictions throughout the range of these species.

SIGNIFICANCE OF RESEARCH

My research has important implications for understanding and addressing aerial insectivore declines. Through taking a multi-species comparative approach when examining aspects of two likely drivers of population declines (i.e., insect availability and non-breeding conditions), my work demonstrates that population declines for most species are likely driven by factors during the non-breeding period, like weather conditions and land-use change. It also demonstrates that conservation efforts addressing these threats will likely have beneficial effects for multiple species. Furthermore, these multi-species comparisons which provide insight into whether species are affected in a similar manner by the same threats.

My research, also demonstrates how the use of multiple intrinsic markers (i.e., stable isotopes, CORT_f and telomere dynamics) can provide insight into the effects of conditions during one part of the annual cycle on a subsequent part. This may be increasingly important, as the logistics and costs of conducting research on all stages of the annual cycle may be prohibitive.

Finally, although much research in the past has been devoted to understanding the effects of conditions during breeding on performance and population dynamics, there is now a greater awareness that to fully understand population declines, it is important to consider factors throughout the annual cycle. My research adds to this growing body of literature that examines the effects of ecological factors on species throughout their annual cycle.

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Appendix 1. Supplementary Material for Chapter 2

Table A1. Summary of the number of nests, mean ± SE hatching dates and nestling mass, and nestling survival for each species and the number of insect samples and mean ± SE insect abundance by site.

	variable[1]	BEFV	JO	WE	total
Barn	N	2	11	17	30
	mean ± SE HD (range)	52.0 ± 3.0 (49 – 55)	55.6 ± 2.2 (47 – 74)	52.7 ± 1.5 (42 – 63)	53.7 ± 1.1 (42 – 74)
	surviving nestlings (%)	10/10 (100.0)	39/39 (100.0)	71/75 (94.7)	120/124 (96.8)
	mean ± SE nestling mass (range)[2]	18.20 ± 0.74 (13.0 – 21.0)	16.11 ± 0.36 (10.5 – 20.0)	16.65 ± 0.31 (6.0 – 21.0)	16.59 ± 0.23 (6.0 – 21.0)
Cliff	N	–	25	26	51
	mean ± SE HD (range)	–	51.5 ± 0.8 (42 – 58)	55.3 ± 1.1 (41 – 63)	53.4 ± 0.7 (41 – 63)
	surviving nestlings (%)	–	63/83 (75.9)	47/85 (55.3)	110/168 (65.5)
	Mean ± SE nestling mass (range)[2]	–	22.35 ± 0.38 (12.5 – 28.0)	21.09 ± 0.37 (11.5 – 26)	21.79 ± 0.27 (11.5 – 28)
Tree	N	70	26	34	130
	mean ± SE HD (range)	47.1 ± 0.8 (39 – 66)	49.6 ± 1.0 (41 – 60)	49.9 ± 0.9 (41 – 66)	48.3 ± 0.5 (39 – 66)
	surviving nestlings (%)	350/371 (94.3)	107/133 (80.5)	150/165 (90.9)	607/669 (90.7)
	mean ± SE nestling mass (range)[2]	22.42 ± 0.10 (15.5 – 27.5)	22.35 ± 0.22 (15.0 – 27.0)	21.89 ± 0.16 (16.0 – 26.0)	22.28 ± 0.08 (15.0 – 27.5)
Insect abundance	N	64	65	68	197
	mean ± SE daily (range)	-0.55 ± 0.06 (-1.62 – 0.56)	-0.70 ± 0.08 (-2.30 – 0.69)	-0.78 ± 0.07 (-2.15 – 0.42)	-0.68 ± 0.04 (-2.30 – 0.69)

	variable[1]	BEFV	JO	WE	total
	mean ± SE IA_M (range)	-0.33 ± 0.02 (-0.73 – -0.09)	-0.42 ± 0.02 (-0.70 – -0.08)	-0.46 ± 0.01 (-0.69 – -0.21)	-0.41 ± 0.01 (-0.73 – -0.08)
	mean ± SE IA_{B1} (range)	-0.33 ± 0.02 (-0.73 – -0.09)	-0.42 ± 0.02 (-0.91 – -0.04)	-0.45 ± 0.01 (-0.69 – -0.24)	-0.40 ± 0.01 (-0.91 – -0.04)
	mean ± SE IA_{MB} (range)	-0.47 ± 0.04 (-1.03 – 0.60)	-0.64 ± 0.05 (-1.43 – 0.01)	-0.60 ± 0.05 (-1.35 – 0.13)	-0.57 ± 0.03 (-1.43 – 0.60)

[1] Abbreviations: N = number of nests or daily samples, HD = hatching date (May 1 is day 1), IA_M = mean insect abundance up to and including day 12; and IA_{B1} = mean insect abundance on and one day prior to banding day; IA_{MB} = mean insect abundance up to and including banding day.

[2] Does not include nestling mass for nests where the mean nestling mass was than two standard deviations below the mean for all nests.

Appendix 2. Supplementary Material for Chapter 3

Decision rules for data compiled from the Maritime Nest Records Scheme

Clutch initiation date: I identified the first day that an egg was laid as the clutch initiation date. I assumed that breeding swallows laid one egg a day on consecutive days. To identify clutch initiation dates, I required 1) at least two nest checks with the first nest check occurred when the clutch was incomplete (i.e., fewer eggs than later checks with more eggs or nestlings) or 2) two nest checks between which laying occurred with one day for each egg in the clutch. If laying occurred between two nests checks where there was one more day than the number of eggs, I identified the clutch initiation date as the first of two potential days when the clutch was initiated (147 of 3,121 observations).

Hatching date: I identified the day when eggs began to hatch as the hatching date. I assumed that all chicks hatched on the same day. To identify hatching dates, I required that nests were monitored at least twice with either daily nest checks (one check occurring prior to hatching and one check after hatching) or one check as the young were hatching (i.e., with fewer young than the next nest check) and a second check afterward to confirm more nestlings had hatched. If nests were monitored every second day and one check was conducted prior to hatching and one check was conducted after hatching, then I identified the hatching date as the first day chicks were observed (301 of 939 observations).

For clutch size, brood size and nestling survival, I assumed that egg-dumping had occurred when nests were observed with more than seven eggs or nestlings for Bank and Barn Swallows, five for Cliff Swallows and eight for Tree Swallows.

Clutch size: To identify the clutch size, I required that nests were monitored at least twice, with 1) one check during egg-laying and the other check occurring after the clutch was complete, 2) two checks during the incubation period with the same number of eggs, or 3) one check during incubation and one after hatching as long as these checks occurred within 16 days of each other.

Brood size: To identify the brood size, I required that nests were monitored at least twice no more than 16 days apart during the nestling period, or, for nests with a known clutch size, one nest check occurred during the nestling period and all the eggs hatched. Similar to hatching date, I assumed that all young hatched on the same day.

Nestling survival: To determine nestling survival to day 12-16, I required that nests were monitored at least twice during the nestling period and that the earliest and latest check occurred within 12-16 days of each other. All of these species have long nestling periods (<18 days, (Brown & Bomberger Brown 1999a; Garrison 1999; Winkler et al. 2011; Brown et al. 2017), therefore during this age range, all young are still present in the nest. Furthermore, I considered nestling survival to 12-16 days to be an indicator of the number of fledged young, because, nestling survival after day 10 is high for these species (Brown & Bomberger Brown 1999b; Ambrosini et al. 2002).

Hatching success: To determine hatching success, I required at least one nest check recording one or more nestlings (successful), or at least two nest checks recording the same number of eggs at least 20 days apart (unsuccessful).

Nest success: To determine nest success, I required at least two nest checks during the nestling period, with the earliest and a latter check occurred within 12-16 days of each other. For successful nests, at least one nestling was recorded on the latter check.

Use of clutch initiation in analyses

For all analyses that used clutch initiation as the response variable, I only included data for clutch initiation date up to and including the median date for each year. This approach excluded known second nesting attempts after failed first nests (all species) and second broods (Barn and Cliff Swallows, only) as these may hinder my ability to detect changes in breeding phenology (Hussell 2003; Williams et al. 2015). This approach may have also removed some young pairs which start breeding later than experienced pairs, and pairs in poor body condition which may delay breeding because of physiological constraints (Hussell & Quinney 1987; Hussell 2003). Removal of these nesting records would allow us to focus on nesting attempts that were initiated by pairs with the experience and physiological condition necessary to time their breeding with environmental conditions.

In all models where clutch initiation date was an explanatory variable, I included all breeding records.

Results of Barn Swallow brood size and nestling survival models with data source

Initially, my full model for Barn Swallow brood size and nestling survival included all four principal components (for temperature and precipitation), year, latitude, longitude, clutch initiation date, data source (a categorical variable that identified the data as from the MNRS or a long-term study) and an interaction between data source and year. The top models (ΔAICc ≤ 2.0) included the interaction (Table A2), suggesting that there was a different trend across time for the long-term data (Table A3). However, graphical inspection of the results suggested that the inclusion of this term was due to smaller broods and lower nestling survival in one year (2016) of the three-year period when long-term data was available (Figure A1). Since this result contrasted with my comparisons of the long-term data from 1962-1972 and 2006-2016 (Table 9), I re-ran my models, but without the term for data source and the interaction between data source and year. These results are presented above in Tables 9 and 11.

Table A2. Model selection table for the best-fitting models for the relationships between temperature and Barn Swallow brood size and nestling survival when the source of the data and its interaction with year was included. Only models within ΔAICc ≤ 2.0 of the top model are displayed.

Response variable	Model[1,2]	df	AICc	ΔAICc	w_i	Log Likelihood
Brood size	Latitude + Source + Source:Year + Year	5	1740.55	0.00	0.05	-865.20
	Latitude + PC1 + Source + Source:Year + Year	6	1741.32	0.77	0.04	-864.55
	Latitude + PC3 + Source + Source:Year + Year	6	1741.71	1.16	0.03	-864.75
	CID + Latitude + Source + Source:Year + Year	6	1741.77	1.22	0.03	-864.78
	Source + Source:Year + Year	4	1742.09	1.54	0.02	-866.99
	Latitude + PC2 + Source + Source:Year + Year	6	1742.16	1.62	0.02	-864.98
	Latitude + Longitude + Source + Source:Year + Year	6	1742.18	1.63	0.02	-864.98
	Latitude + PC4 + Source + Source:Year + Year	6	1742.35	1.80	0.02	-865.07
Nestling survival	PC3 + Source + Source:Year + Year	5	1467.31	0.00	0.05	-728.56
	Source + Source:Year + Year	4	1467.36	0.05	0.05	-729.62
	Latitude + PC3 + Source + Source:Year + Year	6	1468.57	1.26	0.02	-728.15
	PC2 + PC3 + Source + Source:Year + Year	6	1468.58	1.27	0.02	-728.16
	PC2 + Source + Source:Year + Year	5	1468.77	1.46	0.02	-729.29
	PC1 + PC3 + Latitude + Source + Source:Year + Year	7	1468.80	1.49	0.02	-727.22
	Latitude + Source + Source:Year + Year	5	1468.85	1.54	0.02	-729.33
	CID + PC3 + Source + Source:Year + Year	6	1468.89	1.58	0.02	-728.31
	CID + Source + Source:Year + Year	5	1468.91	1.60	0.02	-729.36
	Longitude + Source + Source:Year + Year	5	1469.10	1.78	0.02	-729.45

Response variable	Model[1,2]	df	AICc	ΔAICc	w_i	Log Likelihood
	PC4 + Source + Source:Year + Year	5	1469.13	1.82	0.02	-729.47
	PC3 + PC4 + Source + Source:Year + Year	6	1469.22	1.91	0.02	-728.48
	Latitude + PC1 + Source + Source:Year + Year	6	1469.24	1.93	0.02	-728.49

[1] PC1-4 represents principal components 1-4 identified in Table 2.

[2] Source was a categorical variable representing data that was collected as part of the Maritime Nest Records Scheme or long-term monitoring projects.

Table A3. Model coefficients, SE and 95% confidence intervals (CI) for the best-fitting models explaining the relationships between temperature, precipitation and Barn Swallow brood size and nestling survival when the source of the data and its interaction with year was included. Bolded explanatory values indicated those with an effect on the response.

Response	Explanatory variables[1,2]	Estimate	SE	Lower 95% CI	Upper 95% CI	Relative importance (N[3])
Brood size	(Intercept)	560.70	213.20	141.64	979.72	
	CID	0.00	0.00	-0.01	0.00	0.12 (1)
	Latitude	-0.07	0.05	-0.16	0.01	0.90 (7)
	Longitude	0.00	0.01	-0.07	0.03	0.10 (1)
	PC1	0.00	0.02	-0.02	0.09	0.15 (1)
	PC2	0.00	0.01	-0.07	0.03	0.10 (1)
	PC3	0.00	0.01	-0.03	0.09	0.12 (1)
	PC4	0.00	0.01	-0.05	0.09	0.09 (1)
	Source	-561.00	213.10	-979.91	-142.10	1.00 (8)
	Source:Year	0.28	0.11	0.07	0.49	1.00 (8)
	Year	-0.28	0.11	-0.48	-0.07	1.00 (8)
Nestling survival	(Intercept)	656.70	233.50	197.49	1115.94	
	CID	0.00	0.00	-0.01	0.00	0.13 (2)
	Latitude	-0.02	0.05	-0.24	0.07	0.27 (4)
	Longitude	0.00	0.01	-0.09	0.05	0.06 (1)
	PC1	0.01	0.02	-0.03	0.13	0.12 (2)
	PC2	0.00	0.02	-0.04	0.11	0.15 (2)
	PC3	0.03	0.04	-0.02	0.14	0.49 (6)
	PC4	0.00	0.02	-0.07	0.12	0.11 (2)
	Source	-669.30	233.60	-1128.69	-209.86	1.00 (13)
	Source:Year	0.33	0.12	0.10	0.56	1.00 (13)
	Year	-0.33	0.12	-0.55	-0.10	1.00 (13)

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[1] PC1-4 represents principal components 1-4 identified in Table 2.

[2] Source was a categorical variable representing data that was collected as part of the Maritime Nest Records Scheme or long-term monitoring projects.

[3] Number of averaged models.

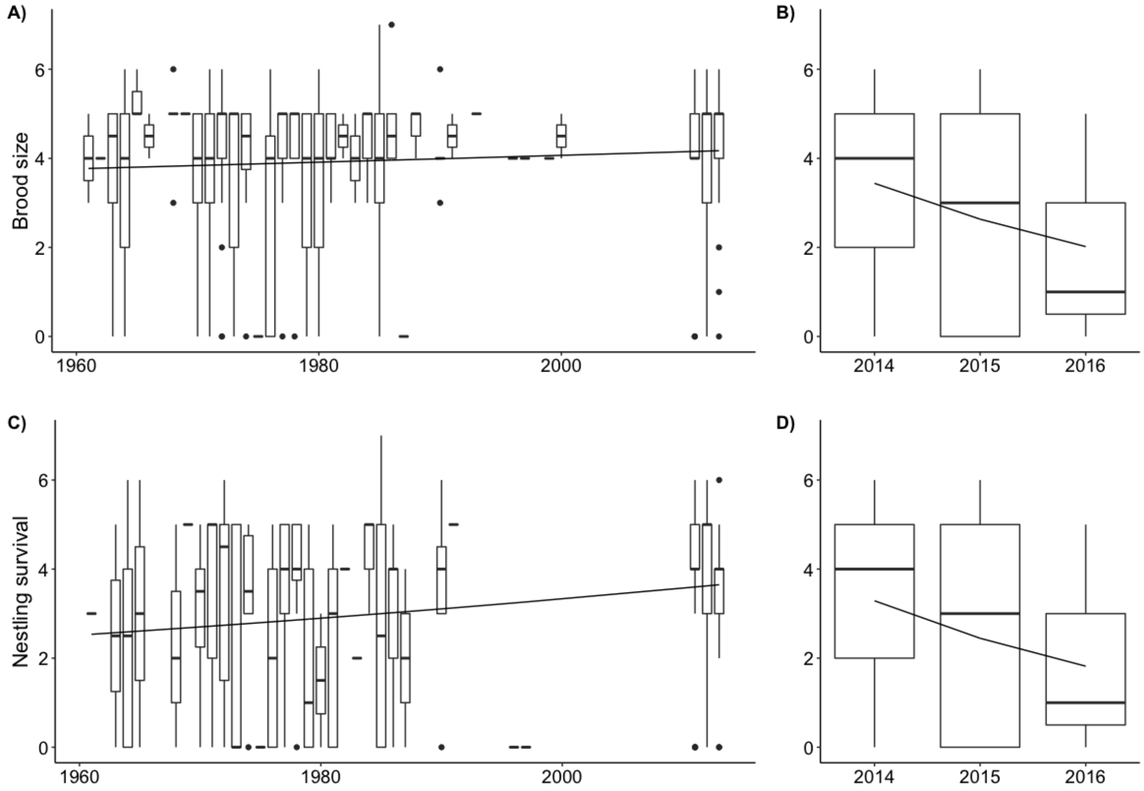

Figure A1. Relationships between Barn Swallow brood size (A, B) or nestling survival (C, D) and year for data from the Maritime Nest Records Scheme (A, C) and a long-term study (B, D). The decline in breeding performance during the long-term study was attributed to lower performance in 2016, compared to 2014 and 2015.

Appendix 3. Supplementary Material for Chapter 5

Isotope composition of rectrix and contour feathers

Recent research suggests that body molt for all three species may occur throughout the annual cycle (Imlay et al. 2017a), rather than just during the winter. Since my analyses of winter locations, migratory connectivity and fidelity relies of these feathers being molted during the winter, I used linear regressions to compare δ^2H in rectrix and contour feathers from the same individual for each of my three species. I considered the feathers were molted in the same location, if the relationship between δ^2H in rectrix and contour feathers was significant, and the slope was between 0.90 and 1.10.

For Bank Swallows, I found a significant relationship between δ^2H in contour and rectrix feathers ($p = 0.01$), however the slope was not within my acceptable limit (slope of 0.53) (Figure 1A), suggesting that these feathers were not consistently molted at the same location. For Barn Swallows, I found a significant relationship ($p < 0.001$) and a slope within my acceptable limit (slope of 0.91) (Figure 1B), suggesting that the feathers were molted at the same location. Finally, for Cliff Swallows, I did not find a significant relationship between δ^2H in rectrix and contour feathers ($p = 0.13$) nor was the slope within my acceptable limit (slope of 0.27) (Figure 1C), indicating that these feathers were not molted at the same location.

Although contour and rectrix feathers were not molted at the same location for Bank and Cliff Swallows, this does not preclude these contour feathers from being molted during the winter, especially since the values of δ^2H in contour feathers are consistent with isotope values throughout their wintering range (Bank: -124.94 to -19.49, Cliff: -124.94 to -19.90). Since swallows may move long distances during the winter (this study Figure 1, Fraser et al. 2017), potentially through isotopically dissimilar habitats, it is likely that, for these species, rectrix and contour feathers are molted at different winter locations. Therefore, I will use the contour feathers collected in 2014 to 2016 to examine winter locations, migratory connectivity and fidelity for all three species, after removing any samples that do not contain isotope values found within the wintering range of these species.

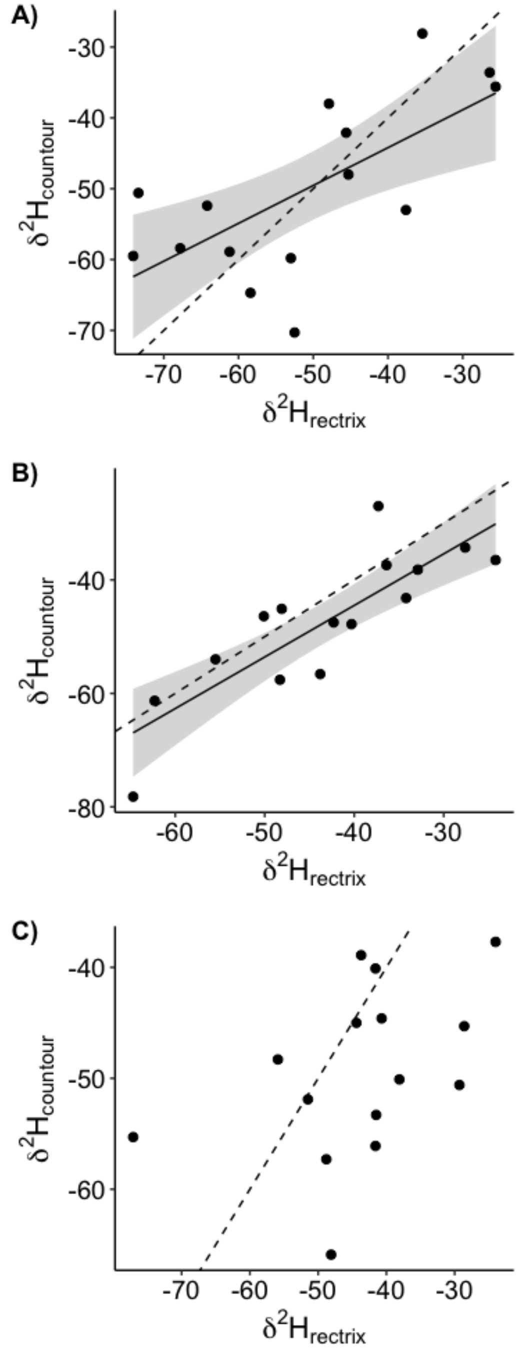

Figure A2. Relationships between δ^2H in contour and rectrix feathers from the same individual for Bank (A), Barn (B) and Cliff Swallows (C). Solid lines and grey areas indicate significant relationships ($p < 0.05$) and 95% confidence intervals between feather type, and dashed lines indicate the reference line with a slope = 1.0. N = 15 samples/species.

Appendix 4. Co-Authorship and Copyright

The following chapters are my own work, but they have been published with a number of co-authors whose contributions were invaluable to the final product. All co-authors gave permission for these papers to be included in this thesis. These contributions and licensing information are detailed below.

Chapter 2. Imlay TL, Mann H, Leonard ML. 2017. No effect of insect abundance on nestling survival and mass in Barn, Cliff and Tree swallows. Avian Conservation and Ecology **12**:19.

HRM assisted with data analysis and both HRM and MLL provided feedback on the manuscript. Under the publisher The Resilience Alliance, publications in the journal Avian Ecology and Conservation are covered under a Creative Commons BY-NC license.

Chapter 3. Imlay TL, Mills Flemming J, Saldanha S, Wheelwright NT, Leonard ML. 2018. Breeding phenology and performance for four swallows over 57 years: relationships with temperature and precipitation. Ecosphere **9**:e02166.

JMF assisted with data analysis, SS, NTW and MLL provided data, and all co-authors provided feedback on the manuscript. Under the publisher the Ecology Society of America, publications in the journal Ecosphere are covered under a Creative Commons BY license.

Chapter 5. Imlay TL, Hobson KA, Roberto-Charron A, Leonard ML. Winter locations, migratory connectivity and fidelity of three declining Nearctic-Neotropical migrant swallows. Animal Migration, *in review*. Manuscript # AMI-D-18-00001.

ARC assisted with analyzing geolocator data, and KAH provided access to R scripts used for the stable isotope assignment. All co-authors provided feedback on the manuscript.