

MIGRATORY CONNECTIVITY AND DIFFERENTIAL PATTERNS OF DECLINE IN
BARN SWALLOW (*Hirundo rustica*) IN NORTH AMERICA: POTENTIAL EFFECTS OF
FACTORS ON BREEDING AND WINTERING GROUNDS

A Thesis

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ABSTRACT

Populations of several Neotropical migratory bird species have experienced declines in the recent decades but long-distance migrant aerial insectivores seem to be declining at greater rates than any other group. The Barn Swallow (*Hirundo rustica*) is a long-distance migrant and an aerial insectivore whose breeding populations have declined drastically in northern regions of North America but remain stable in certain areas of the southern United States. However, reasons for differential population trends and whether factors on breeding and/or wintering grounds could be causing these declines remain unclear. The main objective of this study was to investigate causes of differential population dynamics experienced by Barn Swallows in North America by 1) studying patterns of migratory connectivity of populations using a three stable isotope approach ($\delta^2\text{H}$, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and 2) evaluating evidence for factors on breeding and/or wintering grounds causing regional differences in population trends.

Rectrix feathers (R1) of Barn Swallow grown on the wintering grounds were collected during breeding season in 2009, 2010 and 2011 across the breeding range of the species. Feathers were examined isotopically ($\delta^2\text{H}$, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and used to determine the relative strength of migratory connectivity of populations and to identify approximate wintering regions in South America. Long-term mark-recapture data from two breeding colonies in Washington State and Ontario were compared to the Southern Oscillation Index (SOI) for breeding and wintering months as a measure of El Niño Southern Oscillation (ENSO) to study the fundamental effect of large-scale climatic conditions on annual survival rates. Similarly, long-term reproductive parameters (i.e. fledging success, total number of eggs laid, chicks per nest) of breeding individuals in Washington State and Manitoba were used to determine the effects of local weather variation on reproductive performance. Winter-grown feathers grouped according to

population trends were additionally analyzed for corticosterone (CORT) concentrations to test whether declining northern populations have higher exposure to stressors on their wintering grounds.

Stable isotope ($\delta^2\text{H}$, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) analyses revealed evidence for a diverse pattern of migratory connectivity among breeding populations of Barn Swallow. Four isotopically distinct clusters corresponding to different wintering regions were identified and a progressive longitudinal shift in wintering grounds was detected. For stable and/or increasing populations in southern US, at least half of the entire population occupy areas in north-eastern South America. In contrast, a large proportion of individuals breeding in declining populations overwinter in western and central South America, suggesting that regions in north-eastern South America may be better quality habitats than those in western and central South America. This study found evidence for a differential effect of ENSO-related weather conditions on inter-annual survivorship of two different breeding populations of Barn Swallows in North America. Annual survivorship of Barn Swallows breeding in Washington State was strongly correlated to ENSO during breeding and wintering months, while no correlation was found for birds breeding in Ontario, potentially due to the geographical variation of the effect of ENSO on weather conditions across North America and South America and the differential degree of migratory connectivity of populations. The length of cold periods (total number of consecutive days (≥ 2 d periods) with maximum daily temperatures lower than 11°C) was found to have also a strong effect on annual survival rates of birds breeding in Washington State but not in Ontario. Annual reproductive performance was significantly affected by environmental conditions early in the breeding season related to ambient temperature, while precipitation variables had little effect. However, no significant decrease in reproductive success over time was noted, suggesting that

population declines might not be related with a decrease in reproductive performance modelled based on weather conditions. Wintering ground stressors related to CORT seem to have no significant effect on population size changes, since feather-CORT levels from declining populations were similar to those from stable populations.

This study is the first to provide information on wintering origins of North American Barn Swallows using stable isotopes and to identify factors occurring on breeding and/or wintering grounds that could have an effect on population trends of the species. Further work to understand the profound declines of Barn Swallows and of aerial insectivores should attempt to increase knowledge on winter habitat requirements of the species, as well as to study temporal patterns of change of weather conditions (i.e. La Niña events and extensive cold weather periods early in the spring) and the potential correlation of these changes with the existed patterns of decline.

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CHAPTER 1 GENERAL INTRODUCTION

Several populations of Neotropical migratory avian species have experienced dramatic declines in the last few decades in North America (Terborgh 1989, Askins et al. 1990, Finch 1991, Terborgh 1992, Rappole and McDonald 1994, Peterjohn et al. 1995, Sauer et al. 2011). Aerial insectivores, birds that feed exclusively on aerial insects year around, are experiencing among the greatest decline rates of any bird group. (Bohning-Gaese et al. 1993, Cadman et al. 2007, McCracken 2008, Bird Studies Canada et al. 2012, NABCI Canada 2012). Recent studies have shown that this decline seems to be greater for populations located in the north and northeast of their breeding range. In addition, a stronger pattern of decline has been noticed for long-distance migrants that travel longer distances to their wintering grounds in Central and South America in contrast to short-distance migrants that winter in southern US (Nebel et al. 2010).

1.1. Potential factors of decline for aerial insectivores

In North America, aerial insectivores include nightjars (family Caprimulgidae), swifts (family Apodidae), some flycatchers (family Tyrannidae), martins and swallows (family Hirundinidae) (Sibley 2000). All species of this group feed on flying insects, but they differ in foraging behavior, nesting habitat, and wintering locations. For instance, dominant forage habitat for swifts, martins and swallows are usually open areas in proximity to rivers, lakes and wetlands, while nightjars and flycatchers prefer woodland clearings. Nightjars usually nest on leafy of gravely soils, while flycatchers build cup-shape nests in trees, and swift, martins and swallows prefer man-made structures such as boxes, chimneys and building's walls to place their nests (Poole 2005). In addition, some species are long-distance migrants that migrate to warmer

latitudes in southern South America; while others travel shorter distances to winter in southern North America and the Caribbean.

Potential factors underlying declines for aerial insectivore populations are highly diverse, ranging from 1) habitat loss due especially to human activities, 2) habitat degradation, caused by increase of predation rates, scarcity of food supplies and higher incidence of diseases and ectoparasites, 3) changes in weather patterns, 4) exposure to environmental contaminants, and 5) persecution.

1.1.1. Habitat loss

Human activities centered on the extraction of natural resources have increased dramatically in recent decades. Additionally, development and intensification of agriculture has resulted from conversion to more modern farming techniques. For instance, these transformations have affected the amount of open-grasslands used for foraging (Evans et al. 2007). Mixed livestock and crop farming has been documented to have a positive association with reproductive success of Barn Swallows (*Hirundo rustica*) in Europe, and the reductions of these activities could be another potential reason for their decline in North America (Ambrosini et al. 2002, Gruebler et al. 2010). Flycatchers and nightjars are affected by changes in composition and structure of forests and native grasslands (DeGraaf and Yamasaki 2003, COSEWIC 2007). The replacement of old-style structures such as chimneys, flat-gravel roofs, barns or other buildings have reduced the availability of artificial nest sites for certain species like Barn Swallow, Chimney Swift (*Chaetura pelagica*), Common Nighthawk (*Chordeiles minor*) and Cliff Swallow (*Petrochelidon pyrronota*), and have been suggested as a main potential factor for the decline of these species (Brigham et al. 2001, COSEWIC 2011, COSSARO 2011). However, the extent to which a decrease in availability of nesting sites is limiting aerial insectivore populations remains unclear,

since a large number of suitable structures that were previously used by these species in the past remain unoccupied today.

1.1.2. Habitat degradation

1.1.2.1. Predation

Abundance of predators could have important negative effects on the total number of individuals of a population (Thompson 2007, Rogers 2011). High predation rates in the breeding grounds was initially thought to have a significant impact in population declines of many number of insectivorous species of passerines in North America during 1968 to 1987 (Bohning-Gaese et al. 1993). However, follow-up studies have revealed that the situation may be more complex and predation may not play such an important role in the population dynamics of this group (Sauer et al. 1996).

1.1.2.2. Food availability

Reduction in food availability is a limiting factor for bird populations (Martin 1987, Boutin 1990) since abundance of insects correlates with reproductive success of a large number of songbirds species (Strehl and White 1986, Rodenhouse and Holmes 1992, Marshall et al. 2002). This factor might be essential in the understanding of aerial insectivore population trends, since all declining species of this group share the main characteristic of feeding exclusively on flying insects (SCOC Committee 2009). The main potential factors that could be affecting prey availability are 1) increases in frequency and/or intensity of cold weather periods during spring in the northern portion of the breeding range, 2) the mismatch in the timing of insect emergence and reproduction due to changes in weather patterns, and 3) large scale declines of aerial insect populations due to extensive use of pesticides, which will be explained in more detail in section 1.1.4.

1.1.2.2.1. Cold weather periods

Aerial insectivorous migrants are especially vulnerable during cold weather periods because cold temperatures reduce aerial insect activity (Newton 2007). If cold weather periods become more frequent and prolonged, the amount of prey available for aerial insectivores could be considerably reduced (Taylor 1963). This lack of food will affect adult survival (Ligon 1968, Whitmore et al. 1977), but could especially influence body condition of young and their survival to independence (Gardarsson and Einarsson 1997, Bize et al. 2007) and potentially affect population sizes.

1.1.2.2.2. Insect emergence and reproduction mismatch

Vertebrates have evolved to synchronize periods of highest food demands from their young with the peak season of food abundance to maximize their reproductive output (Perrins 1970). In the case of aerial insectivores, the abundance of flying arthropods at the time of maximum food requirements of their young will be a crucial determinant of reproductive success. Warmer spring temperatures over the past decades have modified the breeding phenology of a wide variety of organisms, such as birds, amphibians, and insects (Beebee 1995, Crick and Sparks 1999, Bartomeus et al. 2011). In the case of birds, studies have reported an advance in egg-laying dates for many avian species due to an increase in global average temperature (Walther et al. 2002, Root et al. 2003). However, certain avian species appear unable to adapt to spatial and temporal changes in food resources and tend not to modify their migration and breeding phenology. Therefore, even if the abundance of insects remain stable at a breeding location over the years, this mismatch effect could potentially reduce the productivity of aerial insectivores and increase their mortality rates, with a consequent negative effect to their populations (Visser et al. 1998, Visser et al. 2006, Gaston et al. 2009) .

Several studies have suggested that long-distance migrants might have more difficulties to adapt their breeding and migratory phenology to recent changes in average temperature (Berthold et al. 1998, Faaborg et al. 2010, Jones and Cresswell 2010), and, those species seem to exhibit a greater population decline than short-distance migrants (Nebel et al. 2010). For instance, a comparison study of the short-distance migrant Dalmatian Pelican (*Pelecanus crispus*) and the long-distance migrant Great White Pelican (*Pelecanus onocrotalus*) in Europe has recently suggested that the Dalmatian Pelican has showed a rapid advancement in laying dates due to warmer temperatures over the last two decades, while Great White Pelican exhibited no change, and this could potentially have negative consequences to population size of the long-distance species (Doxa et al. 2012).

Timing of migration for short- and long-distance migrants is controlled by endogenous circannual mechanisms (Berthold 1984, Wikelski et al. 2008). Theoretically, short-distance migrants might be able to adjust their timing of migration more effectively in response to changes in local climate than long-distance migrants, since they winter closer to the breeding grounds and conditions on these wintering-locations might be more correlated with those on breeding areas. In contrast, the cues used for long-distance migrant species to migrate do not necessarily relate to conditions at their breeding areas. Therefore, long-distance migratory birds are more likely to experience a mismatch in peak food abundance for their young and might be more extensively affected by changes in climate (Visser et al. 2004). An example of the negative effect of mistiming of food availability and reproduction on an aerial insectivore is the case of the Pied Flycatcher (*Ficedula hypoleuca*) breeding in Europe (Both and Visser 2001). This long-distance migrant has not changed its arrival date on the breeding grounds over the years and some populations have declined by about 90% in the last twenty years due to a mismatch in

timing of food peaks (e.g. caterpillars) for nestlings early in the season. In contrast, Tree Swallow (*Tachycineta bicolor*), a short-distance migrant breeding in North America whose populations are relatively stable, have adjusted their breeding phenology to warmer temperatures over a 40-year period and egg-laying dates have advanced by an average of nine days in some areas of its range (Dunn and Winkler 1999). Despite these findings, other studies have found little evidence for shifts in breeding phenology (Barrett 2002) or have shown the opposite pattern for short and long-distance migrants (Jonzén et al. 2006). Clearly, the phenomenon of breeding phenology changes due to variation in climate is not always so explicit, possibly due to differences among species and inconsistent temperature trends around the world.

1.1.2.3. Diseases and parasites

Environmental changes in recent decades such as changes in weather patterns, loss and alteration of habitat, and environmental pollution have likely promoted disease emergence and ectoparasitism by forcing pathogens and parasites into new ecological niches and facilitating their establishment or transmission (Holmes 1996). Communal breeding is an attribute shared by many species of aerial insectivores, especially in the swallow family, that presents some potential costs and benefits for the species (Alexander 1974). Aggregation during breeding is usually associated with the reuse of old nests from previous breeding seasons with the consequent cost for the individuals due to higher loads of ectoparasites and higher probability of contracting infectious diseases. These diseases can reduce fecundity rates of adults, as well as survival and body condition of young (Moss and Camin 1970, Brown and Brown 1986, Shields and Crook 1987, Szép and Møller 1999). In the case of West Nile virus, avian influenza, avian cholera or avian tuberculosis, they have the potential to cause rapid declines in bird populations by increasing adult and chick mortality rates (Hochachka and Dhondt 2000, Lachish et al. 2011).

Therefore, infectious diseases could be an especially important factor limiting aerial insectivore populations.

1.1.3. Change in weather

Local weather as well as regional climate patterns may strongly influence avian population dynamics (Sæther et al. 2006). Weather conditions during the non-breeding season often affect population sizes mainly through a weather-dependent loss of individuals. Møller (1989) found that winter mortality during migration or in the wintering grounds was mainly related to environmental factors encountered on the wintering grounds and was the main cause of a population size reduction of Barn Swallows breeding in Denmark. In addition, Baillie and Peach (1992) reported that losses of individuals between fledging and the following breeding season was primarily due to weather conditions on wintering grounds and correlated strongly with population changes for several species of passerines.

Weather during the breeding season can also directly affect survivorship and subsequent breeding densities if they encounter unseasonable cold periods, storms or other severe weather events (Blake et al. 1992, Newton 2007). Individuals with higher body condition usually arrive earlier in the season and benefit from occupying better territories which usually enhance their reproductive success (Møller 1994, Kokko 1999). However, the major cost of early arrival is a high probability of encountering adverse weather conditions (Møller 1994, Newton 2007). For aerial insectivore species, cold snaps and heavy precipitation periods early in the breeding season are one of the major causes of mortality, especially for swallows (Whitmore et al. 1977, Brown and Brown 1998, Brown and Brown 1999b, Brown and Brown 2000). In addition, prolonged periods of precipitation and cold temperatures could be problematic to birds indirectly since they have been previously linked to a reduction of incubation time, more extended incubation periods requirements, and reduction of immune system activity (Lifjeld et al. 2002, Ardia et al. 2010).

1.1.4. Environmental contaminants

1.1.4.1. Direct effect

Persistent organochlorine pesticide contamination has been implicated as a cause for the decline in populations of Neotropical migratory birds in recent decades (Mora 1997, Klemens et al. 2000). Pesticides such as organochlorines (OCs) and polychlorinated biphenyls (PCBs), which accumulate in animal tissues and biomagnify in food chains, were extensively used in North America in the 1950's and 1960's. Although these compounds have since been restricted, their negative effects still persist in the environment (Gard and Hooper 1995). These effects could be especially important in the case of aerial insectivorous birds, since they feed on aerial insects and could therefore directly ingest the compounds that their prey have accumulated (Klemens et al. 2000).

In North America, OCs were largely replaced by a new generation of pesticides such as organophosphorus (OPs) and carbamates, which degrade faster in the environment. However, these compounds are more toxic and are known to be responsible for important bird population declines in North America and Europe (Newton 2004, Mineau et al. 2005). A clear example of their toxicity is the well-known case of the massive poisoning episode of Swainson Hawks (*Buteo swainsoni*) in the grasslands of Argentina due to the widespread use of an OP insecticide to control insect abundance (Goldstein et al. 1999). Despite such poisoning episodes, sublethal effects from constant exposure to OPs (i.e. dermal absorption and exhalation, contact with treated vegetation and poisoned insects, or direct ingestion), may also affect bird populations (Henny et al. 2010). Even if the amount of contaminant on their bodies might not be enough to directly kill them, contaminant exposure could affect avian populations indirectly by reducing the survivorship, fecundity and fitness of their individuals. Contaminant exposure could modify the behavior of adults (Hart 1993, Bustnes et al. 2001) or affect the endocrine system of

nestlings and reduce growth rate (Powell and Gray 1980, Colborn et al. 1993), with a consequent detrimental effect on adult reproductive success (Ratcliffe 1967, Henny et al. 2010).

Migratory birds are potentially more widely exposed to environmental contaminants since their migratory movements allow them to encounter these substances on their breeding and wintering areas, as well as during migration (Gard et al. 1993). The specific use of OCs, OPs and PCBs in Central and South America is not well known but they are likely extensively applied across those regions (Lacher and Goldstein 1997), suggesting that Neotropical migrants could be also exposed to these compounds on their wintering grounds (Gard and Hooper 1995).

1.1.4.2. Effect on insect populations

The use of pesticides in agricultural or forested areas may have reduced the abundance of aerial insects (Scott-Dupree et al. 2009, Van Dijk 2011) and could have affected populations of aerial insectivores indirectly. These effects are more difficult to detect but have been seen in insectivorous species such as woodpeckers (family Picidae) that forage in bark beetles (Morrissey et al. 2008) and species of the family Emberizidae (Brickle et al. 2000, Hart et al. 2006). For aerial insectivores, the use of mosquito-control agents has been correlated with a reduction in clutch size and fledgling survival of House Martins (*Delichon urbicum*) in France due to a decrease in food intake by nestlings and an increase of adult foraging rates (Poulin et al. 2010). A recent study of Chimney Swifts revealed the negative influence of pesticide treatments on their diet (Nocera et al. 2012). The examination of a well-preserved guano deposit showed a clear shift in insect diet from Coleoptera to Hemiptera starting in the 1960's possibly due to the introduction of Dichlorodiphenyltrichloroethane (DDT) pesticides in North America and the associated decrease in beetle populations. More recently, the use of neonicotinoid insecticides have raised significant concern in the scientific community due to evidence of a connection to the honey-bee colony collapse disorder (CCD), which has dramatically reduced populations of

honey bees (Girolami et al. 2009, Maini et al. 2010, Lu et al. 2012). Therefore, these new group of insecticides should be considered carefully as a potential reason for the decline of aerial insectivores in North America due to its high toxicity for aerial insects and persistence in aquatic systems (Van Dijk 2011, Mason et al. in press).

1.1.5. Human persecution

Some species of aerial insectivores are associated with human activities during their breeding season, such as Barn Swallow, Cliff Swallow, Bank Swallow (*Riparia riparia*) and Chimney Swift. Barn and Cliff Swallows often use buildings to place their nests. Colonies of Bank Swallows occur in vertical banks or cliffs but also in human-made sites such as sand and gravel quarries and road cuts (Garrison 1999) and Chimney Swifts use chimneys as well as natural structures (Cink and Collins 2002). This close association with humans has beneficial and detrimental effects. For instance, despite their protection under the *Migratory Birds Convention Act, 1994* (CWS 1991), numerous episodes of colony-site destruction have been reported due to building demolitions, excavations of sand banks, and replacement of old chimney structures (Garrison 1999). Additionally, swallows and swifts are often considered a nuisance and their nests destroyed. Despite the potential implications of these practices, no studies focused on the effects of these disturbances on population trends have been addressed yet.

1.2. Migratory connectivity and seasonal interactions

In North America, migratory birds travel between temperate breeding regions to southern areas with more optimum conditions in response to seasonal changes in habitat suitability (Berthold 2001). These species usually spend five months of their annual cycle on their wintering grounds, four months in their breeding locations and approximately three traveling across these locations (Newton 2008). Populations of migratory birds are therefore influenced

over global spatial scales across their annual cycle by factors on their breeding grounds, wintering grounds and stopover sites (Sherry and Holmes 1995).

There are two main concepts related to annual migratory movements that can have a significant impact on the evolution, behavioral ecology and population dynamics of migratory birds. The first is the degree to which individuals breeding in the same areas migrate to the same wintering areas and vice versa known as “migratory connectivity” (Webster et al. 2002, Boulet and Norris 2006). The strength of this link determines how well populations are connected throughout the annual cycle by the migratory movements of their individuals. In populations with “strong connectivity”, the majority of individuals breeding in the same location spend the non-breeding season in the same wintering areas. In contrast, individuals from populations with “weak connectivity” migrate primarily to different wintering locations. In practice, populations tend to show a broad range of degree of connectivity across species and populations (Webster et al. 2002). The second concept is seasonal interaction whereby carry-over effects from previous seasons can affect subsequent events (Webster and Marra 2005). Thus, events and conditions in one part of their annual cycle can potentially have a negative or positive effect on the behavior and reproductive performance of migratory species at the individual level, as well as on their population dynamics (Webster et al. 2002). At the individual level, seasonal interactions can cause important variation in fecundity and annual survival (Norris and Taylor 2006). At the population level, carry-over effects can disturb population equilibrium and influence the per-capita reproductive rates in the following season, potentially leading to a population decline (Norris and Marra 2007). The magnitude of the effect of seasonal interactions on a population depends on the degree of connectivity of that population (Webster and Marra 2005). Therefore, determining the strength of migratory connectivity and seasonal interactions is essential to

address the potential causes for the widespread declines of aerial insectivores across North America.

To understand migratory connectivity and seasonal interactions, we need to link breeding and wintering areas used by populations of interest and track their migratory movements. However, tracking these movements is extremely challenging and has involved the application of numerous techniques over time, such as extrinsic and intrinsic markers (Boulet and Norris 2006, Hobson and Norris 2008). Geographic variation in plumage and morphology could be used as an extrinsic marker when morphotypes are geographically segregated. Marking of individuals using tags, aluminum or color bands have also produced valuable results since it provides exact information on the start and end points of migratory movements (King 2001, Amirault et al. 2006). However, the low recovery rates and the enormous marking effort necessary to obtain adequate data seriously reduce the value of these approaches. Radio transmitters and geolocator devices have proved to be useful in tracking migratory movements (Stutchbury et al. 2009b, Bächler et al. 2010, Bairlein et al. 2012, Mitchell et al. 2012, Stanley et al. 2012). However, sample size is usually reduced due to high costs and these devices can negatively affect the behavior and ecology of the species studied (Barron et al. 2010). The use of intrinsic markers to track migratory movements has considerably expanded in the last few years, primary due to various advantages over extrinsic markers. For instance, initial marking and subsequent recapture is not necessary, since every capture provides information on origin and less labor effort is required to obtain large sample sizes. This technique relies on the spatial distribution of intrinsic markers such as contaminants, parasites and pathogens, genetic markers, stable isotopes and trace elements to determine migratory origins of birds (Ricklefs et al. 2005, Smith et al.

2005, Boulet et al. 2006, Hobson and Wassenaar 2008, Poesel et al. 2008, Behrooz et al. 2009, Szép et al. 2009, Yogui and Sericano 2009, Chabot et al. 2012).

1.3. Stable isotope techniques

Stable isotopes are atoms of the same element that have different number of neutrons but the same number of protons. Stable isotope abundance of a given element in nature (δX) varies due to physical, biological and chemical transformations and it is usually expressed in delta (δ) notation as parts per mil (‰) as the ratio of the “heavy” and “light” isotopes of a sample (R_A) relative to the isotopic ratio of an international standard (R_S) following the equation:

$$\delta X = [(R_A/R_S) / R_S] * 1000 \quad (1.1)$$

Stable isotopes of natural elements such as hydrogen ($\delta^2\text{H}$), carbon ($\delta^{13}\text{C}$), nitrogen ($\delta^{15}\text{N}$), sulphur ($\delta^{34}\text{S}$) and strontium ($\delta^{87}\text{Sr}$) have been extensively used as intrinsic markers and have provided a key approach in the study of migratory connectivity (Hobson 1999a, Hobson and Wassenaar 2008). This methodology is based on the fact that organisms incorporate isotopic signals of local food webs and ambient water through their diet. Keratinous tissues are metabolically inert once synthesized and reflect the isotopic value of nutrients and ambient water at the specific growing location plus an isotopic discrimination resulting from the transformation of chemical elements along the food chain during nutrients intake and excretion (Wassenaar 2008). Movements of migratory birds can thus be tracked since birds moving among isotopically distinct areas during migration retain information of prior location in their feathers and other tissues (Hobson and Clark 1992, Hobson and Wassenaar 2008).

1.3.1. Hydrogen isotopes

Hydrogen isotopes are particularly useful for studies of avian migratory connectivity since $\delta^2\text{H}$ values of feathers are correlated with $\delta^2\text{H}$ values of precipitation at places where those feathers were grown and $\delta^2\text{H}$ in precipitation varies across continents (Hobson and Wassenaar

2008). Feather-precipitation calibration curves for $\delta^2\text{H}$ values have been created for different regions and avian groups to convert precipitation isoscapes into feather isoscapes accounting for the existent isotopic discrimination factor between feather and precipitation (Hobson and Wassenaar 2008, Clark et al. 2009, Hobson 2011). The recent integration of $\delta^2\text{H}$ -feather information and GIS techniques has made possible to create reliable depictions of probability of origin of avian species (Hobson et al. 2009a, Gonzalez-Prieto et al. 2011, Hobson et al. 2012d, Ofukany et al. 2012).

1.3.2. Carbon and nitrogen isotopes

Carbon and nitrogen isotopes are also commonly used in studies of migratory connectivity mainly to identify habitat uses (Marra et al. 1998, Wassenaar and Hobson 2000, Kelly et al. 2008). $\delta^{13}\text{C}$ values in nature are related to different photosynthetic pathways in C3, C4 and CAM plants, since C3 plants clearly discriminate against ^{13}C isotopes during fixation of CO_2 in photosynthesis and are ^{13}C -depleted relative to C4 and CAM plants, which tend not to discriminate so strongly against ^{13}C (Fry 2006, Marshall et al. 2007). In addition to differential photosynthetic pathways, isotopic variation in C3 plant tissues may also result from differences in water-use efficiency. To avoid water loss in dry environments, C3 plants reduce significantly the diffusion of CO_2 into their leaves, leading to an enrichment in ^{13}C during photosynthesis (Marshall et al. 2007). In combination with other isotopes, $\delta^{13}\text{C}$ values could also be used to distinguish inshore versus offshore (France 1995, Fry 2002, Sierszen et al. 2011) and marine versus freshwater environments (Nelson et al. 1989, Bearhop et al. 1999, Pruett et al. 2009). The natural abundance of $\delta^{15}\text{N}$ in leaves relies on a variety of factors such as photosynthesis, mycorrhizal fungi associations, climate, or the large variation in $\delta^{15}\text{N}$ values of soils due to land-use practices (Kelly 2000). Plant species associated with mycorrhizal fungi usually show lower $\delta^{15}\text{N}$ values (3 - 8‰) than non-mycorrhizal plants (Craine et al. 2009). At a local scale, foliar

$\delta^{15}\text{N}$ values seem to be correlated negatively with annual precipitation rates and positively with mean annual temperature (Austin and Sala 1999, Martinelli et al. 1999, Craine et al. 2009).

Variation in $\delta^{15}\text{N}$ values can also reflect the excess of nitrogen-based fertilizers input into the land and water system and has the potential to be used to infer levels of agricultural activity (Hobson 1999b, Hebert and Wassenaar 2001, Yerkes et al. 2008).

Despite their obvious usefulness, the application of stable isotope techniques for assignment of origins could be problematic due to the considerable isotopic variation among feather samples grown in same locations (Hobson 2005, Lott and Smith 2006, Hobson 2011) and the similarity in isotopic values of extensive geographical areas (Bowen et al. 2005). Recent studies have achieved the creation of feather origin depictions using a likelihood assignment methodology, which accounts for sources of variance in the isotope data and incorporate estimates of error (Royle and Rubenstein 2004, Van Wilgenburg and Hobson 2011). Recently, Hobson et al. (2012c) demonstrated that foraging substrate and migratory strategy are potential factors affecting the variance in the relationship between feathers and precipitation- $\delta^2\text{H}$ values among avian species. To account for the problem of low resolution of isoscapes (e.g. hydrogen) in some geographical areas of the globe, some prior information about the species could be used to constrain results of assignment of origin. For instance, some studies have used distribution maps of the studied species to delimit depictions of origin (Royle and Rubenstein 2004, Gonzalez-Prieto et al. 2011) or spatial information related to movement trajectories based on band recoveries (Van Wilgenburg and Hobson 2011, Hobson et al. 2012a). Others have constrained the analysis by previously excluding those individuals feeding in marine environments (Yerkes et al. 2008, Ofukany et al. 2012). Additionally, geographical distribution of $\delta^2\text{H}$, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$

has been recently used as a prior to assign individuals to more constrained origins (Hobson et al. 2012a, Hobson et al. 2012b).

1.4. Studied species

This thesis focuses on Barn Swallow, a long-distance migratory aerial insectivore that breeds throughout most of North America and winters primarily in South America and to a lesser extent in Central America (Figure.1.1 and Ridgely et al. (2007)). Barn Swallows have recently been reported breeding in Argentina during the boreal winter (Martinez 1983). This is the first known case of the species breeding in the Southern Hemisphere within its historical wintering range (Appendix A) and the population is expanding within that region (Billerman et al. 2011). The Barn Swallow is the most widely distributed swallow in the world. It is part of the family Hirundinidae and from six to eight subspecies are found in America, Europe, Africa, Asia and Oceania (Turner 2004, Zink et al. 2006). The species feeds while flying primarily on flies (Diptera), followed by beetles (Coleoptera), true bugs (Hemiptera), leafhoppers (Homoptera), and bees, wasps and ants (Hymenoptera) (Turner 1982, Brown and Brown 1999a, Turner 2004). On the breeding grounds, Barn Swallows associate with man-made structures where they have access to artificial nesting sites (Brown and Brown 1999a). They are usually found in agricultural lands, cities and suburbs up to 1000 m above sea level, and along highways near open areas such as lakes, meadows and fields where they can forage for insects (Turner and Rose 1989). During the non-breeding season, the species roosts communally with other swallow species in sugar-cane fields and open wetlands (Ridgely and Tudor 1989, Winkler 2006). Barn Swallows have a single complete annual molt that occurs shortly after arrival to their wintering grounds (Broekhuysen and Brown (1963), Pyle (1997) and Appendix B). As aerial insectivores, they rely on their flight ability to

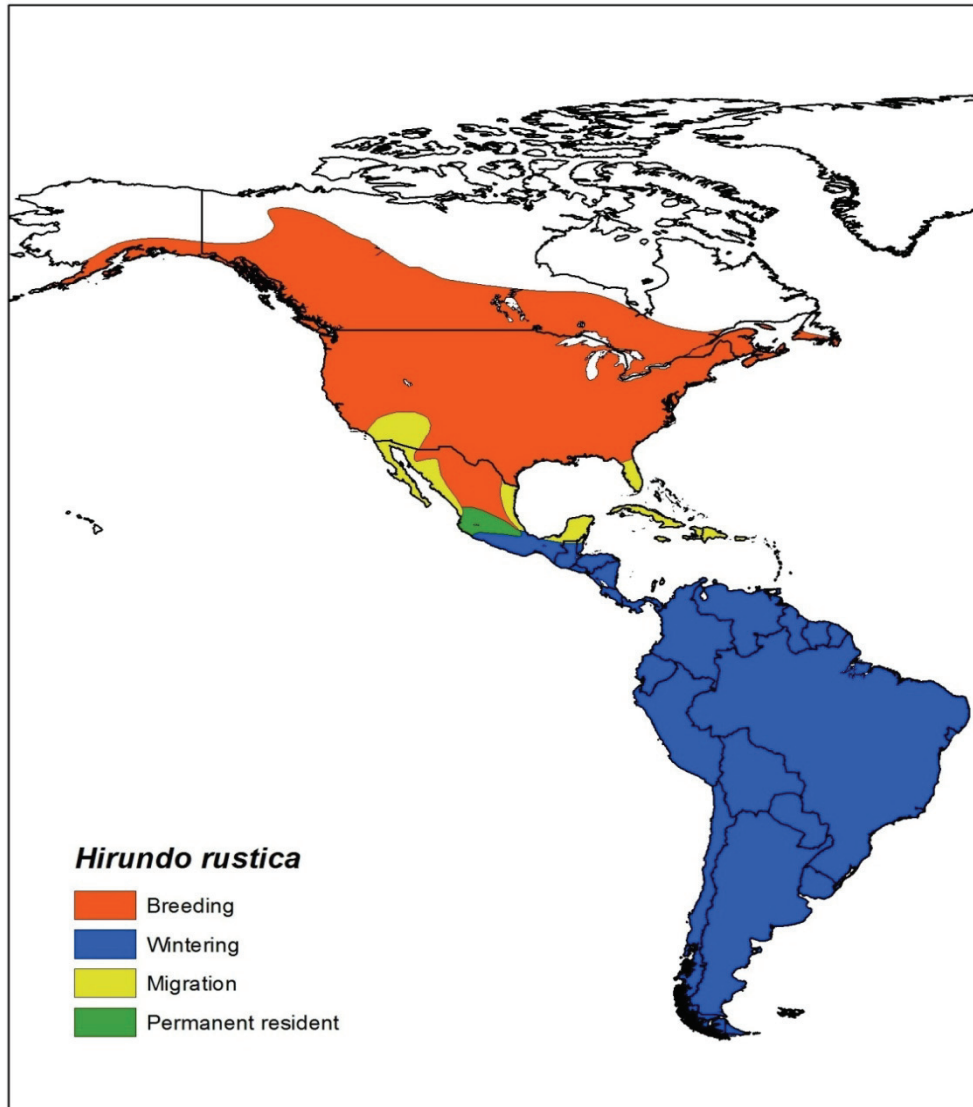


Figure 1.1. Distribution of Barn Swallow (*Hirundo rustica*) in the Neotropical system (Ridgely et al. 2007).

forage and molt flight feathers slowly and gradually presumably to maintain flight efficiency (Rohwer et al. 2005).

The Barn Swallow, despite its wide distribution and historical abundance, has decreased drastically in recent decades in most North America (Cadman et al. 2007, Nebel et al. 2010, Bird Studies Canada et al. 2012). Barn Swallow monitoring data from the Breeding Bird Survey (BBS) collected across North America during spring have shown that populations are in great decline in Canada and northern United States, while they remain stable or increasing in areas of southern United States (Sauer et al. (2011), Figure 1.2.). Results from Environment Canada suggest a clear pattern of decline for populations in Canada with an obvious increase in declining rates starting in the middle 80's (Figure 1.3A). In contrast, U.S. Geological Survey results, calculated based on hierarchical Bayesian models techniques (Link and Sauer 2002, Sauer and Link 2011) also imply a decline of Barn Swallow populations in Canada but without this clear threshold in population change (Figure 1.3B).

Recently, a similar approach using hierarchical Bayesian methods has been applied to the BBS data from the Canadian region and preliminary results suggest that aerial insectivore long-term declines might have extended over 40 years, while the occurrence of a greater decline starting in the middle 80's remains unclear (Adam C. Smith, EC-CWS, personal communication). At a global scale, the species is listed as *Least Concern* in the IUCN Red List of Threatened Species (BirdLife International 2012). In Canada, the reduction of at least 30% of the total number of mature individuals over the last ten years lead to the designation of Barn Swallow in May 2011 as a *Threatened* species (COSEWIC 2011) and to be classified as *Threatened* species in Ontario (COSSARO 2011).

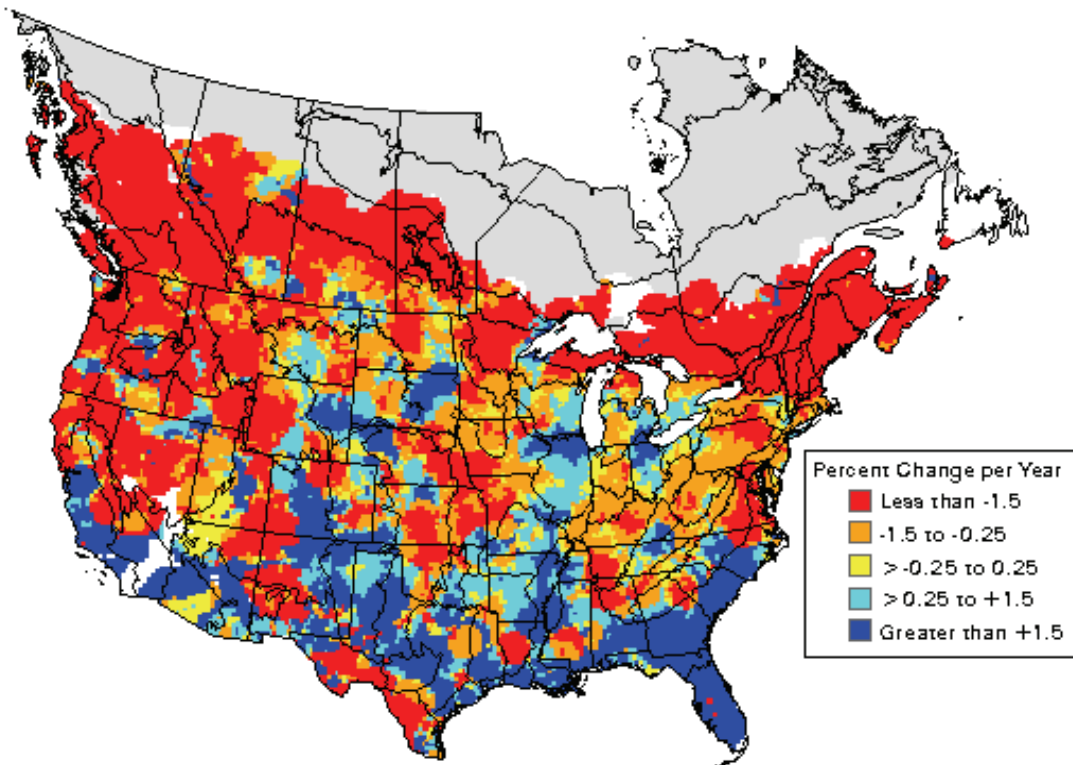


Figure 1.2. Map of geographic patterns of annual population change of Barn Swallow in North America from 1966 to 2010 based on long-term BBS data. Colors in the map represent percentage of population change per year (Sauer et al. 2011).

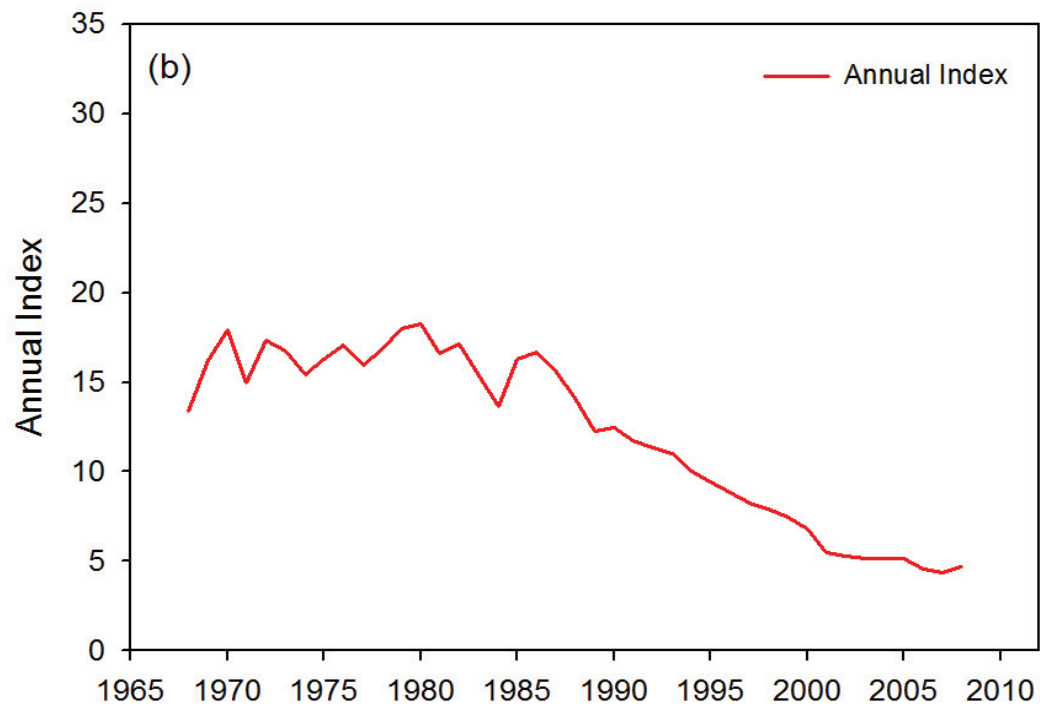
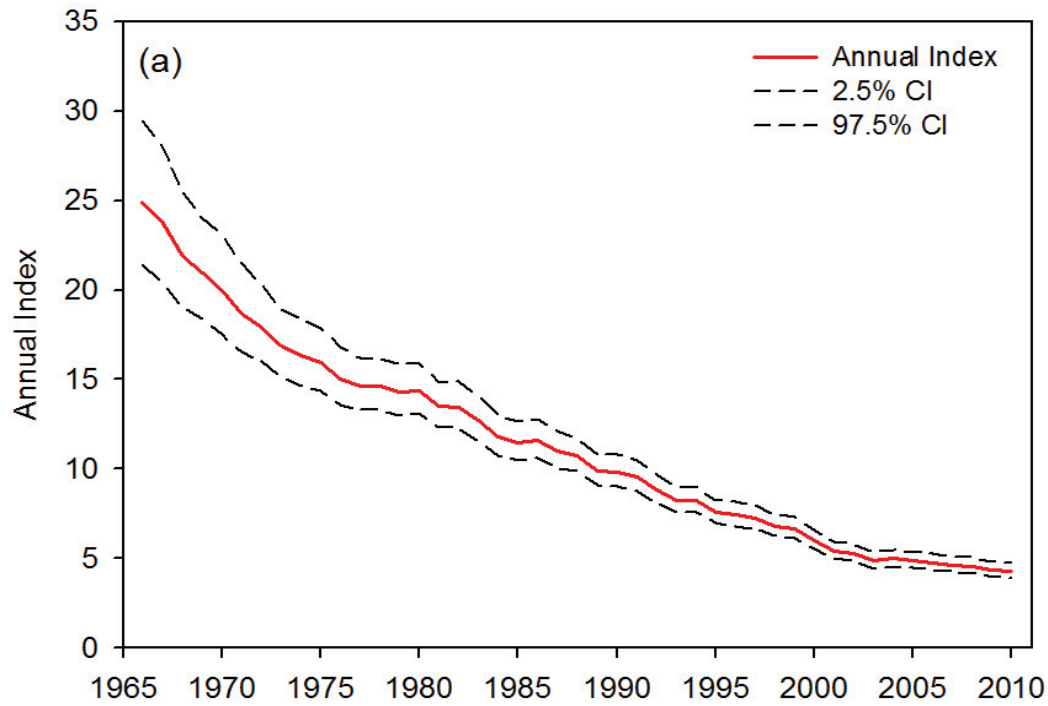


Figure 1.3. Annual population change index for Barn Swallow in Canada based on two different statistical methods: (a) data from 1966 to 2010 using the U.S. Geological Survey (USGS) approach and (b) data from 1968 to 2008 based on the Environment Canada (EC) approach.

1.5. Thesis outline

Barn Swallows have been declining in the northern part of their range, in Canada and northern US, while populations in the southern part (e.g. southern US) have remained relatively stable/increasing. Despite the fact that the overall breeding and winter ranges for the species are known, specific locations where individuals from different populations actually spend the winter and whether different breeding populations mix during winter remain unknown. The main objective of this thesis is to investigate potential causes of differential population trends experienced by Barn Swallows in North America. Potential differences in migratory connectivity between increasing and decreasing populations were examined to evaluate whether factors on the breeding or wintering grounds could be responsible for such differences. I hypothesize that decreasing populations may be influenced by more detrimental factors than increasing populations either on their breeding or wintering grounds. Individuals from declining populations could be carrying over negative effects from one season to the next one due to adverse conditions (i.e. habitat loss, change in weather conditions, environmental contaminants, habitat degradation) experienced during different stages of their annual cycle. In contrast, individuals from increasing populations may occupy more favorable areas (breeding or wintering) where conditions are not limiting populations.

This thesis is organized into 4 chapters and 3 appendices that are formatted for scientific journals except for Chapter 1, “Introduction”, Chapter 4, “Summary and synthesis” and Appendix C.

Chapter 2 (“Estimating wintering origins and migratory connectivity of Barn Swallow (*Hirundo rustica*) in North America: a multi-isotope approach”) addresses patterns of migratory connectivity of populations of Barn Swallow using $\delta^2\text{H}$, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measurements on feathers

and prior information based on distribution of the C3 and C4 vegetation on the wintering grounds. Additionally, it attempts to evaluate the effect of differential migratory connectivity on the distinct north-south population trend experienced by the species in North America. Feathers collected on the breeding grounds and grown on the wintering grounds were analyzed to identify potential areas of feather origin in the winter grounds (South America) based on feather-stable isotope values and existing knowledge of $\delta^2\text{H}$ and $\delta^{13}\text{C}$ isoscapes for that continent. It was hypothesized that birds breeding in northern declining populations migrate to different areas in South America compared to those of individuals from stable populations, and are therefore affected by different wintering conditions. Additionally, to compare $\delta^2\text{H}$ isotopic variation of a highly colonial migratory bird, Cliff Swallow (*Petrochelidon pyrrhonota*), relative to a less colonial Barn Swallow, a small sample of Cliff Swallow feathers were examined.

Chapter 3 (“Evaluation of possible factors occurring on breeding and wintering grounds influencing declines on breeding population of Barn Swallows (*Hirundo rustica*) in North America”) investigates factors on breeding and wintering grounds that could be playing a role in the differential decline of populations of Barn Swallows in North America.

The importance of weather conditions during breeding and non-breeding seasons on the apparent survival rates of Barn Swallow was evaluated by studying the effect of ENSO-related weather and the length of cold periods in the spring, which has been previously shown to have an effect on aerial insectivore species mortality rates. The effects of local climatic variation on the reproductive performance of Barn Swallow in North America were investigated by selecting the best model comprising weather variables having a significant effect on reproductive success. Long-term changes in reproductive success were additionally tested by generating predictions of antecedent reproductive rates of the species based on weather patterns. I anticipated that

reproductive performance of Barn Swallows has declined over time according to population declines experienced by the species. Barn Swallow feather-deposited corticosterone (CORT) concentrations were used to test for exposure to stressors on the wintering grounds. I hypothesized that stressors on the wintering grounds play an important role in the differential population trends shown by breeding populations of the species in North America. Therefore, higher feather CORT values for those populations in decline were expected when compared with values of stable populations. I additionally tested whether the specific breeding and wintering location of individuals and winter-habitat use could have an effect on their stress response based on $\delta^2\text{H}$, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values on winter-grown feathers.

Appendix A, “A multi-isotope ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, $\delta^2\text{H}$) approach to infer wintering location and habitat of the disjunct Argentinean breeding population of Barn Swallow (*Hirundo rustica*)”, focuses on identifying potential wintering areas of a population of Barn Swallows now breeding in the historic winter range of the species using a multi-isotope approach and prior information similarly to Chapter 2. Feathers grown prior to the breeding season and during breeding were analyzed for $\delta^2\text{H}$, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ to locate areas where feathers were grown to test for a potential switch in molt pattern and migratory behavior of individuals. Appendix B, “Molt in Barn (*Hirundo rustica*) and Cliff (*Petrochelidon pyrrhonota*) Swallows at a winter roost site in Argentina”, provides a first and detailed description of molt of Barn and Cliff Swallows in the early austral summer and reports an important wintering site for migratory swallows in Argentina. Appendix C shows the relationship between $\delta^2\text{H}$ values on tail and contour feathers $\delta^2\text{H}$ of Barn Swallows sampled from same individual, used in this study for feather samples collected in the states of New York and New Jersey.

CHAPTER 2. ESTIMATING WINTERING ORIGINS AND MIGRATORY CONNECTIVITY OF BARN SWALLOW (*Hirundo rustica*) IN NORTH AMERICA: A MULTI-ISOTOPE APPROACH

2.1. Introduction

Despite its wide distribution and historical abundance, Barn Swallow (*Hirundo rustica*) populations have decreased drastically in the recent decades within North America (Cadman et al. 2007, McGowan and Corwin 2008, Nebel et al. 2010, Bird Studies Canada et al. 2012). These trends appear to be characteristic of several aerial insectivores breeding in North America (SCOC Committee 2009, Nebel et al. 2010, NABCI Canada 2012). Worldwide, Barn Swallow is listed as *Least Concern* in the IUCN Red List of Threatened Species (BirdLife International 2012). In Canada, a decrease in the total number of adults of at least 30% of over the last ten years, has recently resulted in its designation as *Threatened* (COSEWIC 2011) and has been also classified as *Threatened* in Ontario (COSSARO 2011). Results from the Breeding Bird Survey (BBS) have shown most negative trends have occurred in Canada and the northern USA since 1968; while more southern breeding populations have remained stable or have increased (Sauer et al. 2011). Currently, factors responsible for differential population trends for Barn Swallows in North America remain unknown.

As a long-distance Neotropical migrant, Barn swallow spends much of the annual cycle at sites separated by thousands of kilometers and populations may be limited by factors occurring at breeding and wintering grounds and at stopover sites (Sherry and Holmes 1995, Newton 2008). Interaction among factors in different seasons may also occur, resulting in individuals carrying-over effects from previous seasons that could ultimately influence overall reproductive success and survival (Webster et al. 2002). For instance, birds occupying good quality wintering habitats can acquire appropriate physical condition for migration and will arrive earlier to their breeding

grounds, with a consequent benefit on reproductive performance (Marra et al. 1998, Norris et al. 2004). Saino et al. (2004) also found that environmental conditions on the African wintering grounds, as measured by the normalized difference vegetation index (NDVI), influenced first egg dates and clutch sizes of Barn Swallows breeding in Europe (see also Robinson et al. (2008), Ambrosini et al. (2011), Wilson et al. (2011)). In addition, Rockwell et al. (2012) recently showed that males of Kirtland's Warbler (*Setophaga kirtlandii*) arrived on breeding grounds later following drier winters and that total rainfall in the wintering grounds, delayed arrival and nest initiation were significantly associated with lower fledgling success in the species.

Deciphering the relative effects of factors influencing populations on wintering compare to breeding grounds can be enhanced by a knowledge of the strength of migratory connectivity (Webster et al. 2002). Strong connectivity between breeding and wintering populations suggests that most individuals from the breeding population will be influenced by similar factors on both breeding and wintering areas. In contrast, individuals in populations characterized by weak connectivity will typically be differentially affected by factors operating on the wintering grounds (Webster et al. 2002). Determining the strength of migratory connectivity between breeding and wintering populations is essential, then, to unravel changes in populations of Barn Swallow in North America, as well as to implement effective conservation strategies for the species (Webster et al. 2002, Rubenstein and Hobson 2004, Webster and Marra 2005 , Martin et al. 2007).

Determining the nature of connectivity for target populations of migratory birds requires the ability to track movements across the annual cycle and numerous extrinsic and intrinsic markers have successfully been used to track such movements (Boulet and Norris 2006, Hobson and Norris 2008). Recent studies have effectively applied radio transmitters and geolocator devices

to derive approximate migratory movements of relatively small species (Stutchbury et al. 2009b, Bächler et al. 2010, Bairlein et al. 2012, Mitchell et al. 2012, Stanley et al. 2012), but such markers necessarily have been applied to small numbers of individuals due to expense. In addition, all extrinsic markers can have negative effects on the behaviour of studied individuals (Barron et al. 2010). Spatial distributions of intrinsic markers such as contaminants, parasites, pathogens, genetics, trace elements and stable isotopes also have the potential to be used to track migration (Ricklefs et al. 2005, Behrooz et al. 2009, Yogui and Sericano 2009) and are typically unbiased by the choice of an initial studied population (Hobson and Norris 2008). However, intrinsic markers require an *a priori* understanding of the spatial distribution in nature of intrinsic markers and this has proven to be challenging.

Stable isotope measurements of animal tissues have been extensively used to track migratory movements of individuals to study migratory connectivity and seasonal interactions (Hobson and Wassenaar 1997, Marra et al. 1998, Hobson 1999a, Bearhop et al. 2004, Norris and Taylor 2006, Hobson et al. 2009a, Rohwer et al. 2011). This technique is based on the fact that isotopic ratios in animal tissues reflect those in local foodwebs and ambient water and such ratios can vary geographically in a predictable manner (Hobson and Wassenaar 2008). Keratinous tissues, such as feathers, are especially useful since they are metabolically inert once synthesized and reflect the isotopic value of nutrients and ambient water at time of growth (Wassenaar 2008). Spatial patterns of the water isotopes ($\delta^2\text{H}$ and $\delta^{18}\text{O}$) in particular have proven useful to create “isoscapes” of expected feather values at continental scales (West et al. 2010). Recently, plant- $\delta^{13}\text{C}$ isoscapes based on predictions of the distribution and relative abundance of C3 and C4 vegetation have also been established for Africa (Still and Powell 2010) and South America (Powell et al. 2012). Similarly, Craine et al. (2009) has provided a global theoretical plant- $\delta^{15}\text{N}$

isoscape. These developments have led to attempts to simultaneously combine isoscapes based on several elements (Hobson et al. 2012a, Hobson et al. 2012b, Hobson et al. 2012d). In South America, the distribution of $\delta^2\text{H}$ in amount-weighted mean growing season precipitation shows a structure with the potential to be used in identification of origins of winter-grown feathers (Bowen et al. 2005). In addition, there is significant structure in the distribution of plant $\delta^{13}\text{C}$ values to potentially increase the resolution of assignments based upon $\delta^2\text{H}$ measurements (Powell et al. 2012).

Here, I investigated the strength of migratory connectivity between North American breeding and South American wintering populations of Barn Swallow and whether connectivity could be a potential factor for the north-south differential population trend shown by the species in North America. If factors on the wintering grounds are responsible for differential population trajectories of Barn Swallows in North America, breeding populations in the northern part of the breeding range were expected to differ in their feather-stable isotope values from breeding colonies in the south. Individuals were additionally assigned to wintering regions in South America, independently of their breeding location, to identify any geographical structure in wintering origin. Finally, $\delta^2\text{H}$ values of feathers for a smaller sample of Cliff Swallows (*Petrochelidon pyrrhonota*) were examined in order to contrast isotopic variation for this highly colonial species compared to the less colonial Barn Swallow. A stronger pattern of connectivity for more colonial Cliff Swallows relative to Barn Swallows was predicted.

2.2. Methods

2.2.1. Sample collection

Adult Barn Swallows were captured using mist-nets during the breeding seasons (May to late August) of 2009, 2010 and 2011 at eight sites where swallows were declining (British Columbia, California, Quebec, Manitoba, New York State, Ontario, Saskatchewan, and Washington State)

and at five sites where they were stable or increasing (Alabama, Colorado, Mississippi, New Jersey, and Texas) (Figure 2.1.). All birds were banded using USFWS aluminum bands and sex, age and body measurements (wing length, tail length and weight) were recorded following the North American Banding Council guidelines (NABC 2001). One inner tail feather grown in the wintering grounds (Pyle 1997) was collected for each bird for stable isotope analyses and stored in labeled paper envelopes. For locations in New York and New Jersey, five or six contour feathers were collected. Both types of feathers (tail and contour feathers) were used for stable isotope analyses based on the linear relationship found between $\delta^2\text{H}$ values of tail and contour feathers (Appendix C), which support the occurrence of a complete molt of flight and contour feathers in the wintering grounds (Pyle 1997). Adult Cliff Swallows were also captured in 2010 and 2011 in four breeding colonies located in Manitoba ($n = 76$), Ontario ($n = 73$), Nebraska ($n = 134$) and Texas ($n = 10$) and feathers grown in the wintering grounds were collected (Pyle 1997). Federal banding and collection permits for Canada and the US were obtained through the Bird Banding Laboratory part of the North American Bird Banding Program. All field protocols were approved by the University of Saskatchewan Animal Research Ethics Board and followed the guidelines of the Canadian Council on Animal Care.

2.2.2. Stable isotope analyses

Feather samples were cleaned of surface oils using a 2:1 (v/v) chloroform/methanol soak for 24 hours and dried at room temperature under a fume hood for 48 hours. Samples were prepared and analyzed for stable isotope analyses ($\delta^2\text{H}$, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in the National Hydrology Research Centre of Environment Canada in Saskatoon, Canada. A total of 644 Barn Swallow feather samples were analyzed for $\delta^2\text{H}$ involving the subsampling of 0.35 ± 0.02 mg of feather material collected from the right side of the feather tip and weighed into silver capsules. Additionally, 405 feathers were analyzed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, and approximately 1 mg of feather



Figure 2.1. Sampling sites in North America where Barn Swallow feathers were collected during breeding season of 2009, 2010 and 2011.

tissue was collected from the left side of the tip of the feather and loaded into tin capsules. A total of 293 Cliff Swallow feather samples were also analyzed for $\delta^2\text{H}$ using the same methodology explained above.

Stable-hydrogen isotope measurements in Barn and Cliff Swallow feathers were performed on H_2 derived from high-temperature flash pyrolysis (1350°C) of feathers using a Eurovector elemental analyzer (Milan, Italy - www.eurovector.it) interfaced with an Elementar IsoprimeTM (Isoprime Ltd., Cheadle, Stockport, UK) continuous-flow isotope-ratio mass spectrometer (CFIRMS). Analyses of $\delta^2\text{H}$ were conducted using the comparative equilibration method described by (Wassenaar and Hobson 2003) using three calibrated keratin isotope reference materials corrected for linear instrumental drift: Caribou Hoof (CBS: $-197\text{‰} \pm 1.8\text{‰}$), Kudu Horn (KHS: $-54.1\text{‰} \pm 0.6\text{‰}$) and a commercial keratin powder standard (Spectrum: $-121.6\text{‰} \pm 1.9\text{‰}$). Feather samples were analyzed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ at the Department of Soil Science Laboratory, University of Saskatchewan, Saskatoon, using a Costech ECS4010 elemental analyzer (Costech Analytical Technologies Inc. Valencia, California) coupled to a Delta V Advantage mass spectrometer with Conflo IV interface (Thermo Scientific. Bremen, Germany). Two reference materials were used to calibrate $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ results, Bowhead Whale Baleen Keratin (BWB-II: $\delta^{13}\text{C}=-18.50\text{‰}$, $\delta^{15}\text{N}=14.22\text{‰}$) and an egg albumen ($\delta^{13}\text{C}=-23.57\text{‰}$, $\delta^{15}\text{N}=6.24\text{‰}$). All isotope measurements were reported in the delta (δ) notation as parts per mil (‰) relative to Vienna Standard Mean Ocean Water – Standard Light Antarctic Precipitation (VSMOW-SLAP) for $\delta^2\text{H}$, Vienna Standard PeeDee Belemnite (PDB) for $\delta^{13}\text{C}$, and atmospheric nitrogen (AIR) for $\delta^{15}\text{N}$. Within-run analytical precision was estimated as $\pm 0.2\text{‰}$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, and $\pm 2.2\text{‰}$ for $\delta^2\text{H}$.

2.2.3. Statistical analyses

An Analysis of Variance (ANOVA) was applied to identify differences in feather mean $\delta^{13}\text{C}$, $\delta^2\text{H}$ and $\delta^{15}\text{N}$ values independently for all breeding populations of Barn Swallow followed by a post-hoc Tukey-test to compare isotopic differences among specific populations. Stable isotope results from ten breeding locations ($n = 405$), for which feather values for $\delta^{13}\text{C}$, $\delta^2\text{H}$ and $\delta^{15}\text{N}$ were available, were analyzed using a three-dimensional k-means clustering analysis (Hartigan 1975) to arrange individuals into groups based on similarities in stable isotope profiles. This method assigns each case (i.e. feather sample) to a cluster by minimizing the “Euclidean distance” from the case to the corresponding cluster centroid and requires *a priori* specification of the number of clusters into which the samples will be placed. Two main criteria were used to determine the number of clusters that best reflected natural groupings in the data. First, an exploratory agglomerative hierarchical clustering analysis was used employing Ward’s criterion. Second, four sets of potential clustering centroids ($k = 2-5$) were selected and k-means clustering analysis was applied for the four selected sets. The validity of each of the four sets was assessed based on significant differences among centroids by performing a multivariate analysis of variance (MANOVA) for the three isotopes ($\delta^2\text{H}$, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in each set. The k-means clustering solution which maximized the number of centroids while maintaining also statistically significant multivariate ($\delta^2\text{H}$, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) differences in the cluster means was selected. The final selection of four clusters to be applied in the k-means cluster analysis was based on the greatest consistency between results from both hierarchical and MANOVA analyses. All statistical analyses were performed using IBM SPSS Statistics 19.0.0.

2.2.4. Assignment of feather origins

Feather samples grown in the wintering grounds ($n = 405$) were clustered in four groups (G1: $n=38$; G2: $n=111$; G3: $n=154$ and G4: $n=102$) and these were assigned as putative wintering-

origins in South America using normal probability density functions (Royle and Rubenstein 2004, Hobson et al. 2009b, Van Wilgenburg and Hobson 2011) to assess the likelihood that the observed data ($\delta^2\text{H}_f$) could have resulted from growth at given locations within the $\delta^2\text{H}$ isoscape of (Bowen et al. 2005) and prior information about the distribution of C3 and C4 plants in South America (Powell et al. 2012) following methodology described in (Hobson et al. 2009b).

A raster surface of the amount-weighted mean precipitation $\delta^2\text{H}$ isoscape ($\delta^2\text{H}_p$) for South America for growing season months (Bowen et al. 2005) was used as a proxy of distribution of $\delta^2\text{H}$ values in rainfall in the continent. To limit the analysis to regions within the wintering range of the species, areas higher than 3,000 meters above sea level were removed from the isoscape (Brown and Brown 1999a). The empirical equation:

$$\delta^2\text{H}_f = -17.57 + 0.95 \delta^2\text{H}_p \quad (2.1)$$

reported for non ground-foraging Neotropical migrants (Hobson et al. 2012c) was applied to convert the altitude clipped $\delta^2\text{H}_p$ isoscape to an equivalent feather $\delta^2\text{H}$ ($\delta^2\text{H}_f$) isoscape. The expected standard deviation (σ_c) between individuals growing their feathers at the same locality for $\delta^2\text{H}$ ($\sigma = 14.4\text{‰}$) was estimated using the standard deviation of the residuals from the same regression equation reported by Hobson et al. (2012c). To depict the probable molting origins of individuals, a normal probability density function:

$$f(y^*|\mu_c, \sigma_c) = \left(\frac{1}{\sqrt{2\pi}\sigma_c}\right) \exp\left[-\frac{1}{2\sigma_c^2} (y^* - \mu_c)^2\right] \quad (2.2)$$

was applied to assess the likelihood that a given pixel in the $\delta^2\text{H}_f$ isoscape represented a potential origin for each feather sample.

A theoretical spatial distribution of $\delta^{13}\text{C}$ based on vegetation types in South America was obtained from Powell et al. (2012) (see also Figure 2.2.). From this, a dichotomous surface of C3- and C4-dominated vegetation zones was created. Cells with $\delta^{13}\text{C}$ values $< -20 \text{‰}$ were

classified as C3-dominated and those with $\delta^{13}\text{C}$ values $> -20\text{‰}$ were classified as C4-dominated (Kelly 2000). These zones were then converted to equivalent feather- $\delta^{13}\text{C}$ values assuming an isotopic discrimination factor of 2‰ between plant and feather, calculated based on known discrimination factors of $\sim 1\text{‰}$ between plants and herbivorous insects (DeNiro and Epstein 1978, Peterson and Fry 1987, France and Peters 1997), and $\sim 1\text{‰}$ between insects and bird feathers (Hobson 2007).. The expected mean and standard deviation (SD) of feather- $\delta^{13}\text{C}$ for each region were calculated based on modeled $\delta^{13}\text{C}$ values extracted from the dichotomous feather- $\delta^{13}\text{C}$ isoscape. Equation A.2 was then applied to assess the probability that the observed $\delta^{13}\text{C}$ of the feather represented growth in a C3 versus C4-dominated winter origin for each feather sample.

Following Hobson et al. (2009b), our assignment algorithm used Baye's Theorem to compute the probability of each pixel x_i being the origin of a feather sample, given the observed feather value y_j , where j indexes the C3 or C4 vegetation zone.

$$f_X(x_i|Y = y_j) = \frac{f_Y(y_j|X=x_i)f_X(x_i|J=j)}{\sum_i f_Y(y_j|X=x_i)f_X(x_i|J=j)} \quad (2.3.)$$

The random variables Y and X are both continuous and represent the observed feather- $\delta^2\text{H}$ values for Barn Swallows and the pixels within the feather- $\delta^2\text{H}$ isoscape, respectively. The random variable J describes potential origins in C3 or C4-dominated zones and is thus categorical with a dimension of two.

Spatially explicit probability densities were normalized to the sum of likelihoods, thus yielding a single probability of origin surface for each feather sample. To statistically assign individuals to molt origin the calculated spatially explicit probability densities for each feather sample were reclassified using 3:1 odds ratios of correctly assigning an individual to its molt origin. The set of cells that defined the upper 75% of estimated probabilities of origin was coded

as “1” (likely) and the rest as “0” (unlikely) (Van Wilgenburg and Hobson 2011). Results of the assignment of each individual were summed and mapped to obtain the most probable molting origin of the population. All analyses were performed using scripts adapted from (Van Wilgenburg and Hobson 2011) and employing the ‘raster’ package within R Statistical Computing environment, Version 2.10 (R Development Core Team 2011) and ArcGIS Version 9.3 (ESRI 2011).

2.3. Results

Winter-grown feathers of Barn Swallows showed significant differences across breeding populations in $\delta^2\text{H}$ (ANOVA, $F_{12,600} = 13.95$, $p < 0.001$), $\delta^{13}\text{C}$ (ANOVA, $F_{9,395} = 6.47$, $p < 0.001$) and $\delta^{15}\text{N}$ values (ANOVA, $F_{9,397} = 6.75$, $p < 0.001$) (Table 2.1.). However, feather- $\delta^2\text{H}$ values were not significantly different for most breeding populations in North America (ANOVA and Tukey-Test, $p < 0.05$), with the exception of British Columbia. This breeding population differed from all populations except Saskatchewan, and showed $\delta^2\text{H}$ feather values more depleted in ^2H than any other group (Figure 2.3a.). When $\delta^2\text{H}$ standard deviations (SD) of feathers from Barn and Cliff Swallows grouped by breeding location were compared, the range of $\delta^2\text{H}$ values was larger for Barn Swallows (range of SDs: 8.1 - 17.3‰) than for Cliff Swallows (range of SDs: 6.1 - 8.3‰) (Table 2.1., Figure 2.3.).

K-means cluster analysis suggested four distinct clusters, corresponding to wintering regions, that were consistently different from each other in $\delta^{13}\text{C}$, $\delta^2\text{H}$ and $\delta^{15}\text{N}$ values simultaneously (MANOVA, $F_{9,971} = 171.7$, $p < 0.001$) (Table 2.2.). For breeding colonies in Alabama, Mississippi, British Columbia, Quebec and California, 50% of the total population or greater were assigned to a single cluster, suggesting a stronger pattern of migratory connectivity. Birds breeding in Washington State also showed a strong segregation on wintering grounds with most

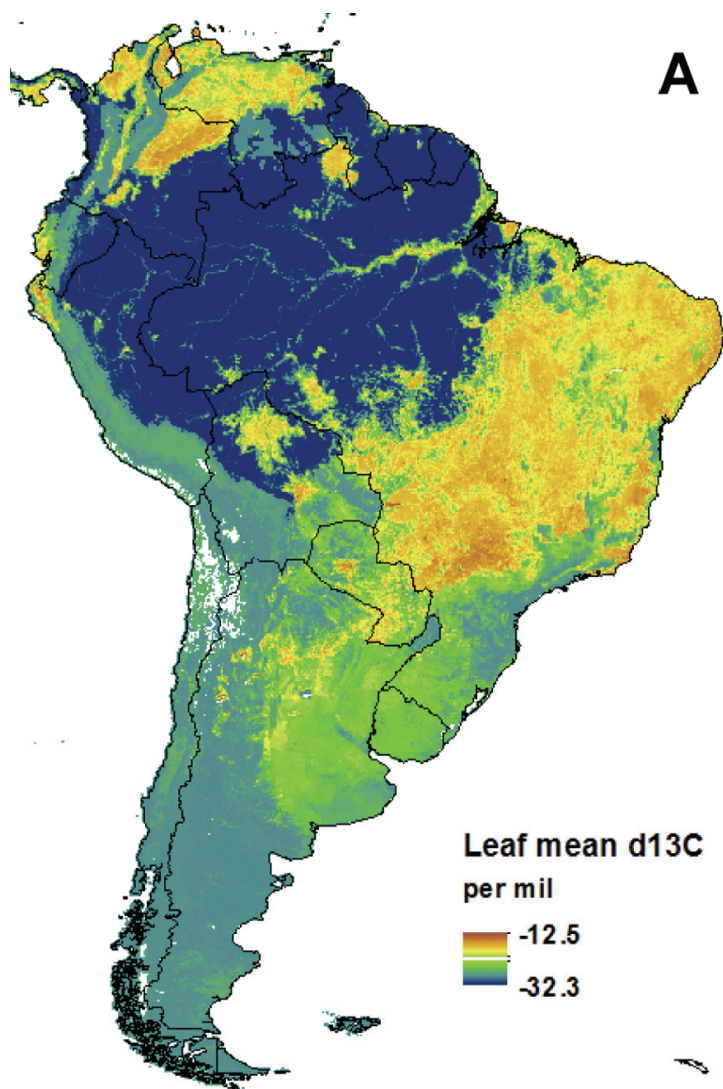


Figure 2.2. Estimated mean leaf $\delta^{13}\text{C}$ (‰) per 5-min grid cell extracted from Powell et al. (2012)

Table 2.1. Stable isotope values (‰) of winter-grown feathers of Barn and Cliff Swallows collected from different breeding populations across North America.

Species/Location	$\delta^2\text{H}$			$\delta^{13}\text{C}$			$\delta^{15}\text{N}$		
	n	Mean	SD	n	Mean	SD	n	Mean	SD
Barn Swallow (<i>Hirundo rustica</i>)									
British Columbia	22	-73.1	15.5	12	-21.2	1.5	12	10.8	1.9
Saskatchewan	8	-62.8	16.6						
Manitoba	83	-60.5	10.7	78	-20.5	2.8	78	10.0	1.1
California	30	-54.6	10.2	19	-20.5	1.7	17	10.1	1.2
Washington State	21	-58.4	14.9	14	-19.5	2.2	14	10.6	1.8
Quebec	13	-54.0	12.0	10	-16.0	2.4	10	11.9	1.7
Ontario	253	-48.5	10.7	163	-17.8	2.5	163	11.3	1.4
Colorado	39	-46.6	13.3	25	-19.7	3.0	25	10.7	1.4
New Jersey State	25	-47.6	11.0						
New York State	29	-47.5	13.7						
Mississippi	48	-38.8	10.3	33	-17.8	3.7	33	11.4	1.4
Alabama	31	-40.7	8.1	21	-16.5	3.8	20	11.4	1.3
Texas	38	-46.2	11.0	31	-18.8	4.0	31	11.0	1.6
Cliff Swallow (<i>Petrochelidon pyrrhonota</i>)									
Manitoba	76	-56.5	8.3						
Ontario	73	-55.3	8.1						
Nebraska	134	-52.5	6.3						
Texas	10	-44.6	6.2						

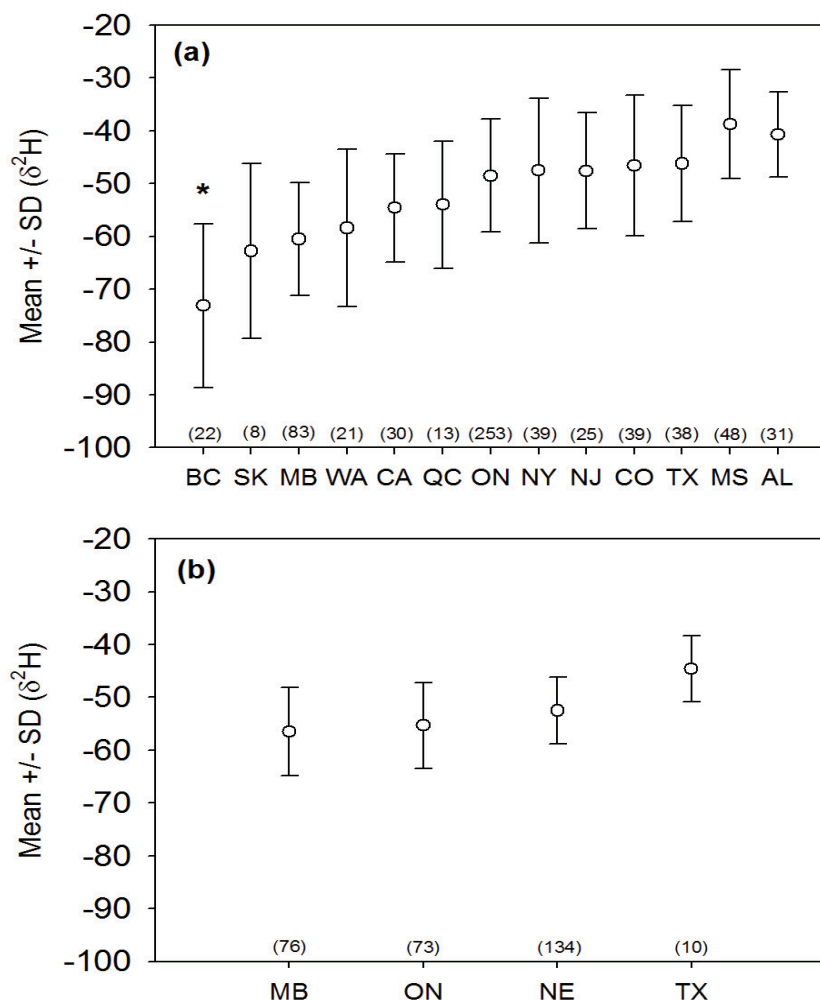


Figure 2.3. Mean and standard deviations of $\delta^2\text{H}$ values (‰) of breeding populations of Barn Swallow (a) and Cliff Swallow (b) in North America. Letters represent provinces and states (BC=British Columbia, SK=Saskatchewan, MB=Manitoba, WA=Washington State, CA=California, QC=Quebec, ON=Ontario, NY=New York, NJ=New Jersey, CO=Colorado, TX=Texas, MS=Mississippi, AL=Alabama, and NE=Nebraska). Numbers above locations represent sample sizes. Star symbol denotes significant differences in mean comparisons (Tukey's HSD test; $p < 0.05$) among British Columbia and the rest of breeding populations except Saskatchewan.

Table 2.2. Stable isotope values (‰) for the four groups created using k-means analysis. Letters denote significant differences in mean comparisons by a Tukey's HSD test ($p < 0.05$).

	$\delta^2\text{H}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
Group 1 (a)	-77.4 ^{bcd}	-20.8 ^{cd}	11.1
Group 2 (b)	-61.3 ^{acd}	-19.3 ^c	10.6 ^d
Group 3 (c)	-47.8 ^{abd}	-17.9 ^{ab}	10.8 ^d
Group 4 (d)	-33.4 ^{abc}	-18.1 ^{ac}	11.4 ^{bc}

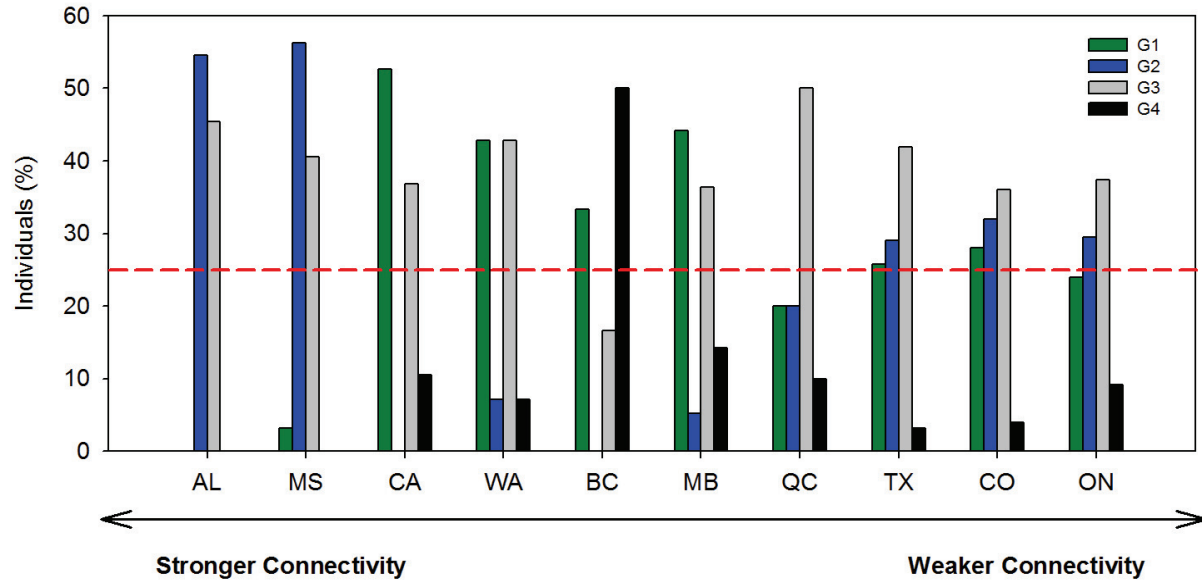


Figure 2.4. Percentage of individuals from each breeding populations assigned to the four groups created from k-mean analyses. (BC=British Columbia, MB=Manitoba, WA=Washington State, CA=California, ON=Ontario, QC=Quebec, CO=Colorado, TX=Texas, MS=Mississippi, and AL=Alabama. Red-dotted line denotes the 25% threshold corresponding to a complete panmixing of individuals.

Table 2.3. Percentage of individuals from each breeding population assigned to the four groups created applying k-means analysis based on $\delta^2\text{H}$, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of winter-grown feathers of Barn Swallows.

Population	n	Group 1 (%)	Group 2 (%)	Group 3 (%)	Group 4 (%)
Ontario	163	9	24	37	29
Manitoba	77	14	44	36	5
Quebec	10	10	20	50	20
British Columbia	12	50	33	17	0
Colorado	25	4	28	36	32
California	19	11	53	37	0
Washington State	14	7	43	43	7
Mississippi	32	0	3	41	56
Alabama	22	0	0	45	55
Texas	31	3	26	42	29

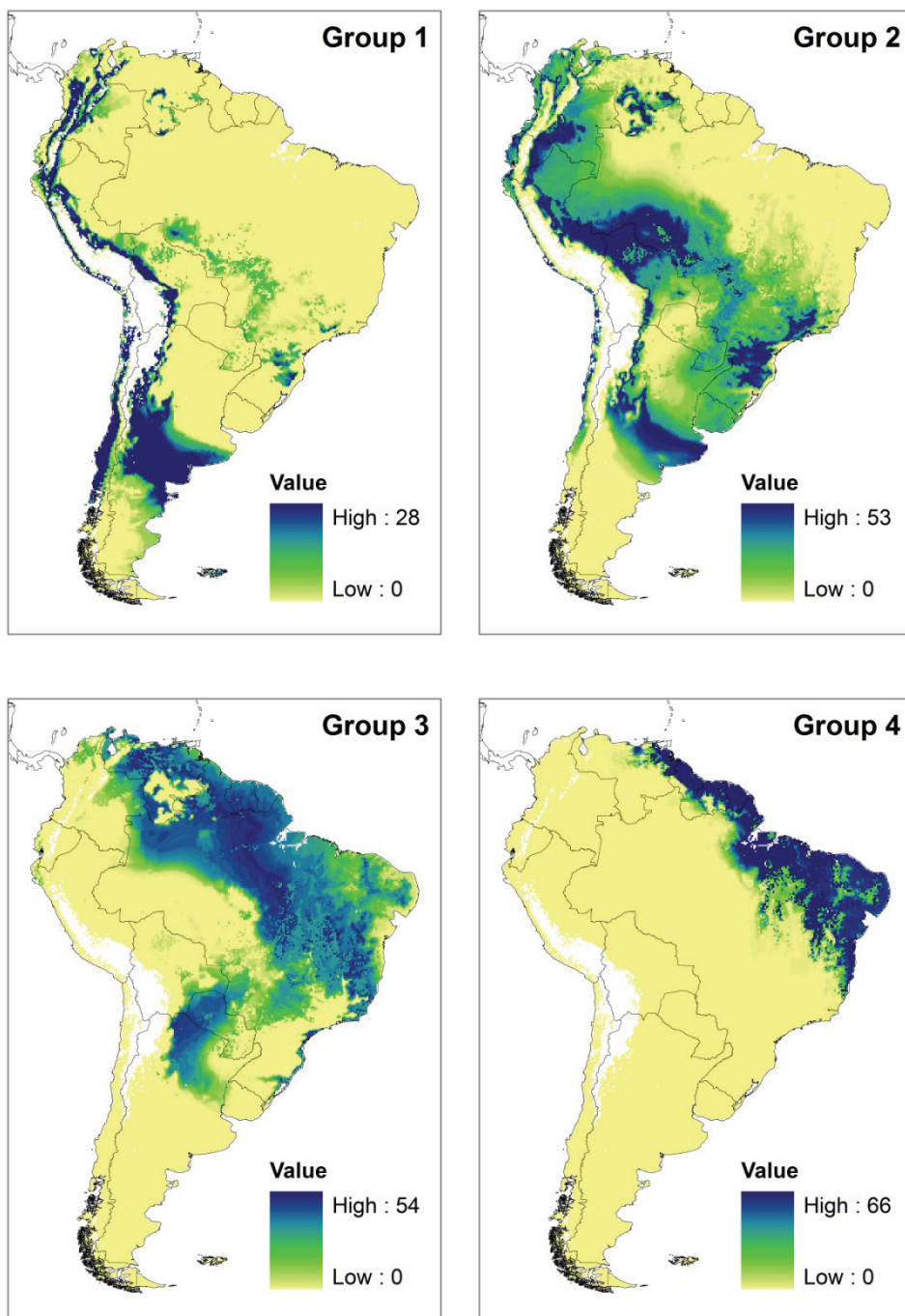


Figure 2.5. Depicted potential molting origins in South America of 405 Barn Swallows breeding across North America sampled in 2009, 2010 and 2011 separated in the four isotopically distinct groups. Maps were created using $\delta^2\text{H}$ and $\delta^{13}\text{C}$ values of winter-grown feathers. Values depicted on maps represent the number of individuals in the total sample that were assigned to each cell in the map, representing a potential molting origin according to a 3:1 odds ratio.

individuals being distributed across two single clusters. In contrast, the rest of breeding populations showed a weaker pattern of connectivity. Individuals from these breeding colonies were more uniformly distributed across the four clusters, with each cluster comprising approximately 10 % to 30 % of the total population for each colony (Figure 2.4., Table 2.3.).

Depicted molting origins of the four groups suggested a progressive longitudinal change in geographic locations of wintering grounds for North American Barn Swallows. Groups 1 and 2 were mainly comprised of individuals from northern and western breeding regions and their most likely overwintering areas corresponded with western and central South America. Wintering areas for individuals in Group 1 and 2 were located along the west and east side of the Andes respectively. In contrast, potential molting regions for birds classified in Groups 3 and 4, composed mainly of eastern and southern breeding birds, corresponded with areas in north-eastern and central-eastern South America respectively (Figure 2.5.).

2.4. Discussion

Breeding populations of Barn Swallow in North America exhibited significant variation in degree of migratory connectivity and populations in eastern and western North America generally were more segregated on the wintering grounds than those in central regions. Populations in Mississippi and Alabama showed the strongest pattern of connectivity with more than half of their individuals being assigned to a single cluster and the rest to a different cluster. Birds breeding in Washington State were mainly distributed across two clusters, showing relatively strong migratory connectivity. Similarly, breeding colonies in British Columbia, California, Manitoba and Quebec also showed a relatively strong connectivity with half of the total population grouped in one single cluster and the other half distributed between two other clusters. Populations in Texas, Colorado, and Ontario showed the weakest migratory

connectivity overall with individuals from these populations uniformly distributed among three different clusters.

This diverse pattern of migratory connectivity among populations agrees with previous studies of Barn Swallows in Europe. Hobson et al. (2012a) recently found differential levels of connectivity among populations in Europe, showing higher heterogeneity of winter origins for Barn Swallow populations in western than in eastern regions. These findings are additionally supported by Ambrosini et al. (2009), who examined ring recovery data for Europe and Africa and found that the species winters over large areas but populations in northern Europe tend to segregate more in the wintering grounds than those in south-western Europe.

Assignment of wintering origins by combining multiple stable isotope profiles and the theoretical distribution of C3 and C4 plants in South America showed a progressive longitudinal shift in wintering locations of Barn Swallows across North America. Birds breeding in northern and western North America tended to winter in western regions, while those breeding in southern and eastern populations wintered in the north-east of South America. This coarse longitudinal gradient in wintering regions is likely maintained by distinct flyways already described for the Neotropical Nearctic migratory system.

Hobson et al. (2012a) similarly found evidence for large-scale spatial structuring of wintering locations in European Barn Swallow populations. That study suggested that breeding populations from Eastern Europe tend to overwinter in southern Africa, while most birds from the western part of their breeding range seem to migrate to more northern regions. Using feather- $\delta^{13}\text{C}$ values, Evans et al. (2003) also found this longitudinal pattern and showed that breeding populations of European Barn Swallows from geographically separated areas in the west and east part of Europe wintered in isotopically distinct habitats.

Populations of Barn Swallow that present a stable/increasing population trend (i.e. Mississippi and Alabama) showed stronger patterns of connectivity than the rest of the breeding populations I examined in North America. These findings contrast with previous studies showing a higher vulnerability to factors in the wintering grounds of populations with strong migratory connectivity, mainly due to their more restricted wintering locations and their lack of flexibility in migratory behavior (Dolman and Sutherland 1995, Webster et al. 2002, Webster and Marra 2005). Most of birds breeding in these stable/increasing regions occupy areas in north-eastern South America. In the north, these regions correspond with the Amazon Delta and tropical, subtropical moist forest biomes and cultivated areas (i.e. rice and sugar cane). Almost 60% of the total surface is occupied by forested areas and 40% by marshes and water bodies, and semi-desert biomes are present in the east (Morelo 2002). These northern areas of South America could indeed represent high-quality habitats for Barn Swallows and individuals occupying these areas could be subjected to more beneficial conditions (i.e. large availability of insects, constant temperatures, etc.) than birds overwintering in dryer or more temperate locations. For example, most Barn Swallows from declining populations tended to overwinter in western and central South America, where temperatures and precipitation rates are significantly lower and marsh areas are less common (Morelo 2002). However, there is no evidence for a recent change in habitat quality for those western regions in the past few decades when population declines started to be more severe. Therefore, we are not able to relate those population declines with habitat quality.

Significant differences in migratory connectivity were found between Barn and Cliff Swallows based on feather- $\delta^2\text{H}$ values. Standard deviations in $\delta^2\text{H}$ values of breeding locations of Barn Swallows were significantly larger than those of Cliff Swallows, suggesting broader

wintering ranges and an overall weaker migratory connectivity pattern for Barn Swallow compare to Cliff Swallows. I hypothesize that the differential strength of migratory connectivity found for these species could be potentially explained based on their degree of coloniality, although to my knowledge no studies have reported this relationship. Cliff Swallow is a highly colonial bird which typically nests in large colonies (Brown and Brown 1995) and exhibit a significantly high adult and young site fidelity (Brown and Brown 1996). In contrast, Barn Swallows show lower coloniality (Shields 1984, Brown and Brown 1999a). The existence of a strong heritable element on Cliff Swallows from the same breeding colony which force individuals to return to the same breeding location (Brown and Brown 2000) could potentially result in a high degree of segregation during the non-breeding season. Since this degree of coloniality and site fidelity is less remarkable for Barn Swallows, the effect of this heritable element of segregation may not be so intense for this species, causing a more extensive dispersion of individuals on the wintering grounds.

In this study, information on feather $\delta^2\text{H}$, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ was applied and additionally combined with information on geographic distribution of vegetation types in South America. Despite the advantages of using stable isotopes in studies of geographical origins, there is ambiguity in evaluating migratory connectivity using this approach based on three main limitations. First, this technique relies on the estimation of geographical distribution in nature of $\delta^2\text{H}$ across continents (i.e. isoscapes), and these isoscapes are based on a long-term dataset of averaged $\delta^2\text{H}$ -precipitation values (Bowen et al. 2005). Therefore, uncertainty related to inter-annual variations in precipitation $\delta^2\text{H}$ from the long-term GNIP average at local scales remains an issue when using $\delta^2\text{H}$ isoscapes to identify molting origins. Secondly, the relatively large variance in within-population $\delta^2\text{H}$ profiles of known-origin feathers must be considered (Hobson 2011). The

statistical approach used in this study propagates this error in the assignment but the magnitude of variance in feather $\delta^2\text{H}$ values within populations growing feathers at the same location and the nature of the isoscapes over continental areas results in the isotope approach being a weak tool for identifying the strength of migratory connectivity *per se* (Hobson et al. 2012c). The broad range of longitudinal variation in $\delta^2\text{H}$ isoscapes for most continents is also a contributing factor here (Bowen et al. 2005). Therefore, while different isotope values of feathers (i.e. greater than the variance expected at a single site) strongly implies different geographic areas of feather growth, similar isotope values do not necessarily mean growth at the same location, since areas with similar isotopic values can be extensive. In order to constrain these areas of origins of migrants, $\delta^2\text{H}$ analyses can be combined with other markers that show a better longitudinal structure such as other isotopes (strontium), genetics, and trace elements (Sellick et al. 2009, Chabot et al. 2012, Ofukany et al. 2012) or prior information in species distribution, band recoveries and isotopic/geographic clusters (Gonzalez-Prieto et al. 2011, Van Wilgenburg and Hobson 2011, Hobson et al. 2012a, Hobson et al. 2012b, Hobson et al. 2012d).

In conclusion, these results showed that populations of North American Barn Swallows presented diverse levels of migratory connectivity as indicated by the assignment of individuals from same populations to a single (strong connectivity) or multiple (weak connectivity) isotopic clusters. A progressive longitudinal shift of wintering grounds was detected, with breeding populations in more northern and western regions wintering in western South America, and breeding populations in southern and eastern North America occupying areas in north-eastern South America. Stable populations of Barn Swallow exhibit an overall stronger pattern of connectivity than declining populations and occupied better quality regions characterized by warmer temperatures and higher precipitation rates. In contrast, declining populations tend to

occupy areas subjected to colder and drier conditions, less suitable for Barn Swallows. However, we were not able to relate population declines with habitat quality since there is no evidence for a recent change in habitat quality for those western regions when population declines started to be more severe.

This is the first study that attempts to identify winter origins of a Neotropical long-distance migrant using stable isotopes analyses and presents a plausible explanation of potential reasons for the differential decline of Barn Swallows in North America. However, the broad range of feather isotope values representing wintering areas, even for those populations with strongest connectivity, suggests a large number of potential molting areas for Barn Swallows in South America. Indeed, we should not deny the possibility that populations may have stronger connectivity than shown in this study but we are not able to detect it due to limitations in stable isotope analyses. These results can be now investigated further by using more direct-tracking techniques such as low-weight geolocators or by combining stable isotopes with distributions of trace elements in South America.

CHAPTER 3. EVALUATION OF POSSIBLE FACTORS OCCURRING ON BREEDING AND WINTERING GROUNDS INFLUENCING DECLINES IN BREEDING POPULATIONS OF BARN SWALLOWS (*Hirundo rustica*) IN NORTH AMERICA

3.1. Introduction

Populations of declining aerial insectivores breeding in North America could be limited by ecological factors operating during more than one stage of their annual cycle on their breeding areas (Budnik et al. 2000, Hayden et al. 2000), wintering areas (Yalden and Pearce-Higgins 1997), stopover sites (Newton 2008), or wintering and breeding locations (Silleet et al. 2000, Newton 2008). These ecological factors could be density-dependent, and so involve competition for limited resources, density dependent predation, etc. (Baillie and Peach 1992, Ferrer and Donazar 1996), or density-independent (i.e. weather, contaminants, habitat degradation, and other environmental stressors) (Blake et al. 1992, Williams et al. 1993, Ferrer and Donazar 1996, Klemens et al. 2000, Gill et al. 2001). However, specific effects of these impacts on population sizes are difficult to evaluate because of the large variety of factors that can separately or jointly influence survival and reproduction of migratory species at different stages of their annual cycle (Sherry and Holmes 1995).

Barn Swallow populations have decreased drastically in recent decades in most of North America but reasons for these declines remain unknown (Cadman et al. 2007, McGowan and Corwin 2008, Nebel et al. 2010, Bird Studies Canada et al. 2012). Data from the Breeding Bird Survey (BBS) collected across North America have shown extensive declines from 1968 to 2010 in Canada and northern United States, while populations in southern United States remain stable or increasing for the same period (Sauer et al. (2011) and Table 3.1.).

Table 3.1. Population trends estimates for Barn Swallow based on percentage of annual population change (% change) for a long- and short- term intervals for locations where sampling was performed. Star symbol denotes those locations where population trends are negative. Sample size represents the number of BBS survey routes on which the species was encountered during the long-term interval.

Location	Long-term (1966-2010)			Short-term (2000-2010)	
	n	% change	95% CI	% change	95% CI
British Columbia *	108	-4.9	-5.8, -3.9	-4.6	-7.2, -1.7
Manitoba *	67	-2.6	-3.9, -1.7	-2.0	-3.6, -0.3
Quebec *	112	-6.0	-7.0, -5.1	-5.4	-7.0, -3.6
Ontario *	146	-2.3	-3.0, -1.7	-2.5	-4.1, -0.8
California *	169	-1.4	-2.0, -0.8	-1.2	-3.0, 0.4
Colorado	129	0.4	-0.7, 1.5	-1.4	-3.7, 1.0
New York state *	123	-1.2	-1.7, -0.8	-1.0	-2.3, 0.4
New Jersey state *	40	-1.2	-2.1, -0.3	-1.0	-2.5, 0.6
Mississippi	51	3.0	2.0, 4.2	0.1	-2.8, 2.7
Alabama	104	3.9	2.8, 5.1	-0.7	-2.8, 1.4
Texas	212	4.1	3.3, 4.9	1.0	-0.7, 2.8
Washington State *	82	-2.3	-3.0, -1.7	-2.6	-4.2, -0.9
Saskatchewan *	87	-3.2	-4.0, -2.3	-3.3	-5.3, -1.4

3.2.1. Annual survival and weather

The El Niño Southern Oscillation (ENSO) is a reliable measurement of wide-scale climatic fluctuations which can be used to study the effects of weather conditions in a large-scale geographic context. The ENSO phenomenon consists of a cycling of warming and cooling of the central and eastern Pacific Ocean surface and it is an important source of inter-annual weather variation over broad regions of the world (Philander 1990). The Southern Oscillation Index (SOI) is a quantitative measurement of the ENSO phenomenon and it is defined as the difference in sea level pressure between the tropical Pacific Ocean (Tahiti) and the Indian Ocean (Darwin) (Philander 1990). In North America, negative SOI values correspond to the warm phase of the ENSO phenomenon called El Niño; while positive SOI values are indicative of the La Niña phase, which has opposite effects to the El Niño phase. ENSO has a differential effect on weather conditions across North America. During El Niño phase, northern and western regions encounter drier and warmer conditions while southern United States experience higher precipitation rates and colder temperatures (Shabbar and Khandekar 1996, Shabbar et al. 1997). In South America, two distinct areas of ENSO-related weather conditions can be defined. Regions in the north and north-eastern South America show scarce precipitation during the El Niño phase, while regions in southern and western South America experience high precipitation rates (Ropelewski and Halpert 1987). In Central America, the west and east coasts differ significantly in the effect of the El Niño phase, since the west coast exhibit drought episodes and the east coast is subjected to intense precipitation (Ropelewski and Halpert 1987).

Since El Niño and La Niña events have a clear impact on ambient temperatures and precipitation at a global scale, ENSO-related weather conditions could affect populations of migratory birds by indirectly affecting their survivorship and fecundity. On the breeding grounds, annual variation in ENSO has been previously related to fluctuations in adult survival

of Yellow Warblers (*Dendroica petechia*) in Manitoba (Mazerolle et al. 2005) and of Swainson's Thrushes (*Catharus ustulatus*) across the western region of its breeding range (LaManna et al. 2012). On the wintering grounds, Sillett et al. (2000) found that annual survival rates of Black-throated Blue Warblers (*Dendroica caerulescens*) in Jamaica were strongly associated with annual SOI values, and Flockhart and Wiebe (2008) showed a similar correlation for adult Northern Flickers (*Colaptes auratus*) breeding in British Columbia. Variation in large-scale weather conditions have been previously shown to have a negative effect on population dynamics of Barn Swallow in Europe. Ambrosini et al. (2011) found that Barn Swallows have shifted their wintering locations in Africa northwards due to changes in temperature and precipitation. These changes favoured individuals that winter in warmer and drier regions, which are less favorable for them, and may have contributed to the overall decline of the species.

3.1.2. Reproductive success and spring weather

Local-weather patterns have important implications for reproductive success of avian species since they can affect reproduction parameters directly. For instance, severe drought episodes in western North Dakota in 1988 caused substantial reductions in grassland bird productivity and density (George et al. 1992). More recent studies on Lark Bunting (*Calamospiza melanocorys*) breeding in north-eastern Colorado have found that productivity was positively related to annual precipitation and negatively related to average temperatures during the breeding season (Skagen and Adams 2012). Weather on the breeding grounds, specifically extensive cold weather periods shortly after arrival, can also have an indirect effect on reproductive success of aerial insectivores by reducing insect activity and availability (Taylor 1963, Newton 2007). Warmer spring temperatures over the past decades have modified the breeding phenology of insects (Bartomeus et al. 2011). For aerial insectivore species, this change has involved adapting their breeding phenology to the new emergence dates of insects (Walther et al. 2002, Root et al.

2003). However, not all bird species are able to adapt so rapidly to these temporal changes in food sources, and this mismatch can potentially reduce their productivity and can have a negative effect on population sizes (Visser et al. 1998, Visser et al. 2006, Gaston et al. 2009).

3.1.3. Stressors on the wintering grounds

The term “stressor” can be defined as unpredictable and/or uncontrolled stimuli that an animal is exposed to (Romero et al. 2009). To cope with this stimuli, glucocorticoid stress hormones such as cortisol and corticosterone (CORT) are released in the organism to induce behavioral and physiological changes known as the “stress response” (Romero 2004). When these environmental perturbations persist in time, individuals need to allocate greater effort to keep their physiological parameters within normal levels and this could have important detrimental consequences for reproduction, survival and body condition (Dallman et al. 1992, Romero 2004, Romero et al. 2009). Therefore, CORT levels can be applied as a physiological index of the overall health of individuals and, by extension, the health of a population.

Environmental factors, such as habitat quality, food availability or weather, and the physiological stress response tend to correlate; although this relationship is sometimes complex. For instance, Marra et al. (1998) and Marra and Holberton (1998) found that American Redstarts (*Setophaga ruticilla*) wintering in low- and high-quality habitats differed significantly in baseline plasma CORT levels, mainly due to sex-related inter-individual competition. CORT levels have been also correlated with annual changes in food availability. Doody et al. (2008) found that CORT levels in Common Murres (*Uria aalge*) were significantly higher in years where there was a prey-mismatch compared to years where food availability at periods of elevated demand was higher. Additionally, baseline CORT levels of adult Cliff Swallows breeding in Nebraska were significantly higher during a prolonged cold and windy weather event, potentially due also to the effect of food scarcity (Raouf et al. 2006). Weather conditions seem also to influence

CORT secretion in certain stages of the annual cycle of migratory birds. For example, variation in CORT levels in the blood of two migratory species during molt on the Arctic-breeding grounds was shown to be significantly correlated with weather conditions at those regions (Romero et al. 2000). Similar results were found for Barn Swallows in Switzerland, where unexpected reductions in ambient temperature, food availability and/or body condition led to an increase in plasma CORT concentrations of breeding adults (Jenni-Eiermann et al. 2008). Measuring CORT in feathers represents a convenient means of monitoring the physiological response of avian species to stressors during the period of feather growth (Bortolotti et al. 2008, Bortolotti et al. 2009). Since Barn Swallows undergo a complete molt of their flight feathers on their wintering grounds (Pyle (1997) and Appendix B), measures of feather-CORT levels will provide information of hypothalamic-pituitary-adrenal (HPA) axis activity on their wintering grounds

Here, several factors potentially affecting survival of Barn Swallows operating on breeding and wintering grounds were investigated. Specifically, I examined 1) the effects on annual survival rates of Barn Swallows of weather conditions at breeding and non-breeding seasons related to ENSO, 2) the influence of spring weather on fecundity rates and 3) the differential effect on stable and declining populations of stressors on the wintering grounds as indicated by feather CORT levels.

3.2. Methods

3.2.1. Annual survival study

Adult Barn Swallows were captured using mist nets at two locations during the breeding season from April to August: 1) from 2002 to 2011 in Ontario, Canada, while breeding in agricultural farms in the Guelph area (approximate coordinates: 80°19'W, 43°37'N); and 2) from 1999 to 2011 in Washington State, USA, in a breeding colony located at the facilities of

Woodland Park Zoo in Seattle (122°21'W, 47°40'N). Individuals were captured and banded following the guidelines of the North American Banding Council (NABC 2001). Age and sex were also determined based on tail length and evidence of breeding status (Pyle 1997). When captured individuals were found to be already banded from previous years, band number, age and sex were recorded to obtain mark-recapture data.

Mean monthly values of SOI were obtained from the National Oceanic and Atmospheric Administration (NOAA) website (<http://www.cpc.ncep.noaa.gov>) as a measure of ENSO annual conditions (Philander 1990). ENSO conditions on the wintering grounds (SOI_w) were quantified by the mean monthly SOI values from September to March, and from April to August to reflect ENSO conditions on the breeding areas (SOI_b). Since no correlation between SOI_w and SOI_b was found for the years included in the analysis (ON: $r^2=0.05$ and WA: $r^2=0.05$), I assumed that these indexes could be used separately to measure the effect of conditions on breeding and wintering grounds.

3.2.2. Reproductive success

Reproductive success of Barn Swallow was defined as the number of young which survived to 16 days old per total number of active nests in the studied population (i.e. fledgling success) following methodology by Barclay (1988) and was estimated for two well-established breeding colonies in Manitoba and Washington State. All nest structures were monitored over the entire breeding season from early May to September. Nests destroyed by humans were not included in estimates of reproductive success. Variables such as arrival date (date the first individual of the season is seen) and total number of nests, and variables related with fecundity (total number of eggs, chicks per nest, and fledglings) were recorded for each active nest. In Manitoba, birds were captured using mist nets and tail feathers were coloured with enamel paint to identify individuals from a distance. The study colony in Manitoba was located at the University of Manitoba Field

Station (Delta Marsh; 98°22'W, 50°11'N), a forested area in the south shore of Lake Manitoba where several buildings are used by swallows for nesting. Data on reproductive success for this population were obtained from a previous study performed on the same breeding location in 1984, 1985 and 1986 (Barclay 1988) and by me in 2009 and 2010. The colony in Washington State was located at the Woodland Park Zoo and data on reproductive success for this breeding colony have been recorded for 12 consecutive years from 1999 to 2010.

Daily temperature and precipitation data for both locations for the period from arrival through pre-fledgling of young were obtained online from two weather stations considered representative of the weather experienced by birds in their respective breeding colonies. Data for Manitoba were obtained from the Environment Canada Weather Office website (<http://www.weatheroffice.gc.ca>) from May 1 to June 31 for Delta Marsh Weather Station, Manitoba. Data for Washington State were obtained through the National Climatic Data Center (NOAA) website (<http://www.ncdc.noaa.gov>) from April 5 to June 31 for Mc. Millin Reservoir Weather Station, Washington State, located 50 km from the breeding colony. Seasonal temperature was expressed as average maximum (“MaxTemp”) and minimum (“MinTemp”) temperatures during the study period. The existence of exceptionally low temperature periods have been previously shown to have a negative effect on survival and reproductive success (Brown and Brown 1998, Jenni-Eiermann et al. 2008) of aerial insectivore species. Therefore, the variable “ColdDays”, defined as the total number of consecutive days (≥ 2 d periods) with maximum daily temperatures lower than 11°C was selected to account for this phenomenon. The cut-off point (11°C) followed from studies by Brown and Brown (1998) and Brown and Brown (1999b) on responses of Cliff Swallows (*Petrochelidon pyrronota*) and Barn Swallows, respectively, to weather conditions on the breeding grounds (see also Brown and Brown (2000)).

Precipitation was expressed as the average daily precipitation of the season (“AvePrecip”) and the potential effect of interactions between temperature and precipitation was accounted for by adding interaction parameters to the set of candidate models.

3.3.3. Hormone analyses

Adult Barn Swallows were captured using mist-nets during the breeding season (May to late August) of 2010 and 2011 in British Columbia (Alaksen National Wildlife Area, Delta. 122°54'W, 49°8'N), Ontario (Guelph area. 80°6'W, 43°54'N), Saskatchewan (Prince Albert National Park. 106°1'W, 53°54'N), Washington State (Seattle. 122°21'W, 47°40'N), Mississippi (Greenville area. 89°23'W, 32°21'N), Alabama (Montgomery area. 86°59'W, 32°19'N) and Texas (Dallas area. 97°5'W, 32°20'N). All birds were banded using USFWS aluminum bands. Sex, age and body measurements (wing length, tail length and weight) were recorded following the North American Banding Council guidelines (NABC). One inner tail feather grown in the wintering grounds (Pyle 1997) was collected for each adult for stress hormone analyses and stored in labeled paper envelopes.

CORT was first extracted from feathers using a methanol-based extraction technique following procedures described by Bortolotti et al. (2008). Feather length was measured before and after removal of the calamus. Feather vanes were cut in small pieces (less than 5 mm) with scissors. Ten mls of methanol (HPLC grade, Fisher Scientific, Fairlawn, NJ, USA) was added to the cut feather sample and feathers were placed in a sonicating water bath for 30 minutes at room temperature followed by incubation at 50°C overnight in a shaking water bath. Methanol was separated from feather material by vacuum filtration using a plug of synthetic polyester fibre in the filtration funnel. The methanol extract was then placed in a 50°C water bath and subsequently evaporated in a fume hood under air. Extract residues were reconstituted in a small

volume of phosphate-buffered saline (0.05 M, pH 7.6) and final samples were frozen at -20°C until analysed for CORT. Samples were extracted in a single extraction where $> 89\%$ of the radioactivity was recoverable. CORT levels in Barn Swallow feathers were measured by radioimmunoassay (RIA). Measurements were performed on reconstituted methanol extracts and samples were analyzed in two separate assays. Assay variability was defined as the percentage of coefficient of variation (CV), which was 7.3% within assays, and 2.3% and 4.9% for first and second assays. CORT values are expressed as pg CORT per millimeter of feather as an estimation of CORT per unit time of feather growth (Bortolotti et al. 2008, Bortolotti et al. 2009, Bortolotti 2010). All CORT analyses were performed at the laboratory facilities in the Biology Department, University of Saskatchewan, Canada.

3.3.4. Statistical analyses

3.3.4.1. Annual survival study

Mark-recapture data from adult Barn Swallows breeding in Ontario and Washington State were used separately to estimate apparent annual survival (Φ) and recapture (p) rates for both populations using live-recapture or Cormack–Jolly–Seber (CJS) models (Cormack 1964, Lebreton et al. 1992). The term “apparent survival” was defined as the probability of survival of a bird considering that it remains alive but is not recaptured. Recapture rate represents the probability of encountering an animal that was previously marked. All analyses were performed using the program MARK (White and Burnham 1999). An initial model including sex (g) and time (t) dependency in both survival and recapture parameters was developed (Φ_{g*t}, p_{g*t}). The fit of this global model was assessed using the parametric bootstrap procedure (White et al. 2002). A total of 300 simulated bootstrap data sets which met the model assumptions of no overdispersion and independence were generated. The distribution of the deviance from the

original data was then compared with that generated from the bootstrap data sets to determine the probability of encountering a deviance equally or higher than the one obtained from the original data. Additionally, a measure of the degree of overdispersion of the observed data (\hat{c}) was calculated based on the mean of the deviance from both the observed and simulated results (White et al. 2002).

Reduced parameter models were developed to test whether weather conditions in the breeding and wintering grounds could have an effect on survival rates of colonies located in Ontario and Washington State. First, a model that allowed parallel variation over time of survival rates of males and females (Φ_{g+t}) was created. Then, survival estimates were constrained to be a linear function of breeding and wintering weather conditions. SOI_w and SOI_b were used as a measure of weather conditions on the wintering and breeding grounds respectively. Survival was then modeled to vary in parallel and dependently of weather variables and sex. Additionally, models which allow simple variation of survival based on sex (Φ_g), wintering weather conditions (Φ_{SOIw}), breeding weather conditions (Φ_{SOIb}), year (Φ_t), and constant variation of survival over time (Φ) were included in the analysis. Recapture probabilities were also modeled as constant over time (p), as a function of year (p_t) or group (p_g), as a parallel variation over time between sexes (p_{g+t}) and as full year and sex dependency (p_{g*t}). The final candidate set comprised 70 models including 14 different parameter-combinations for survival estimates and 5 parameter combinations for recapture estimates. All model notations followed Lebreton et al. (1992). To select the statistically most relevant model among all models from the candidate set, model selection methods based on the Akaike's Information Criterion (AIC) were used (Akaike 1973, Johnson and Omland 2004). Models in both candidate sets from Washington State and Ontario data were ranked based on second-order variant of AIC (AIC_c) differences, adjusted for small

sample sizes. The model with the lowest AIC_c was selected as the most parsimonious model, although it was assumed that models with AIC_c values differing by less than 2 units had equally substantial level of support (Burnham and Anderson 2002). The probability that a selected model was a better fitted model to the data was assessed using the AIC_c weight value (Burnham and Anderson 2002). A model averaging procedure was applied to calculate average survival estimates when model selection uncertainty was evident (Anderson et al. 2000, Burnham and Anderson 2002).

An additional analysis following the same methodology explained above was used to evaluate the effect on apparent survival on both breeding colonies of length of cold periods in the breeding grounds. A set of candidate models was created using the total number of consecutive days with maximum daily temperatures lower than 11°C measured in a year (COLD) as a covariate and model selection was performed based on AIC values (Akaike 1973, Johnson and Omland 2004). Historical weather data for the period 1968 to 2011 were collected from weather stations in Alabama and Mississippi where populations remain stable and compared with data from weather stations close to the studied breeding colonies in Ontario and Washington State, where Barn Swallows are declining (Table 3.1.). Weather data for Alabama was collected from Selma Weather Station (87° 0'W, 32° 24'N) and from Moorhead Weather Station (90° 30'W, 33° 27'N) for Mississippi. The dataset was searched for the frequency and extent of the occurrences of consecutive days with spring maximum daily temperatures equal to or lower than 11°C. The search was confined to the period from the first day Barn Swallows have been reported to arrive to the areas to June 30.

3.3.4. 2. Reproductive success study

A General Linear Model (GLM) was applied to evaluate the relative importance of spring weather variables (explanatory variables) on reproductive success rates (response variable) of

colonies in Manitoba and Washington State. The most parsimonious model was selected among a class of competing models with different numbers of parameters using AIC_c (Akaike 1973), which accounts for the relative goodness of fit of a statistical model to the data and its complexity in the number of parameters. An initial model with the maximum number of explanatory variables and interactions (“Maximal”) was created and fitted to the data. The function “drop1” was used to identify the least explanatory variable in the maximal model and a new model was created when that parameter was removed. Variables were consecutively removed and the minimal adequate model was selected based on AIC_c and residual deviance values. In order to investigate how well the model selected fit the real data, residuals of the model were plotted to examine heterocedasticity (homogeneity of variance of residuals versus fitted values) and normality of residuals was tested using a q-q plot (Wilk and Gnanadesikan 1968). All analyses were performed using Program R.

The best approximating model was applied to historical weather data from 1968 to 2010 to estimate past productivity rates (fledgling/nest) over time for both breeding colonies and to identify any significant change which could be related to population declines.

3.3.4.3. Winter stressors

To determine whether birds from stable and declining populations in North America had differential stress levels on the wintering grounds, feathers were initially grouped based on the nature of their population trends (Table 3.1.). Two different groups including samples from stable and declining populations were defined for analytical purposes. Differences in CORT values between breeding populations were tested using ANOVA for the two groups. Differences in CORT levels across the seven studied breeding colonies and among the four distinct wintering locations in South America identified based on $\delta^2\text{H}$, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ values of feathers (see Methodology Chapter 2) were additionally tested using Tukey-HSD tests.

3.3. Results

3.3.1. Annual survival and weather

3.3.1.1. Effect of ENSO

Model selection (Table 3.2. and Table 3.3.) and estimates of annual apparent survival probabilities (Table 3.4. and Table 3.5.) modeled based on ENSO conditions on breeding and wintering grounds differed for Barn Swallows breeding in Ontario and Washington State. The statistically best model for the Ontario data was the one in which apparent survival was constant over time (Φ, p_{g+t}) (Table 3.2.). The other two models in which survival varied with SOI_b (Φ_{SOI_b}, p_{g+t}) and SEX (Φ_g, p_{g+t}) differed in AIC_c values less than 2 units ($AIC_c = 0.86$ and 1.55 , respectively), suggesting significant support. However, they only differed from the best model in having one extra parameter, and in this specific situation the best model is considered that with the lowest AIC_c ($AIC_c = 0$) (Burnham and Anderson 2002, Arnold 2010). Model averaging results suggested that neither SOI in the breeding or the wintering grounds could be considered to have an effect on inter-annual survival probabilities (Figure 3.1.). In Washington State, the model which incorporated variation in survival relative to ENSO conditions in the spring (Φ_{SOI_b}, p_t) was selected as the best-fit model (Table 3.3.). Two other models in which apparent survival varied in parallel as a linear-logistic function of SOI_b and SOI_w ($\Phi_{SOI_b+SOI_w}, p_t$) and those of the model which only included $SOIs$ as explanatory variable (Φ_{SOI_b}, p_{g+t}) differed in AIC_c values less than 2 units. However, $\Phi_{SOI_b+SOI_w}, p_t$ only differed from the best model in having one extra parameter, and therefore, the best model is considered that with $AIC = 0$ (Burnham and Anderson 2002, Arnold 2010). Model averaging results suggested that SOI in the breeding or the wintering grounds have a significant effect on inter-annual survival probabilities (Figure 3.2. and Figure 3.3.).

Table 3.2. Summary output of candidate models of annual survival (Φ) and recapture (p) probabilities for Barn Swallows breeding in Ontario from 2002 to 2011 based on ENSO. Model notations denote: g = sex groups (male and female), SOI_b = average Southern Oscillation Index for breeding season, t = year, SOI_w = average Southern Oscillation Index for wintering season, No subscript = constant over sex groups and year. Only models with AIC_c weights ≤ 0.01 are shown.

Model	Num. parameters	AIC_c	ΔAIC_c	AIC_c weight	Deviance
Φ, p_{g+t}	11	1332.38	0.00	0.208	119.72
Φ_{SOI_b}, p_{g+t}	12	1333.24	0.86	0.136	118.53
Φ_g, p_{g+t}	12	1333.93	1.55	0.096	119.22
Φ_{SOI_w}, p_{g+t}	12	1334.41	2.03	0.076	119.69
Φ_t, p_g	11	1334.86	2.47	0.060	122.19
Φ_{g+SOI_b}, p_{g+t}	13	1335.00	2.62	0.056	118.23
Φ, p_t	10	1335.31	2.93	0.048	124.69
Φ_{SOI_b}, p_t	11	1335.65	3.27	0.041	122.99
Φ_{g*SOI_b}, p_{g+t}	14	1335.72	3.34	0.039	116.89
Φ_{g+SOI_w}, p_{g+t}	13	1335.96	3.58	0.035	119.19
Φ_g, p_t	11	1336.27	3.89	0.030	123.61
Φ_{g+t}, p_g	12	1336.32	3.93	0.029	121.60
Φ_{g+SOI_b}, p_t	12	1336.52	4.14	0.026	121.81
Φ_{g*SOI_b}, p_t	13	1336.70	4.32	0.024	119.93
Φ_{SOI_w}, p_t	11	1337.35	4.97	0.017	124.68
Φ_{g*SOI_w}, p_{g+t}	14	1337.90	5.52	0.013	119.07
Φ_{g+SOI_w}, p_t	12	1338.32	5.94	0.011	123.61

Table 3.3. Summary output of candidate models of annual survival (Φ) and recapture (p) probabilities for Barn Swallows breeding in Washington State from 1999 to 2011 based on ENSO. Model notations denote: g = sex groups (male and female), SOI_b = average Southern Oscillation Index for breeding season, t = year, SOI_w = average Southern Oscillation Index for wintering season, No subscript = constant over sex groups and year. Only models with AICc weights ≤ 0.010 are shown.

Model	Num. parameters	AICc	$\Delta AICc$	AICc weight	Deviance
Φ_{SOI_b}, p_t	14	463.30	0.00	0.254	153.83
$\Phi_{SOI_b+SOI_w}, p_t$	15	465.10	1.80	0.103	153.37
Φ_{SOI_b}, p_{g+t}	15	465.30	1.99	0.094	153.57
Φ_{g+SOI_b}, p_t	15	465.46	2.16	0.086	153.73
Φ_{SOI_w}, p_t	14	466.25	2.94	0.058	156.77
$\Phi_{SOI_b+SOI_w}, p_{g+t}$	16	467.12	3.81	0.038	153.11
$\Phi_{g+SOI_b+SOI_w}, p_t$	16	467.29	3.98	0.035	153.29
Φ_{SOI_b}, p	3	467.37	4.06	0.033	181.50
Φ_{g+SOI_b}, p_{g+t}	16	467.52	4.21	0.031	153.52
Φ_{g*SOI_b}, p_t	16	467.59	4.28	0.030	153.59
$\Phi_{SOI_b+SOI_w}, p$	4	467.89	4.59	0.026	179.96
Φ_{SOI_w}, p_{g+t}	15	467.93	4.63	0.025	156.20
Φ_{g+SOI_w}, p_t	15	468.46	5.16	0.019	156.73
Φ_{g*SOI_w}, p_t	16	468.94	5.63	0.015	154.94
Φ, p_t	13	469.28	5.98	0.013	162.04
Φ_{SOI_b}, p_g	4	469.35	6.05	0.012	181.42
$\Phi_{g+SOI_b+SOI_w}, p_{g+t}$	17	469.36	6.06	0.012	153.07
Φ_{g+SOI_b}, p	4	469.38	6.07	0.012	181.45
Φ_{g*SOI_b}, p_{g+t}	17	469.69	6.38	0.010	153.40

Table 3.4. Survival rates estimates and standard errors of male and female Barn Swallows breeding in Ontario calculated using model averaging and respective values of average Southern Oscillation Index for breeding season (SOI_b). SOI_w values are not shown since there were no observed effects of SOI_w on survival rates.

ONTARIO					
Year	SOI_b	Males		Females	
		Survival	SE	Survival	SE
2003	-0.1	0.468	0.050	0.458	0.047
2004	-0.3	0.475	0.054	0.463	0.050
2005	-0.1	0.528	0.051	0.517	0.048
2006	-0.3	0.518	0.048	0.507	0.045
2007	0.1	0.494	0.043	0.484	0.039
2008	0.6	0.487	0.043	0.483	0.040
2009	0.2	0.503	0.042	0.496	0.038
2010	1.4	0.451	0.056	0.451	0.053
2011	0.8	0.466	0.066	0.465	0.063

Table 3.5. Survival rates estimates and standard errors of Barn Swallows breeding in Washington State calculated using model averaging and respective values of average Southern Oscillation Index for breeding season (SOI_b) and Southern Oscillation Index for wintering season (SOI_w).

WASHINGTON STATE				
Year	SOI _b	SOI _w	Survival	SE
2000	0.5	1.0	0.416	0.045
2001	-0.1	1.1	0.512	0.044
2002	-0.5	0.2	0.600	0.054
2003	-0.1	-0.5	0.554	0.051
2004	-0.3	0.0	0.576	0.048
2005	-0.1	-0.6	0.552	0.051
2006	-0.3	0.8	0.553	0.048
2007	0.1	-0.4	0.514	0.047
2008	0.6	1.3	0.393	0.050
2009	0.2	1.2	0.461	0.042
2010	1.4	-0.5	0.317	0.076
2011	0.8	2.2	0.345	0.067

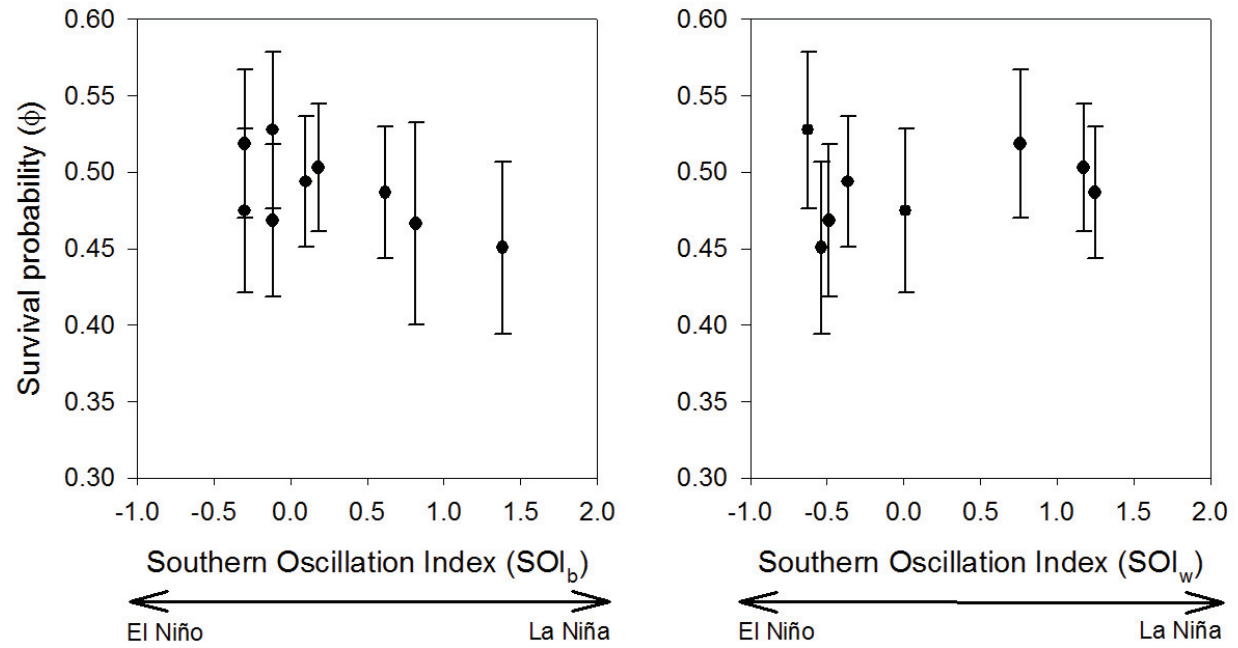


Figure 3.1. Apparent annual survival rates (± 1 SE) of adult Barn Swallows breeding in Ontario from 2002 to 2011 relative to the mean SOI values of breeding (SOI_b) and wintering (SOI_w) season.

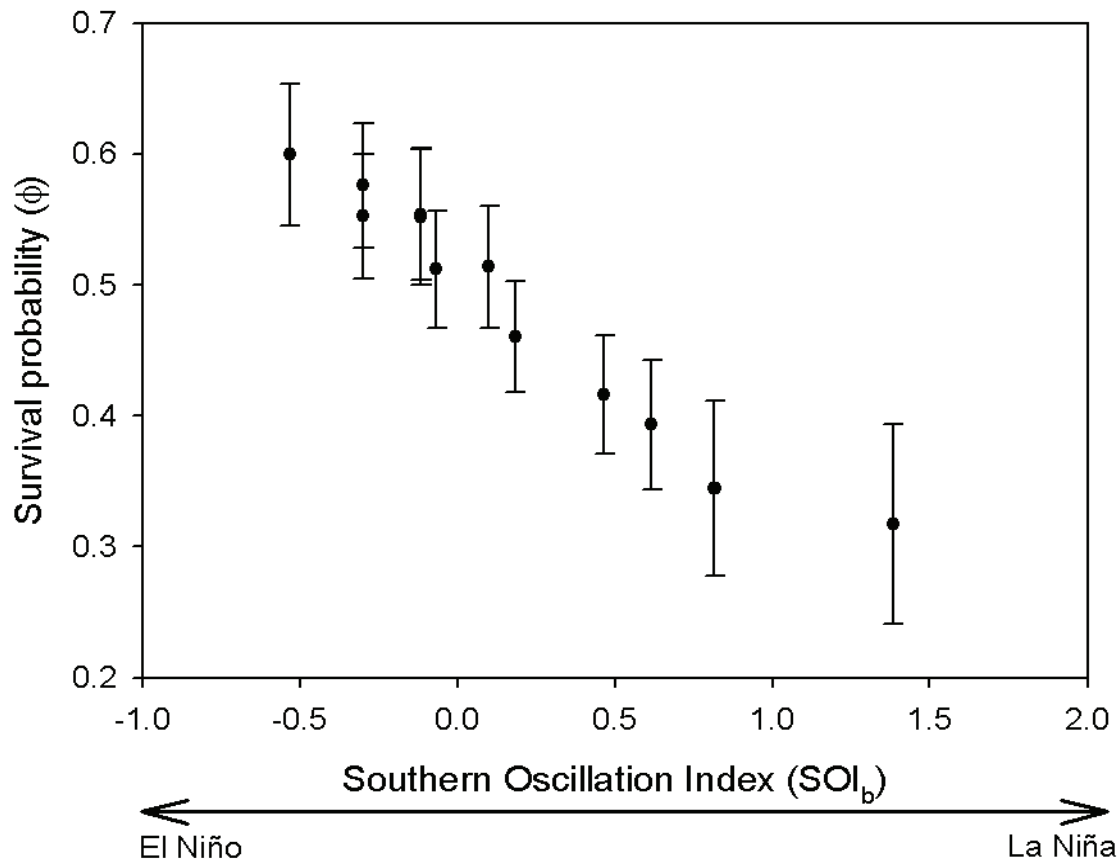


Figure 3.2. Apparent annual survival rates (± 1 SE) of adult Barn Swallows breeding in Washington State from 1999 to 2011 relative to the mean SOI values of breeding season (SOI_b). Negative values of SOI denote El Niño weather conditions while positive values correspond with La Niña conditions.

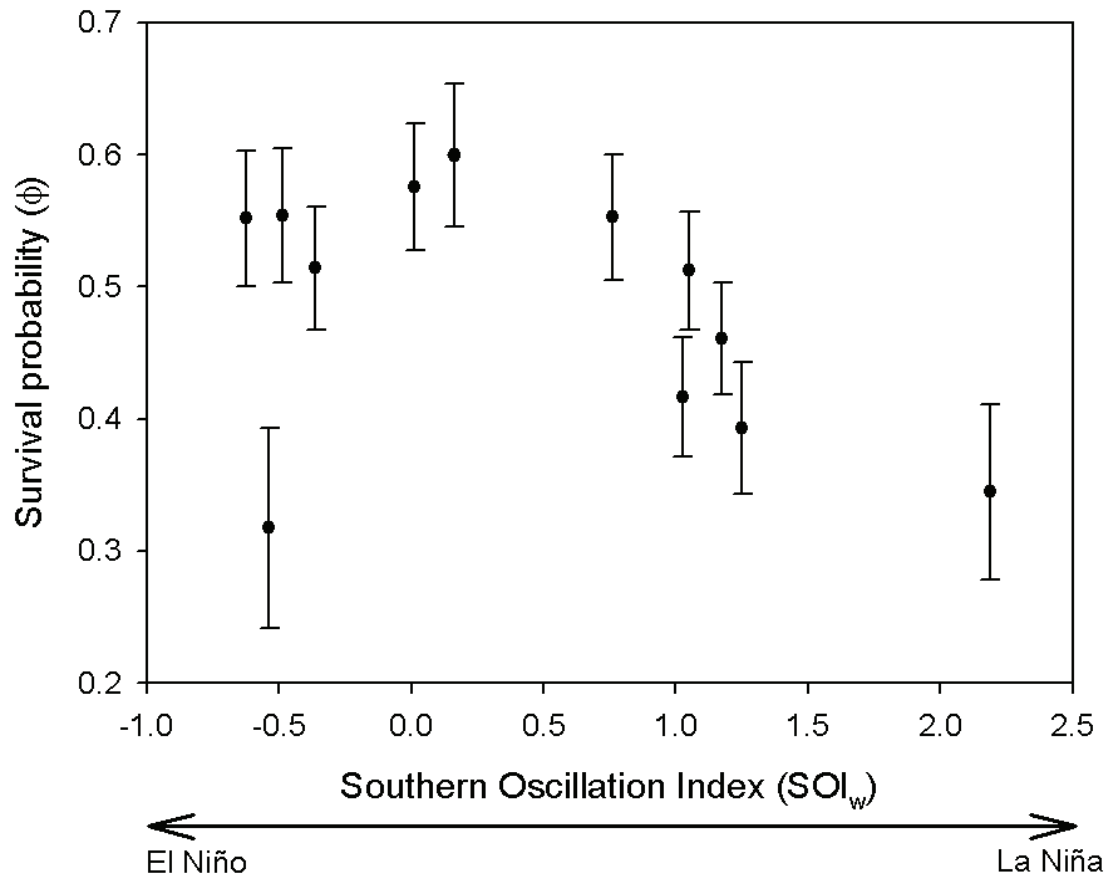


Figure 3.3. Apparent annual survival rates (± 1 SE) of adult Barn Swallows breeding in Washington State from 1999 to 2011 relative to the mean Southern Oscillation Index in the wintering grounds (SOI_w). Negative values of SOI denote El Niño weather conditions while positive values correspond with La Niña conditions.

Survival parameters estimates for Washington State calculated using model averaging methods to account for model selection uncertainty showed that survival probability (Mean \pm SD = 0.495 \pm 0.094) was higher in years with more negative SOI_b values (El Niño years) (Table 3.5. and Figure 3.2). In addition, Barn Swallows breeding in Washington State seem to be also affected to some degree by ENSO conditions in the wintering grounds (SOI_w), since apparent survival rates showed a clear tendency to decline in years with more positive SOI_w values (La Niña years) and to increase in years with more negative values (El Niño years) (Figure 3.3).

Recapture probability for the Ontario colony was best modeled as differing among years and between sexes (Table 3.2.). Model averaging results for Ontario showed that recapture rates for males and females were not different. In Washington State, the most parsimonious model incorporated the variation of recapture probability over time (Table 3.3.). Recapture rate estimates for birds breeding in Washington State calculated using model averaging methods ranged from 0.949 to 0.322 recaptured birds per year (Mean \pm SD = 0.733 \pm 0.218).

3.3.1.2. Effect of length of spring cold periods

Model selection suggested that the number of consecutive days within periods of cold temperatures in the spring (COLD) had a significant negative effect on apparent survival rates of Barn Swallows breeding in Washington State but not in Ontario. In Ontario, the model with best support assumed constant variation of survival (Φp_{g+t}) (Table 3.6.). Inter-annual survival probabilities for Ontario birds based on model averaging suggested that survival probability did not differ over years (Figure 3.4). In Washington State, the model with strongest support assumed the effect of the length of cold periods in the spring in inter-annual survival (Φ_{COLD, p_t}) (Table 3.7.). Survival estimates of birds breeding in Washington State were overall significantly lower in years with a high number of cold periods (Figure 3.5). Historical cold weather data

Table 3.6. Model selection summary output of candidate models of annual survival (Φ) and recapture (p) probabilities for Barn Swallows breeding in Ontario from 2002 to 2011 based on the number of consecutive cold days in the spring. Model notations denote: g = sex groups (male and female), COLD= number of days within periods with maximum daily temperatures $\leq 11^\circ\text{C}$, No subscript = constant over sex groups and year. Only models with AIC_c weights ≤ 0.010 are shown.

Model	Num. parameters	AICc	ΔAICc	AICc weight	Deviance
Φ, p_{g+t}	11	1332.38	0.00	0.296	119.72
Φ_g, p_{g+t}	12	1333.93	1.55	0.136	119.22
$\Phi_{\text{COLD}}, p_{g+t}$	12	1334.19	1.81	0.120	119.47
Φ_t, p_g	11	1334.86	2.47	0.086	122.19
Φ, p_t	10	1335.31	2.93	0.068	124.69
$\Phi_{g+\text{COLD}}, p_{g+t}$	13	1335.64	3.26	0.058	118.87
Φ_g, p_t	11	1336.27	3.89	0.042	123.61
Φ_{g+t}, p_g	12	1336.32	3.93	0.041	121.60
$\Phi_{g*\text{COLD}}, p_{g+t}$	14	1336.65	4.27	0.035	117.82
Φ_{COLD}, p_t	11	1337.30	4.92	0.025	124.63
Φ_t, p	10	1338.22	5.84	0.016	127.60
$\Phi_{g+\text{COLD}}, p_t$	12	1338.25	5.87	0.016	123.54
Φ_{COLD}, p_g	4	1338.52	6.14	0.014	140.08
Φ_{g+t}, p	11	1339.11	6.73	0.010	126.44

Table 3.7. Model selection summary output of candidate models of annual survival (Φ) and recapture (p) probabilities for Barn Swallows breeding in Washington State from 1999 to 2011 based on the number of consecutive cold days in the spring. Model notations denote: g = sex groups (male and female), COLD= number of days within periods with maximum daily temperatures $\leq 11^\circ\text{C}$, No subscript = constant over sex groups and year. Only models with AICc weights ≤ 0.010 are shown.

Model	Num. parameters	AICc	ΔAICc	AICc weight	Deviance
Φ_{COLD}, p_t	14	465.78	0.00	0.347	156.30
$\Phi_{g+\text{COLD}}, p_t$	15	467.73	1.96	0.130	156.00
$\Phi_{\text{COLD}}, p_{g+t}$	15	467.82	2.04	0.125	156.08
Φ, p_t	13	469.28	3.50	0.060	162.04
$\Phi_{\text{COLD}}, p.$	3	469.62	3.84	0.051	183.75
$\Phi_{g+\text{COLD}}, p_{g+t}$	16	469.88	4.10	0.045	155.88
$\Phi_{g*\text{COLD}}, p_t$	16	469.98	4.20	0.043	155.98
Φ, p_{g+t}	14	471.16	5.38	0.024	161.68
Φ_t, p_t	24	471.35	5.57	0.021	138.49
Φ_g, p_t	14	471.41	5.63	0.021	161.93
Φ, p	2	471.42	5.65	0.021	187.61
$\Phi_{g+\text{COLD}}, p$	4	471.49	5.72	0.020	183.57
Φ_{COLD}, p_g	4	471.59	5.81	0.019	183.66
$\Phi_{g*\text{COLD}}, p_{g+t}$	17	472.13	6.35	0.015	155.84

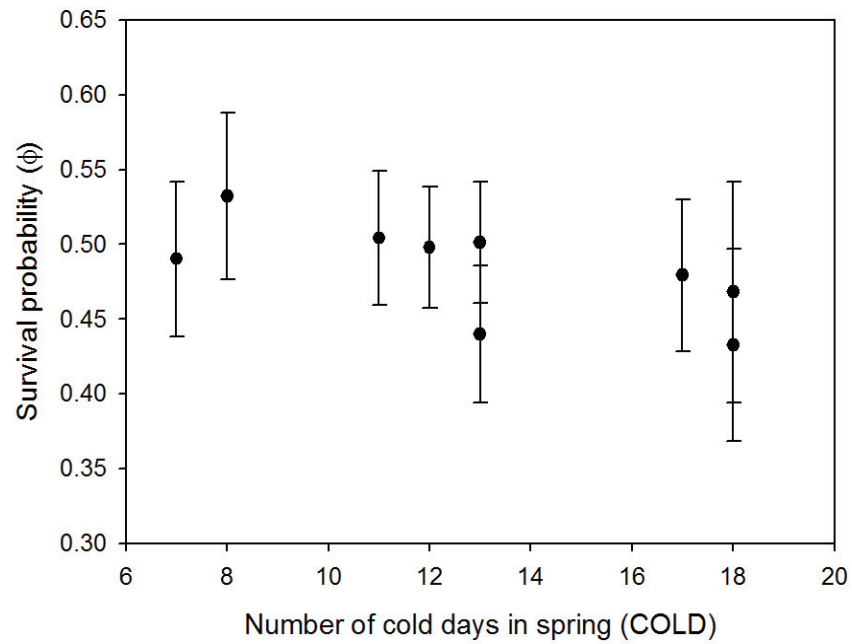


Figure 3.4. Apparent annual survival rates (± 1 SE) of adult Barn Swallows breeding in Ontario from 2002 to 2011 relative to the number of days within periods with maximum daily temperatures $\leq 11^{\circ}\text{C}$ in the spring.

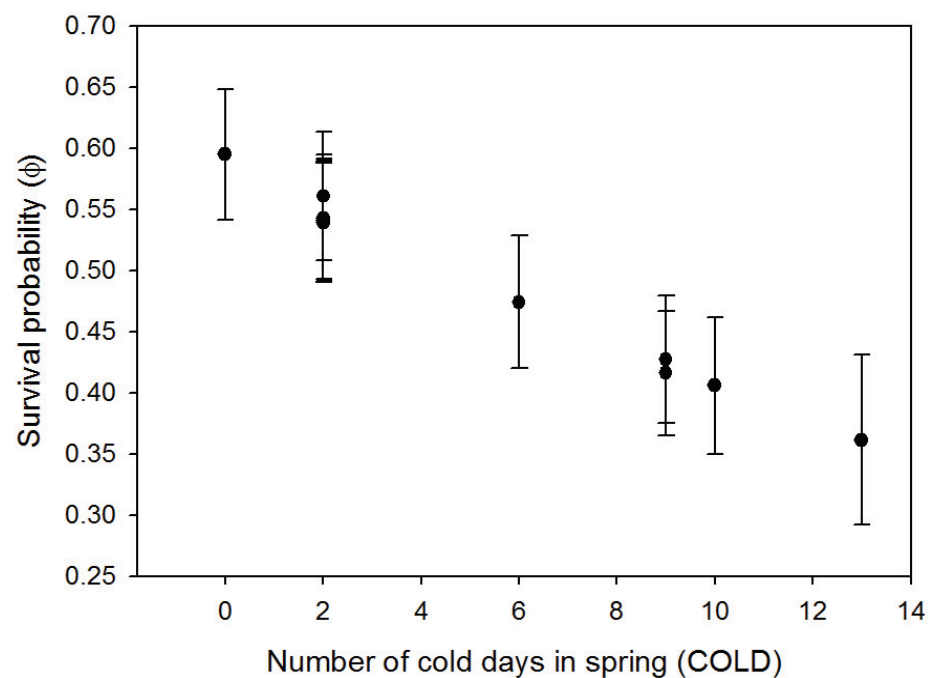


Figure 3.5. Apparent annual survival rates (± 1 SE) of adult Barn Swallows breeding in Washington State from 1999 to 2011 relative to the number of days within periods with maximum daily temperatures $\leq 11^{\circ}\text{C}$ in the spring.

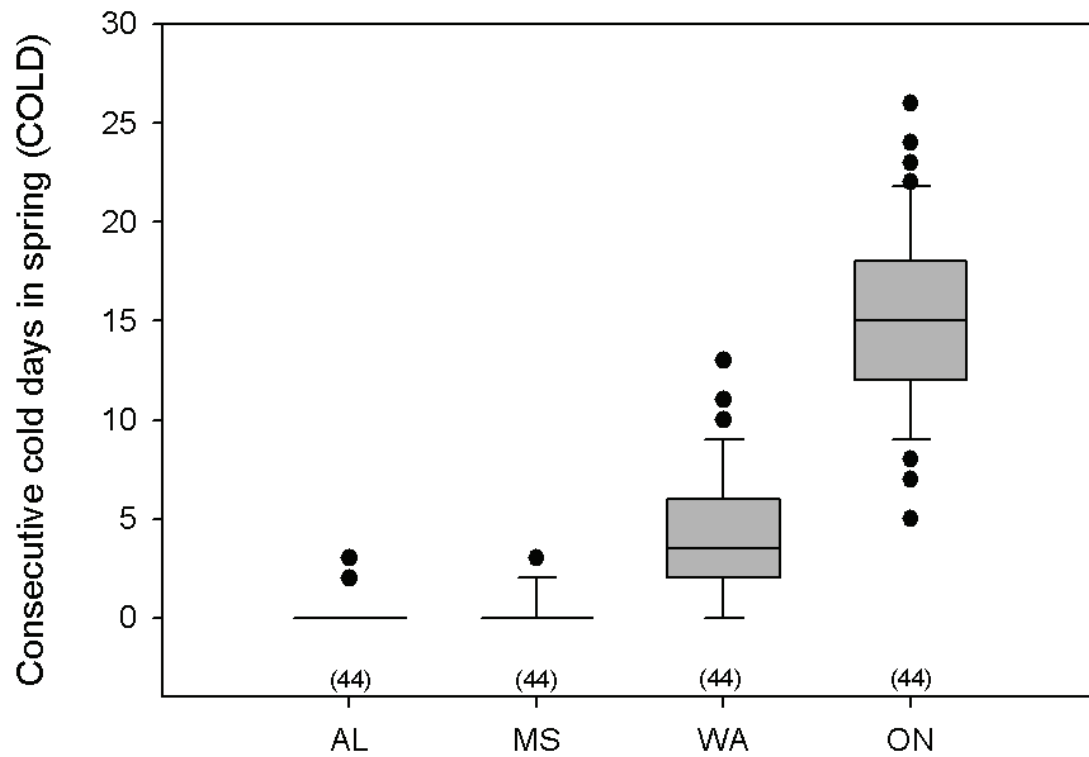


Figure 3.6. Consecutive number of days within periods with maximum daily temperatures $\leq 11^{\circ}\text{C}$ in spring from 1968 to 2011 in Alabama (AL) and Mississippi (MS), where Barn Swallow populations are stable, and in Washington State (WA) and Ontario (ON), where populations are in decline. Numbers in brackets denote number of years included in the study.

comparisons between weather stations in southern US and stations in Ontario and Washington State showed that there were significant differences in the number of consecutive cold days in the spring among areas where populations were stable and in decline (ANOVA: $F_{3,172}=243.8$, $p<0.01$, $n=176$). The extent of periods of consecutive cold days was significantly lower in Alabama and Mississippi, with values between 0 and 4, than in Washington State and Ontario, which ranged between 14 to 2 and 27 to 5 respectively (Figure 3.6).

3.3.2. Reproductive success and spring weather

Reproductive success differed significantly among years in both breeding colonies (Table 3.8.). In Manitoba, reproductive success and number of active pairs in the mid 80's were higher than in 2009 and 2010. Reproductive success from 1984 to 1986 was 3.31 ± 0.27 fledglings/year, while for the two 2009 to 2010 period was 2.20 ± 0.35 fledglings/year. Fewer active pairs were found at this site in 2009 and 2010 (12 – 14 pairs) compared the 80's (17 – 25). In Washington State, reproductive success was particularly low in 2008 but otherwise varied between 3.1 and 3.9 over the 1999 to 2010 period. Total active nests in Washington State varied significantly over the 12-year period, with three minimums in 2001, 2005 and 2010 and two maximums in 2004 and 2007. Values of reproductive success were similar for Barn Swallows breeding in Manitoba and Washington State. However, when reproductive success for the same years (2009 and 2010) was compared between different colonies; values in Washington State were significantly higher than in Manitoba.

The most parsimonious model included four variables related to spring temperature but not precipitation, suggesting a larger effect of temperature on reproductive performance (Table 3.9.). When the actual values of reproductive success were plotted against estimated values calculated using the best model selected (Figure 3.7), a poor fit of the model to the data was found ($r^2 = 0.17$), suggesting some explanatory power of the model selected but also some caveats.

Table 3.8. Arrival date to the site, total number of active pairs (Manitoba) and nests (Washington State) in the breeding season and reproductive success (fledglings/nest) over the years for two breeding colonies of Barn Swallow in Manitoba (Delta Marsh) and Washington State (Seattle). Data from 1984-1986 was obtained from Barclay (1988).

Year	Arrival date	Total pairs/nests	Reproductive Success
Manitoba			
1984	Early May	25	3.1
1985	Early May	25	3.2
1986	Early May	17	3.6
2009		14	2.5
2010	11-May	12	2.0
Washington State			
1999	22-Apr	25	3.4
2000	17-Apr	21	3.8
2001	19-Apr	13	3.6
2002	08-Apr	19	3.4
2003	20-Apr	24	3.5
2004	13-Apr	32	3.1
2005		16	3.9
2006	16-Apr	26	3.9
2007	07-Apr	30	3.3
2008	05-Apr	28	2.2
2009	07-Apr	20	3.2
2010	11-Apr	18	3.9

Table 3.9. Competing general linear models of effects of spring weather variables on reproductive success of Barn Swallow in Manitoba and Washington State over the years. Models are based on the number of fledglings/nest from 1984-1986 and 2009-2010 for Manitoba and 1999-2010 for Washington State. Interactions between explanatory variables were included in the analysis and are denoted with a colon symbol. Model in bold denotes the most parsimonious model.

Models	df	Residual deviance	AIC _c
COLD + MeanPrecip + COLD:MeanPrecip + MaxTemp + MinTemp + MaxTemp:MinTemp	8	1.61	24.17
COLD + MeanPrecip+ MaxTemp + MinTemp + MaxTemp:MinTemp	7	1.83	24.37
COLD + MaxTemp + MinTemp + MaxTemp:MinTemp	6	1.95	23.43
MaxTemp + MinTemp + MaxTemp:MinTemp	5	2.79	27.51

Table 3.10. Parameter estimates, standard error, t statistic, p-value, and upper and lower confidence limits (95%) for the weather variables included in the model selected as the model that best fit data on reproductive success of breeding colonies of Barn Swallows in Manitoba (1984-1986, 2009, 2010) and Washington State (1999-2010). All variables and intercept are significantly significant.

Parameters	Estimate	Standard Error	t	p-value	95% CI	
					Lower	Upper
Intercept	-96.09	26.982	-3.56	0.004	-154.89	-37.31
COLD	-0.07	1.436	3.72	0.003	2.21	8.46
MinTemp	14.35	3.817	3.76	0.003	6.04	22.67
MaxTemp	5.34	0.031	-2.27	0.042	-0.14	-0.003
MinTemp:MaxTemp	-0.77	0.202	-3.79	0.003	-1.21	-0.33

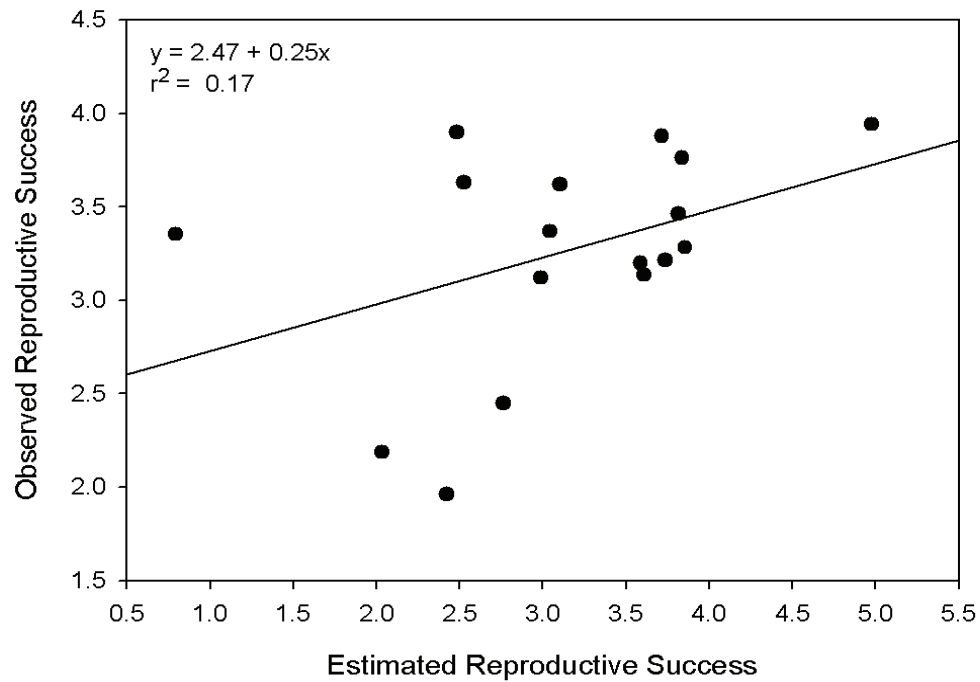


Figure 3.7. Model validation graph showing estimated values of reproductive success for Barn Swallows breeding in Manitoba (1984-1986, 2009, 2010) and Washington State (1999-2010) in the X axis and observed values of reproductive success for those colonies in the Y axis.

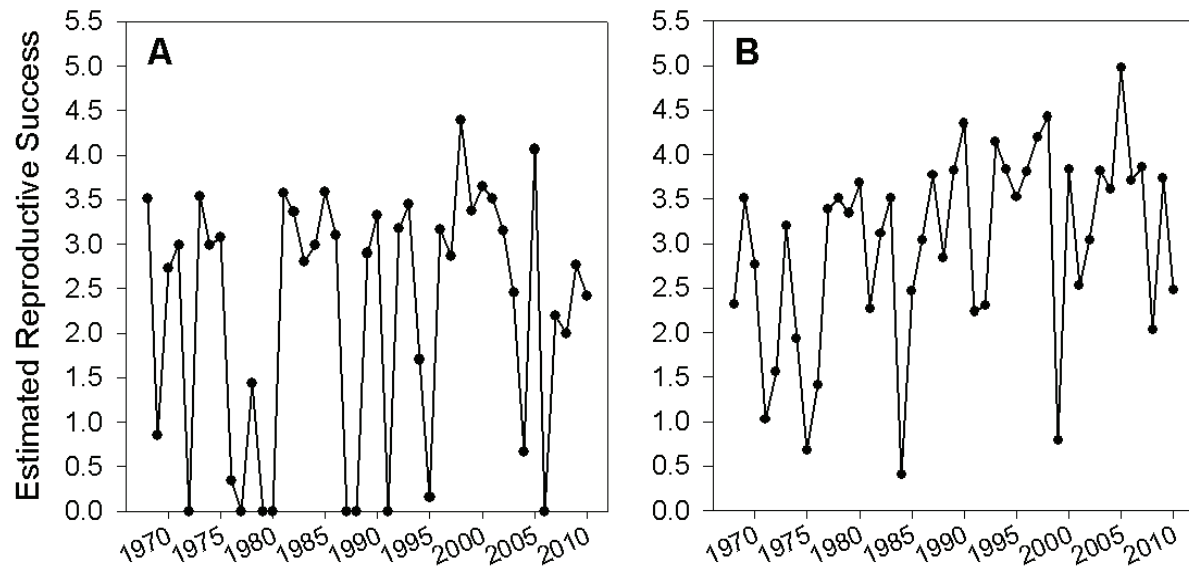


Figure 3.8. Estimated reproductive success values for Barn Swallow colonies in Manitoba (A) and Washington State (B) since 1968 to 2010. Values were calculated based on the most parsimonious model selected using model selection and AICc criterion.

The length of consecutive day-periods of cold weather and the interaction between average minimum and maximum temperatures in spring were negatively correlated with reproductive success. In contrast, minimum and maximum temperatures were positively correlated (Table 3.10.).

Estimations of reproductive success since 1968 using the created model for breeding colonies in Manitoba and Washington State suggest no clear pattern of change in the mid 80's for either of the colonies (Figure 3.8). Manitoba had higher number of years with values of 0 of reproductive success (Figure 3.8a), while Washington State did not experience years with that low fecundity. In fact, values in this colony seem to have increased over the years starting in the early 80's (Figure 3.8b).

3.3.3. Wintering ground stressors

Overall, feathers of Barn Swallow did not differ in CORT levels between stable and declining breeding populations (Table 3.11. and Figure 3.9a; ANOVA: $F_{1,87}=1.502$, $p=0.22$, $n=89$), as well as among breeding populations throughout North America (Table 3.11. and Figure 3.9b.; ANOVA, Tukey HSD: $F_{6,82}=1.965$, $p=0.08$, $n=89$). Additionally, there were not significant differences in CORT levels among wintering locations in South America (Table 3.11. and Figure 3.9c. ANOVA, Tukey HSD: $F_{3,38}=0.735$, $p=0.54$, $n=42$). No significant relationship between CORT and stable isotope values of feathers was found (Figure 3.10; $\delta^2\text{H}$: Pearson correlation= 0.109 , $p>0.1$, $n=42$; $\delta^{13}\text{C}$: Pearson correlation= 0.070 , $p>0.1$, $n=42$; $\delta^{15}\text{N}$: Pearson correlation= -0.012 , $p>0.1$, $n=42$), suggesting that feather-CORT levels were not related with geographical origin of feathers.

Table 3.11. Sample size, mean, standard deviation and standard error of feather corticosterone (CORT) values (pg/mm) of adult Barn Swallows grouped based on breeding population origin, population trend of state/province where samples were collected, and wintering areas in South America. Group 1, Group 2, Group 3, Group 4 notations denote groups created using hydrogen, carbon and nitrogen stable isotope values of feathers.

	n	Mean (pg/mm)	SD	SE
Breeding areas				
Ontario	25	4.31	1.01	0.20
British Columbia	5	3.29	1.64	0.73
Washington State	10	4.34	0.70	0.22
Saskatchewan	5	4.69	0.90	0.41
Texas	15	4.69	0.70	0.18
Alabama	15	4.73	0.82	0.21
Mississippi	14	4.06	1.21	0.32
Trend				
Stable	44	4.51	0.96	0.15
Declining	45	4.24	1.05	0.16
Wintering areas				
Group 1	8	3.90	1.52	0.54
Group 2	13	4.54	1.02	0.28
Group 3	18	4.58	1.04	0.24
Group 4	3	4.23	1.34	0.78

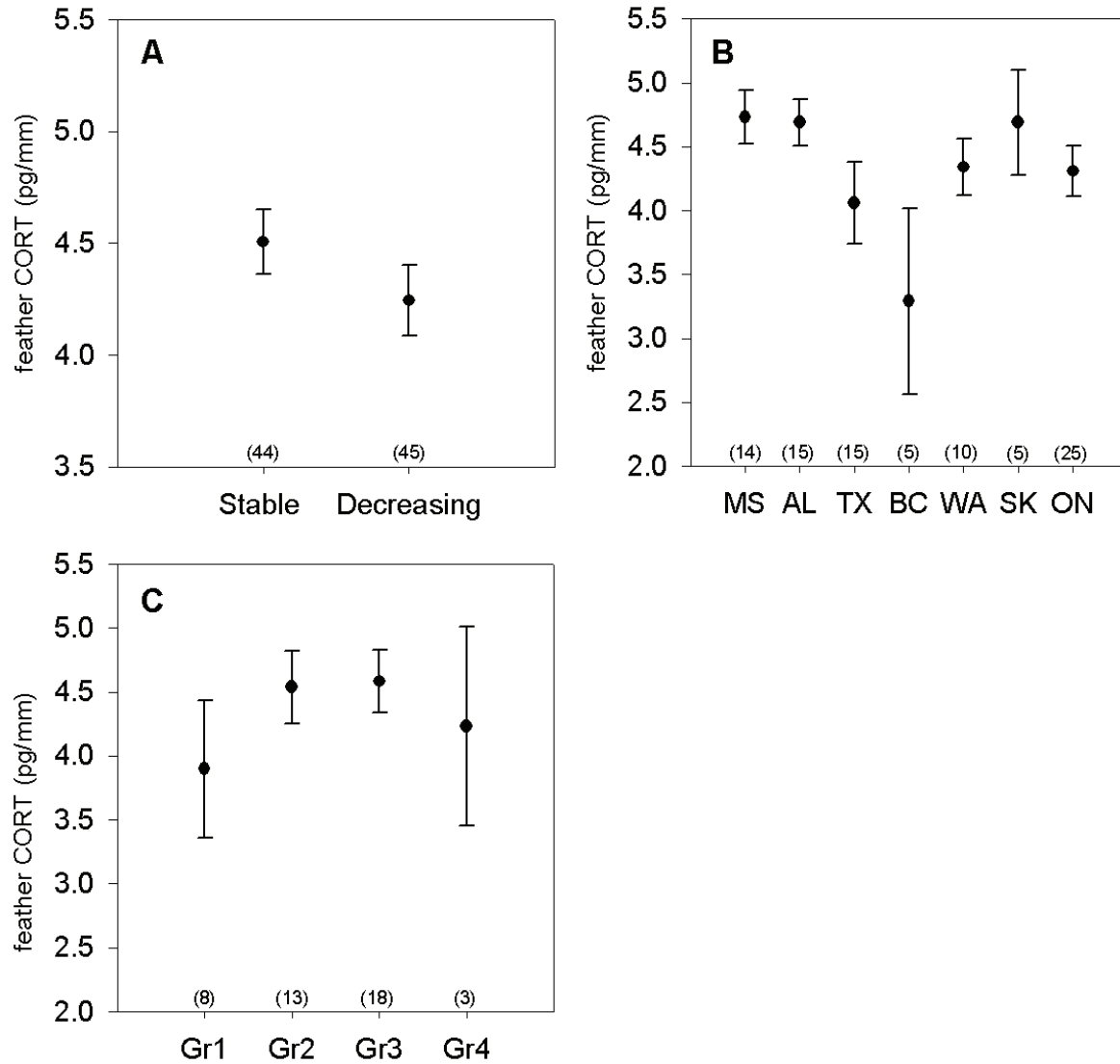


Figure 3.9. Mean (\pm SE) feather corticosterone (CORT) values of adult Barn Swallows. Graph A shows CORT values of stable populations (Stable) and declining populations (Declining); Graph B shows CORT values of breeding populations across North America (Mississippi, MS; Alabama, AL; Texas; British Columbia, BC; Washington State, WA; Saskatchewan, SK; Ontario, ON); Graph C shows CORT values of feathers grown in four different wintering locations in South America (Gr1: Western areas west of Andes, Gr2: Western areas east of Andes, Gr3: North-eastern central areas, Gr4: North-eastern areas). Numbers in brackets denote sample sized. Note different scale of CORT values.

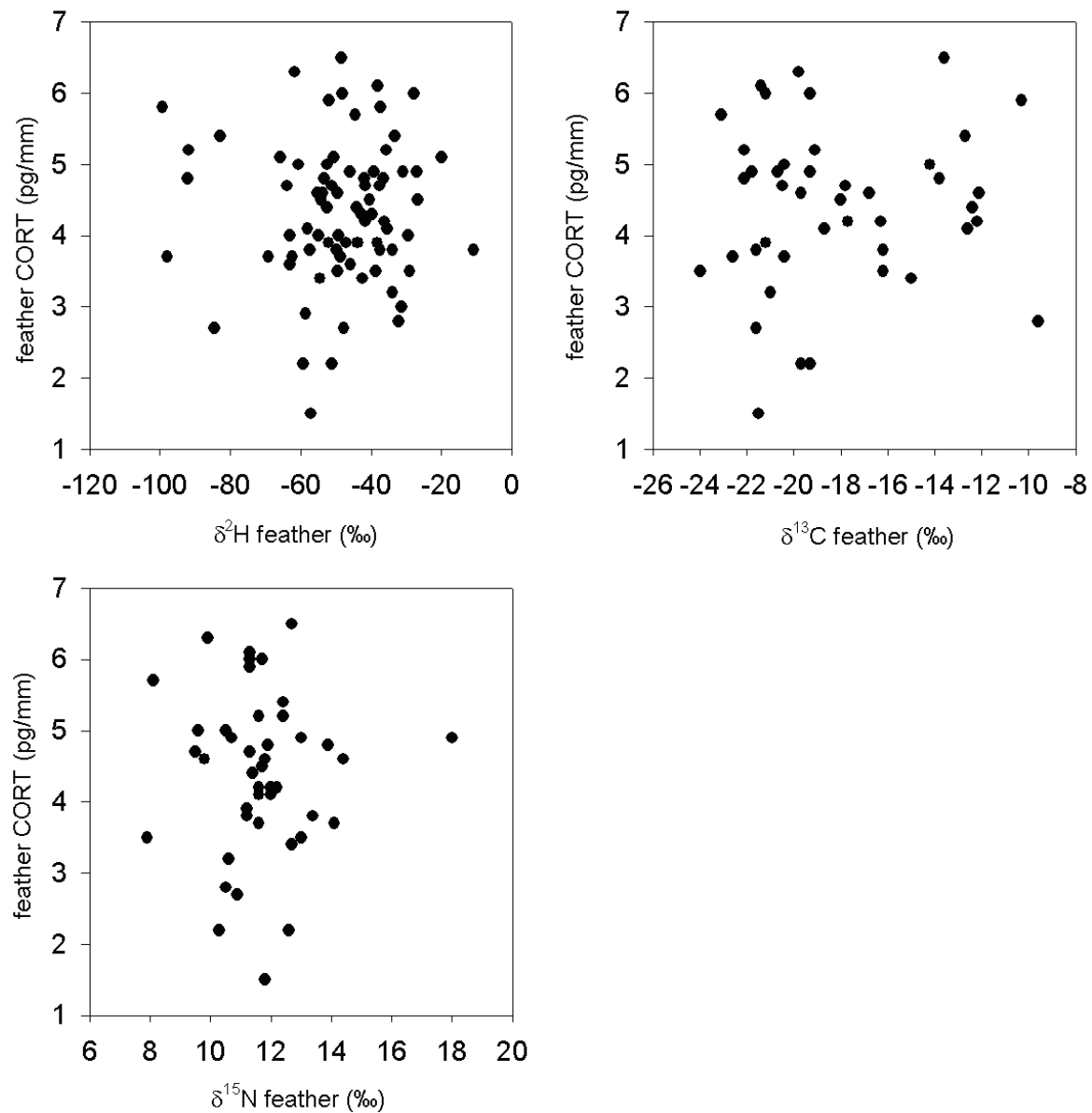


Figure 3.10. Relationships between hydrogen, carbon and nitrogen stable isotope values and measurements of corticosterone (CORT) of feathers of adult Barn Swallows grown in the wintering grounds.

3.4. Discussion

3.4.1. Annual survival and weather

A clear effect of ENSO on inter-annual survival of Barn Swallows was found for birds breeding in Washington State but not for birds breeding in Ontario. Apparent annual survival of swallows in Washington State were strongly and negatively correlated with average SOI values for the breeding months, showing that they were lower during La Niña years and higher during El Niño years, while survival rates for Ontario birds remained constant over time.

These results can be explained based on the differential effect of ENSO across North America. Temperature and precipitation rates in western and northern areas of North America, where the Washington State population is located, tend to be highly affected by ENSO; while north-eastern areas, such as Ontario, tend to be not so affected. (Shabbar and Khandekar 1996, Shabbar et al. 1997). In addition, in western North America La Niña phase characterizes by colder and wetter conditions especially in the winter, and these conditions have been previously shown to have a negative effect on survival of aerial insectivore species (Dence 1946, Ligon 1968, Whitmore et al. 1977, Brown and Brown 1999b).

Weather conditions on the wintering grounds appear to have also differential effects on inter-annual survival rates of Barn Swallows breeding in Washington State and Ontario. Annual survival probabilities of Washington State swallows varied primarily with ENSO-related weather conditions on the breeding grounds, while weather conditions on the wintering grounds seem to have an additional but not so strong effect. Survival rates in Washington State were significantly higher during El Niño-winters, while survival rates decreased in years characterized by La Niña-winters. The fact that the best model for Washington State did not include SOI in the wintering grounds could be due to the effect of the low value of inter-annual survival probability for one El Niño winter.

These results suggest that Barn Swallows breeding in Washington State may migrate to areas in south-eastern South America where ENSO correlates with precipitation rates. In those areas, El Niño-years characterized by high rainfall rates during the wintering months (Ropelewski and Halpert 1987), and since the amount of precipitation on the wintering grounds is positively correlated with the amount of insect biomass available, these individuals may experience lower mortality rates during those years (Szép 1995, Sillett et al. 2000, Strong and Sherry 2000). In contrast, no significant correlation between survival and SOI for the winter months was found for the breeding colony in Ontario. A similar lack of correlation between survival probability of a population and ENSO conditions on wintering grounds have been shown for Black-throated Blue Warblers (*Dendroica caerulescens*) breeding in New Hampshire (Sillett et al. 2000). Annual survival rates of a population wintering in Jamaica correlated with ENSO changes but no correlation was found for a breeding population in New Hampshire. Sillett et al. (2000) suggested that breeding individuals from the New Hampshire site disperse more extensively on the wintering grounds, occupying some areas where the impact of ENSO on weather conditions is important and others where ENSO has no effect. In a study of Purple Martins (*Progne subis*) breeding in north-western Pennsylvania, Stutchbury et al. (2009a) also found no evidence that ENSO influenced adult survival and hypothesized that this lack of correlation was due to low migratory connectivity. In my study, differences in the effect of ENSO-related conditions on the wintering grounds between colonies may be related to the geographical location of the wintering areas and the degree of migratory connectivity of the populations. Since the effect of ENSO on weather conditions in South America is also geographically dependant, birds breeding in Ontario may winter in areas in South America not so severely influenced by ENSO. In addition, results from Chapter 2 suggest significantly weaker migratory connectivity for Barn Swallows breeding

in Ontario, suggesting that these birds may disperse extensively in the wintering grounds. Therefore, the effect of ENSO on the annual survival probability of the population may be difficult to detect since individuals could be affected differently by ENSO at these different geographical locations. In contrast, results of migratory connectivity for birds breeding in Washington State suggest stronger connectivity for this population, so individuals breeding in this location may be segregating more extensively on the wintering grounds going to areas where the effect of ENSO in weather is more significant. I found there was no correlation between winter and summer SOI indices, so they seem to be two independent variables feasible to be used as a measure of weather conditions on breeding and wintering months. However, it should be considered that these variables are additionally including weather conditions during migration and not only breeding and wintering periods.

Extensive cold weather periods early in the breeding season were negatively associated with apparent survival rates of Barn Swallows breeding in Washington State, but there was no correlation for birds breeding in Ontario. I additionally found that the number of consecutive cold spring-days for the period 1968-2011 was particularly high in those areas showing negative population trends (Ontario and Washington State), while regions where Barn Swallow populations tend to be stable or increasing (Mississippi and Alabama) experienced fewer cold weather events, suggesting that this variable can play a role in the differential population dynamics of the species. Although long-term effects of abnormal high mortality episodes are difficult to prove, their immediate effects on population trends have been previously documented for aerial insectivore species. For instance, populations of Barn Swallows breeding in Germany and Denmark were shown to be reduced by 20%-50% due to an early period of cold during fall migration in the previous year (Møller 2011). Similar observations were reported for breeding

Cliff Swallows in the northern Central Plains, where the frequency of unseasonable weather periods in spring caused large mortality events which may have lead to a natural selection of birds arriving late in the season (Brown and Brown 2000). However, the frequency of these cold episodes in the spring seems to have not increased in the last few decades when the intense declines of the species was initiated, and we cannot conclude that this factor therefore driving population declines of Barn Swallows.

Average apparent survival rates of Barn Swallows breeding in Ontario and Washington State were similar and were slightly higher when compared with values from other breeding colonies in Europe. Møller and Szép (2002) found that survival probabilities of a Danish population of Barn Swallows varied over time during a 10-year period, showing survival probabilities for males of 34.3% and 33.8% for females. Additionally, overall survival of Barn Swallows breeding in Britain was approximately 40% (Robinson et al. 2008). A study on the effects of radiation caused by the explosion of the nuclear reactor at Chernobyl on survival of Barn Swallows showed extremely low survival probabilities in highly contaminated areas (28%) in comparison to areas with low contamination levels (40%) (Møller et al. 2005, Møller et al. 2012). Further studies using stable isotope analyses suggested that the Chernobyl population is recruiting individuals from an extensive wintering area (Møller et al. 2006).

Ontario and Washington State birds showed similar inter-annual survival rates between sexes, suggesting that similar factors might be influencing the survival rate of the two sexes. These findings agree with previous studies of survival rates in Sand Martins (*Riparia riparia*) breeding in Hungary (Szép 1995) and Cliff Swallows in the northern Great Plains (Brown and Brown 1996). In the case of European Barn Swallows, survival rates of males and females breeding in

Denmark did not vary in parallel though time and were instead negatively correlated with tail length for males and positively for females (Møller and Szép 2002).

3.4.2. Reproductive success and spring weather

Environmental conditions early in the breeding season related to ambient temperature had a significant effect on the reproductive performance of Barn Swallows breeding in Manitoba and Washington State, while weather variables associated with precipitation had little effect.

In insectivorous birds, timing of breeding is often synchronized with the peak in insect abundance to enhance reproductive performance (Lack 1968, Visser et al. 1998) and previous studies have shown positive relationships between an increase in food supplies and reproductive parameters (Boutin 1990). However, periods of low temperature could reduce the amount of insects available during the breeding season to raise young (Bryant 1975, O'Connor 1979) and can cause smaller egg clutches, reduced immune response and body condition of young and overall lower reproductive success rates (Ojanen et al. 1981, Dawson 2008). In contrast, warmer ambient temperatures could lead to a greater food supply and have been proven to relate to a reduction in incubation time, increase of body mass, as well as with a enhance of development rate of young swallows (Dawson et al. 2005, Dunn 2006, Ardia et al. 2010). Despite previous findings suggesting the negative effect of cool and rainy days on reproductive success of insectivore birds (Collister and Wilson 2007, Arlettaz et al. 2010); this study found no correlation between annual reproductive success and precipitation weather variables, suggesting that precipitation at the areas where the study was performed is not a limiting factor.

Historical reproductive success values estimated from 1968 to 2011 showed some variation over the years, potentially related to normal annual weather anomalies. However, no significant decrease in reproductive performance since 1968 was found for either of the two studied colonies. Apart from the effect that weather conditions could have on the reproductive success of

Barn Swallows, there are other factors especially related to nest predation that could affect fecundity. These results suggest that population declines experienced in those locations might not be related with a decrease in fecundity rates over the years due to weather conditions. However, it cannot be concluded that fecundity has not contributed to population declines, since there might be other factors having an effect on reproductive success that should be considered.

3.4.3. Wintering ground stressors

Barn Swallows experiencing stressors on wintering grounds where they grow feathers were expected to show higher CORT levels than unstressed populations. However, no differences in feather CORT concentrations were found for individuals breeding in stable compare to declining populations, or for individuals occupying different breeding and/or wintering locations, possibly because all populations were exposed to similar wintering conditions. Alternatively, individuals may indeed be exposed to different stressors on the wintering grounds, but the assumption that variation in CORT levels on the wintering grounds is correlated with relative fitness is yet to be proven for this species (Breuner et al. 2008, Bonier et al. 2009, Sheriff et al. 2011).

The no significant correlation between feather-concentrations of CORT and feather $\delta^2\text{H}$, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values corroborates that geographic location of wintering grounds and habitat used during the non-breeding season had little effect on stress-related physiological responses during the molt phase. A recent study has made the first successful attempt to combine stable isotope analyses and CORT level measurement techniques to test the effect of environmental factors on the stress response of birds. Barger and Kitaysky (2012) studied the feeding behavior of two seabird species with highly similar dietary needs based on stable isotope profiles of blood and their physiological stress response to changes in food availability and oceanographic conditions. Additionally, Marra et al. (1998) and Marra and Holberton (1998) showed that individuals wintering in low-quality scrub habitats (with more enriched levels of ^{13}C) presented elevated

plasma CORT concentrations and more deteriorated physical condition than those wintering in high-quality mangrove habitats (with more depleted levels of ^{13}C). Results from my study may not correspond with Marra et al. (1998) and Marra and Holberton (1998) potentially because stressors in the wintering grounds are not limiting factors affecting population sizes of North American Barn Swallows or due to differences in the applied techniques to measure CORT.

Overall, this study suggests a differential effect of ENSO on inter-annual survival rates of Barn Swallows breeding in Washington State and Ontario, potentially due to geographical variation in ENSO effect on weather conditions across North America and the degree of migratory connectivity of populations. Local weather conditions related to temperature variables (especially length of cold weather periods) were shown to have an effect on reproductive success rates of Barn Swallows, but there has not been a clear decline on reproductive success modeled by changes in weather over time. In addition, analyses of CORT levels in feathers did not reveal enough evidence to suggest that declining populations are subjected to stronger winter stressors than stable populations.

CHAPTER 4. SUMMARY AND SYNTHESIS

Establishing geographic links between different stages of the annual cycle (breeding, migration and wintering) of migratory species is fundamental to our understanding of factors limiting their populations (Webster et al. 2002, Webster and Marra 2005). Factors on the breeding grounds have an important effect on fecundity rates as well as age-specific survival, while factors on the wintering grounds mainly have an impact on overwinter survival (Sherry and Holmes 1995). Periods of the annual cycle are inextricably linked and events occurring during previous seasons could have an effect on subsequent seasons and influence population sizes (Webster and Marra 2005). A large variety of extrinsic and intrinsic markers have been used to track migratory movements of avian species. Specifically, the abundance of naturally occurring stable isotopes in avian tissues have been one of the most applied techniques to evaluate migratory connectivity of populations (Hobson and Norris 2008). Other intrinsic markers such as genetics, contaminants, parasites, or trace elements have been also combined with stable isotopes to improve inferences (Ricklefs et al. 2005, Smith et al. 2005, Boulet et al. 2006, Hobson and Wassenaar 2008, Poesel et al. 2008, Behrooz et al. 2009, Szép et al. 2009, Yogui and Sericano 2009, Chabot et al. 2012, Hobson et al. 2012d).

The Barn Swallow (*Hirundo rustica*), a long distance migrant and an aerial insectivore, has declined drastically in most of North America but its populations remain stable in the southern USA (Nebel et al. 2010, Sauer et al. 2011, Bird Studies Canada et al. 2012). Reasons for these differential trends and whether factors on breeding and/or wintering grounds could be causing these declines remain unclear. Some of the most likely factors affecting populations negatively in both breeding and wintering areas are habitat loss, habitat degradation (e.g. predation, food availability, diseases and parasites), weather stochasticity, and human persecution (i.e.

destruction of nests and nest sites). Here, I relied on stable isotope analyses ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, $\delta^2\text{H}$) of Barn Swallow feathers grown on the wintering grounds to establish patterns of migratory connectivity of breeding populations of the species. I also evaluated evidence for factors operating during different stages of the annual cycle causing regional differences in population declines. The approach was to: 1) examine the impacts of ENSO-related weather conditions on breeding and wintering areas on annual survival, 2) investigate the influence of weather conditions on the breeding grounds on annual fecundity rates, and 3) study the potential differential effect of stressors on the wintering grounds on stable and declining populations

4.1. Wintering origins and migratory connectivity

Measurements of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^2\text{H}$ on feathers can provide information about likely geographic origins of birds during molt (Hobson and Wassenaar 2008), and this information could be of great importance in characterizing the degree of migratory connectivity of populations. $\delta^2\text{H}$, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of winter-grown feathers of Barn Swallows and prior information on distribution of vegetation types in South America were used in Chapter 2 to identify potential wintering areas of individuals from different breeding populations in North America and to evaluate migratory connectivity.

Populations of North American Barn Swallows presented a diverse range of migratory connectivity based on $\delta^2\text{H}$, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses and the assignment of individuals from same populations to a single or multiple isotopic clusters. Populations in eastern and western North America showed a stronger pattern of segregation on the wintering grounds than populations located in the central region of the breeding range of the species. This pattern of differential levels of connectivity among populations was also found for the species in Europe (Ambrosini et al. 2009, Hobson et al. 2012a).

When migratory connectivity of Barn Swallows was compared with Cliff Swallows (*Petrochelidon pyrrhonota*), a stronger pattern of connectivity was found for the most colonial species, suggesting a stronger effect of the heritable element which force individuals from the same breeding colony to return to the same breeding location (Brown and Brown 2000) for Cliff than Barn Swallows.

A progressive longitudinal shift of wintering grounds was additionally found for the species combining feather stable isotope profiles and the theoretical distribution of C3 and C4 plants in South America as a prior. Most likely wintering areas for northern and western breeding birds corresponded with western South America, while birds breeding in southern and eastern North America tended to occupy areas in north-eastern South America, suggesting that the dispersal of Barn Swallows is limited differently in some parts of the breeding range than in others, potentially due to different migratory routes followed by individuals. These findings agree with previous studies on European Barn Swallows which suggested a spatial structure in wintering origins for Barn Swallows (Evans et al. 2003, Hobson et al. 2012a).

Populations of Barn Swallow that exhibit a stable/increasing population trend (i.e. Mississippi and Alabama) showed overall stronger patterns of connectivity than the rest of populations in North America. These finding contrast with previous studies which suggested a higher vulnerability to factors in the wintering grounds of populations with strong migratory connectivity (Dolman and Sutherland 1995, Webster et al. 2002, Webster and Marra 2005) and evidence the potential role that wintering grounds factors can be playing in population dynamics of Barn Swallow in North America. The majority of birds breeding in these stable/increasing regions occupy areas in north-eastern South America, which exhibit certain characteristics highly beneficial for Barn Swallows, such as warm temperatures and high precipitation rates all year

around, and high availability of foraging areas (Szép 1995, Sillett et al. 2000, Strong and Sherry 2000, Morelo 2002). In contrast, most of individuals from declining populations tend to overwinter in western and central South America, where temperatures and precipitation rates are significantly lower and good quality foraging areas are significantly less available (Morelo 2002). Despite these findings, there is no evidence for a recent change in habitat quality for those western regions in the past few decades when population declines started to be more severe and we are therefore not able to relate those population declines with habitat quality.

This study has provided novel and significant information on migratory connectivity between breeding and non-breeding areas and wintering origins of Barn Swallows breeding in different locations across North America. Despite the apparent limitations of stable isotope techniques on the identification of geographical origins, the use of a multi-isotope approach and the combination of prior information on geographic distribution of vegetation types has resulted extremely useful to constrain geographic origins of migrants and these results have improved significantly the limited information regarding seasonal linkages of a long-distance migrants' population. However, future studies combining direct-tracking techniques or geographical distribution of trace elements is needed to further constraint the broad geographic origins of Barn Swallows.

4.2. Factors on breeding and wintering grounds

4.2.1. ENSO-related weather conditions

Despite the growing concern regarding declines in populations of aerial insectivore species like Barn Swallow, potential reasons for population declines across North America remain poorly known. Several studies have attempted to identify specific factors that could be driving demographics of migratory aerial insectivore species in decline. However, identifying these factors is extremely challenging due to the large variety of confounding effects that affect annual

survival and reproduction rates across the entire annual cycle of migratory species (Sherry and Holmes 1995). In Chapter 3, I attempted to determine the potential effect of weather factors at a large and local scale on inter-annual survivorship and fecundity of Barn Swallows and to identify some of the ecological factors that could be driving the population declines of Barn Swallows in North America.

Model selection methodology was applied to long-term mark-recapture data of two breeding colonies of Barn Swallow in Seattle, Washington State, USA and Guelph area, Ontario, Canada, to study the effect of large-scale weather conditions on both breeding and wintering grounds on annual survival rates of Barn Swallows in North America. The averaged Southern Oscillation Index (SOI) values for spring and winter months was used to define El Niño Southern Oscillation (ENSO) conditions on breeding and wintering sites respectively. I additionally tested whether the length of cold periods in spring affected negatively individual survival. This study revealed significant differences in the effect of ENSO-related weather conditions on annual survivorship between the two studied populations. Strong evidences for weather conditions related to ENSO on the breeding and wintering grounds causing differential inter-annual survivorship on Barn Swallows breeding were found for the Washington State population. In contrast, no correlation between survival probability and ENSO-related weather conditions was found for birds breeding in Ontario. In Washington State, years characterized by El Niño conditions during breeding months showed significantly higher apparent annual survival rates than years when breeding season-weather was characterized by the La Niña phase. A potential explanation for this finding is that, in North America, La Niña phase corresponded with colder and wetter weather conditions (Shabbar and Khandekar 1996, Shabbar et al. 1997), which have been previously shown to have a negative effect on survival of aerial insectivore species (Dence

1946, Ligon 1968, Whitmore et al. 1977, Brown and Brown 1999b). Weather conditions related to ENSO during wintering months were found to be also of importance for inter-annual survival rates. This finding could be explained by the differential geographical location of wintering areas of the breeding populations of Barn Swallows and the differential degree of migratory connectivity of populations determined in Chapter 2 (Table 2.3. and Figure 2.4.). The effects of ENSO on weather conditions vary significantly across South America and birds breeding in Washington State may be wintering in regions where ENSO has an important effect on weather and the El Niño phase correlates with higher precipitation rates. In contrast, breeding birds from Ontario may occupy areas in South America which weather conditions seem to be less influenced by ENSO. Additionally, birds breeding in Ontario tend to disperse more extensively on the wintering grounds than Washington State birds and the effect of ENSO on the annual survival probability of the population may be difficult to detect since individuals could be affected differently by ENSO-related weather conditions at these different geographical locations. Akaike's Information Criterion (AIC) model selection and averaging analyses suggested that the length of cold periods in spring had a strong negative effect on inter-annual survival for Barn Swallows breeding in Washington State but not for those breeding in Ontario. These results agree with previous studies that showed particularly high mortality rates of insectivorous birds after relatively extensive periods of cold weather in the spring in several areas in North America (Dence 1946, Ligon 1968, Whitmore et al. 1977, Brown and Brown 1999b). I found that North American locations where Barn Swallow populations are in decline encounter significantly longer periods of cold weather in the spring over the years than those breeding in stable areas. These results support the hypothesis that inclement weather after arrival

from spring migration and early in the breeding season could have an important effect on reproductive success and survivorship of Barn Swallows.

4.2.2. Effects of spring weather on fecundity

The effect of weather conditions on the breeding grounds on annual fecundity rates of Barn Swallows from two breeding colonies in North America was examined and weather variables with a significant effect on reproductive success were identified. Results suggested that annual reproductive success of Barn Swallows varies significantly according to maximum and minimum spring temperatures and length of cold periods in the spring, suggesting a larger effect of temperature than precipitation parameters. These results confirm the important role that temperature plays in the reproductive performance of aerial insectivorous birds and open new questions regarding the future impact on the demographics of these species in response to global changes in weather. The extent of cold periods in the spring had been previously shown to have a negative effect on adult survival of aerial insectivore species (Brown and Brown 2000, Newton 2007), and these results confirm the important effect of this factor on the reproductive success of this group. In contrast with previous studies which have suggested the negative effect of both cold and rainy periods during the breeding season on the reproductive performance of insectivore birds (Collister and Wilson 2007, Arlettaz et al. 2010), my results show that spring weather variables related to the length of consecutive day-periods of cold weather and the minimum and maximum daily temperatures were the only weather-related factors that affected the overall productivity of Barn Swallows on the breeding grounds.

4.2.3. Stressors on wintering grounds

Potential differences in stress experienced by birds on the wintering grounds were evaluated using corticosterone (CORT) concentrations on winter-grown feathers. I predicted that birds from declining populations will have higher feather CORT levels than birds from stable

populations, since long-term environmental perturbations can have a profound impact on physiological parameters of organisms, and could consequently affect negatively their population trends (Romero et al. 2009). Despite this assumption, CORT levels of individuals did not differ from stable and declining populations. Similar results were found for birds breeding in geographically separated regions in South America. These results show no evidence for the negative effect of CORT-related stressors on the wintering grounds during molt as potential reasons for the decline of Barn Swallows in North America. However, it is important to recognize that feather-CORT is but one parameter that might honestly reflect environmental conditions during molt and much more research is required to ascertain if wintering ground factors are negatively influencing swallow populations in North America.

4.3. Conclusions

Populations of Barn Swallows in North America experience a diverse range of migratory connectivity. Populations in central regions of North America tended to mix more extensively on the wintering grounds while populations in western and eastern North America exhibited stronger patterns of migratory connectivity with at least half of their entire population overwintering in the same wintering region. Interestingly, those populations with strong connectivity located in southern US showed a more positive population trend in comparison with the rest of populations in North America, suggesting the importance of wintering locations and factors affecting individuals at those locations on the population dynamics of the species.

I found evidence for a differential effect of ENSO-related weather conditions on breeding and wintering grounds on survivorship of Barn Swallows, potentially due to geographical variation in ENSO effect on weather conditions across North America and the degree of migratory connectivity of populations. Local weather conditions related to temperature variables

(especially length of cold weather periods) were shown to have an effect on reproductive success rates of Barn Swallows. In addition, analyses of CORT levels in feathers did not reveal enough evidence to suggest that declining populations are subjected to stronger winter stressors than stable populations.

This study has provided a first attempt to identify factors occurring on breeding and/or wintering grounds that could have an effect on population sizes of Barn Swallows in North America. Further work to understand the profound declines of Barn Swallows, and of aerial insectivores overall, should attempt to study how weather conditions (i.e. La Niña events and extensive cold weather periods early in the spring) have varied over time and whether these changes correlate with the existed patterns of population decline of the species. In addition, future work should focus on enhancing the knowledge on habitat requirements of the species in the wintering grounds, as well as on identifying specific hot-spots in those regions. Geographical differences in habitat quality on the wintering grounds could be studied further by applying geospatial techniques such as the Normalized Difference Vegetation Index (NDVI) for South America (Balbontín et al. 2009). Following studies should also focus on addressing the effects that other factors could have on population size of Barn Swallows, such as contaminants, human persecution and habitat transformation on the breeding grounds.

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APPENDIX A. SWITCHING HEMISPHERES: A NEW MIGRATION STRATEGY FOR THE DISJUNCT ARGENTINEAN BREEDING POPULATION OF BARN SWALLOW (*Hirundo rustica*)

A.1. Introduction

While avian migration systems appear well established, involving the regular periodic movement by individuals of several thousand kilometers (Newton 2008), there are several intriguing cases whereby individuals and populations respond rapidly to changing environmental circumstances leading to a modification of their migratory strategy (e.g. (Snow 1978 , Berthold et al. 1992, Whittington et al. 1999)). Such responses presumably confer significant benefits to those founder populations thereby promoting an evolutionary change in migratory behavior (Pulido 2007). Additionally, the appearance of new migratory traits usually involve further physiological and behavioral changes such as timing of reproduction and onset of molt, associated with changes in circannual rhythms as an adaptation to new climates, photoperiod or other circumstances (Berthold 1984, Gwinner 1987, Gwinner 1996).

However, there are generally few opportunities to examine the evolution of such adaptive processes due to the rarity of well-documented cases of new migratory systems in nature. Moreover, until recently, it has been extremely difficult to infer movements of small birds at continental scales due to limitations in conventional approaches to tracking animal movements (Hobson and Norris 2008). Here, we present the results of a study of a recently established disjunct breeding population of Barn Swallow (*Hirundo rustica*) in Argentina (Martinez 1983) whose movements were inferred using a multiple stable isotopic forensic examination of their feathers. Recent genetic studies indicate that this population was initially derived from the North American breeding population through colonization by migratory individuals (Billerman et al.

2011) but nothing is known of how new migratory and life history strategies may have since rapidly evolved.

A.2. Methods

Breeding Barn Swallows ($n = 100$) were sampled during the austral summer (November-January) of 2006 and 2007 at colonies along the Atlantic coast of Buenos Aires province, Argentina. Tail feathers clearly grown prior to breeding were identified based on wear (Pyle 1997) and collected for all captured birds. For some individuals captured at the beginning of the breeding season tail feathers were induced to regrow and were then collected later in the season.

All feathers were cleaned of surface oils in 2:1 (v/v) chloroform:methanol solvent rinse and prepared for $\delta^2\text{H}$, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis at the Stable Isotope Laboratory of Environment Canada, Saskatoon, Canada. The non-exchangeable hydrogen of feathers was determined using the method described by (Wassenaar and Hobson 2003) and using two calibrated keratin hydrogen-isotope reference materials. Hydrogen isotopic measurements were performed on H_2 gas derived from high-temperature (1350°C) flash pyrolysis of $350 \pm 10 \mu\text{g}$ feather subsamples and keratin standards using continuous-flow isotope-ratio mass spectrometry. Measurement of the two keratin laboratory reference materials (CBS, KHS) corrected for linear instrumental drift were both accurate and precise with typical mean $\delta^2\text{H} \pm \text{SD}$ values of $-197 \pm 0.79 \text{‰}$ ($n = 5$) and $-54.1 \pm 0.33 \text{‰}$ ($n = 5$), respectively. All results are reported for non-exchangeable H expressed in the typical delta notation, in units of per mil (‰), and normalized on the Vienna Standard Mean Ocean Water – Standard Light Antarctic Precipitation (VSMOW-SLAP) standard scale.

For $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses, between 0.5 and 1.0 mg of feather material was combusted online using a Eurovector 3000 (Milan, Italy - www.eurovector.it) elemental analyzer. The resulting CO_2 and N_2 was separated by Gas Chromatograph (GC) and introduced into a Nu Horizon (Nu

Instruments, Wrexham, UK - www.nu-ins.com) triple-collector isotope-ratio mass-spectrometer via an open split and compared to a pure CO₂ or N₂ reference gas. Stable nitrogen (¹⁵N/¹⁴N) and carbon (¹³C/¹²C) isotope ratios were expressed in delta (δ) notation, as parts per thousand (‰) deviation from the primary standards: atmospheric nitrogen and VPDB (Vienna Pee Dee Belemnite carbonate) standards, respectively. Using previously calibrated internal laboratory C and N standards (powdered keratin and gelatin), within runs, precisions for δ¹⁵N and δ¹³C were better than ± 0.15 ‰.

Mean differences in feather δ²H, δ¹³C and δ¹⁵N values between known breeding grounds (i.e. those grown locally) versus unknown wintering grounds were tested using t-tests. Some individuals were sampled for both feathers grown on the breeding and wintering grounds. In those cases, a paired t-test was used to identify differences between growth origins. Multivariate Analysis of Variance (MANOVA) was applied to test simultaneously for isotopic differences among feathers using Pillai's trace statistic. All statistical analyses were performed using R Version 2.10.1 (R Development Core Team 2011).

Naturally molted tail feathers from 100 individuals from Argentina were used to assign Barn Swallows to their molting origins applying a δ²H isoscape and dichotomous prior information on the occurrence of C3- and C4-dominated vegetation zones in South America using methodology described in (Hobson et al. 2009b). The amount-weighted mean precipitation δ²H isoscape corresponding to the growing season of South America (Bowen et al. 2005) was converted into an equivalent feather δ²H (δ²H_f) isoscape using the empirical equation reported for non ground-foraging Neotropical migrants (Hobson et al. 2012c):

$$\delta^2\text{H}_f = -17.57 + 0.95 \delta^2\text{H} \quad (\text{A.1})$$

The expected standard deviation (σ_c) among individuals growing their feathers at the same locality for $\delta^2\text{H}$ ($\sigma = 14.4\text{‰}$) was estimated using the standard deviation of the residuals from the same regression equation reported by (Hobson et al. 2012c). To depict the probable molting origins of individuals, a normal probability density function (Equation A.2.) was applied to assess the likelihood that a given pixel in the $\delta^2\text{H}_f$ isoscape represented a potential origin for each feather sample.

$$f(y^*|\mu_c, \sigma_c) = \left(\frac{1}{\sqrt{2\pi}\sigma_c}\right) \exp\left[-\frac{1}{2\sigma_c^2} (y^* - \mu_c)^2\right] \quad (\text{A.2})$$

where $f(y^*|\mu_c, \sigma_c)$ represents the probability that a given cell (pixel) represents a potential origin for an individual of unknown origin (y^*), given the expected mean $\delta^2\text{H}_f$ for that cell (μ_c) based on the predicted value for that cell within the isoscape, and the expected standard deviation (σ_c) of $\delta^2\text{H}_f$ among individuals growing their feathers at the same locality.

A theoretical spatial $\delta^{13}\text{C}$ -distribution of vegetation in South America was obtained from (Still and Powell 2010, Powell et al. 2012). From this, we created a dichotomous surface of C3- and C4-dominated vegetation zones. Cells with $\delta^{13}\text{C}$ values $< -20\text{‰}$ were classified as C3-dominated and those with $\delta^{13}\text{C}$ values $> -20\text{‰}$ were classified as C4-dominated (Kelly 2000). These zones were then converted to equivalent feather- $\delta^{13}\text{C}$ values assuming an isotopic discrimination factor of 2‰ between plant and feather, calculated based on known discrimination factors of $\sim 1\text{‰}$ between plants and herbivorous insects (DeNiro and Epstein 1978, Peterson and Fry 1987, France and Peters 1997), and $\sim 1\text{‰}$ between insects and bird feathers (Hobson 2007). The expected mean and standard deviation (SD) of feather- $\delta^{13}\text{C}$ for each region were calculated based on modeled $\delta^{13}\text{C}$ values extracted from the dichotomous feather- $\delta^{13}\text{C}$ isoscape. Equation A.2 was then applied to assess the probability of a C3 or C4-dominated winter origin for each feather sample.

I used Baye's Theorem to compute the probability of each pixel x_i being the origin of a feather sample, given the observed feather value y_j , where j indexes the C3 or C4 vegetation zone.

$$f_X(x_i|Y = y_j) = \frac{f_Y(y_j|X=x_i)f_X(x_i|J=j)}{\sum_i f_Y(y_j|X=x_i)f_X(x_i|J=j)} \quad (\text{A.3})$$

The random variables Y and X are continuous and represent the feather- $\delta^2\text{H}$ values for Barn Swallows breeding in the disjunct population and the pixels within the feather- $\delta^2\text{H}$ isoscape, respectively. The random variable J is categorical with dimension two and describes potential origin in C3 or C4-dominated zones.

Spatial probability densities were normalized to the sum of likelihoods to finally obtain a single probability density surface for each feather sample. To statistically assign individuals to molt origin the calculated spatially explicit probability densities for each feather sample were reclassified using 3:1 odds ratios of correctly assigning an individual to its molt origin. The set of cells that defined the upper 75% of estimated probabilities of origin was coded as "1" (likely) and the rest as "0" (unlikely) (Van Wilgenburg and Hobson 2011). Results of the assignment of each individual were summed and mapped to obtain the most probable molting origin of the population. All analyses were performed using R Version 2.10. (R Development Core Team 2011) and GIS Version 9.3 (ESRI 2011).

A.3. Results

Feathers grown on unknown wintering locations ($n = 84$) and those grown locally in Buenos Aires province ($n = 16$) differed significantly for the three isotopes simultaneously (MANOVA, $F_{3,96} = 26.21$, $P < 0.001$) and for $\delta^2\text{H}$ ($t_{98} = 3.96$, $P < 0.001$) and $\delta^{15}\text{N}$ ($t_{98} = 8.06$, $P < 0.001$), but not in $\delta^{13}\text{C}$ values ($t_{98} = -1.77$, $P > 0.05$) when tested separately (Table A1.). Similar results were found for feathers grown on unknown wintering ($n = 16$) and known breeding ($n = 16$) locations

collected from the same individuals. Feather types varied isotopically for the three isotopes (MANOVA, $F_{3,28} = 32.06$, $p < 0.001$) as well as in $\delta^2\text{H}$ ($t_{15} = 4.98$, $p < 0.001$) and $\delta^{15}\text{N}$ ($t_{15} = 8.04$, $p < 0.001$) but not in $\delta^{13}\text{C}$ values ($t_{15} = -0.17$, $p > 0.1$) (Table A1.). Feathers grown on the Argentinean breeding grounds ($n = 16$) formed a tight group (SD: $\delta^{15}\text{N} = 0.2\text{‰}$, $\delta^2\text{H} = 5.0\text{‰}$, $\delta^{13}\text{C} = 0.2\text{‰}$), while feathers grown outside of the breeding season ($n = 100$) were more broadly distributed (SD: $\delta^{15}\text{N} = 2.0\text{‰}$, $\delta^2\text{H} = 20.7\text{‰}$, $\delta^{13}\text{C} = 2.8\text{‰}$) (Figure A1).

Depicted molt origins based on $\delta^2\text{H}$ and $\delta^{13}\text{C}$ values corresponded to regions in north-eastern South America, more specifically in northern Brazil, French Guiana, Suriname, Guyana, and Venezuela (Figure A2).

A.4. Discussion

Feathers grown by swallows breeding in Buenos Aires province differed isotopically from those grown outside of the breeding grounds presumably during the austral winter. Thus, the ancestral (boreal) molt phenology was replaced by a new (austral) migratory strategy in this newly formed breeding population. Our isotopic assignment of wintering locations corresponded with the northeastern region of South America (specifically northern Brazil, French Guiana, Suriname, Guyana, and Venezuela), areas known to also be frequented by wintering swallows from North America (Paynter 1995, Brown and Brown 1999a). These findings agree with previous reports of sporadic observations of Barn Swallow in northern South America during the months of June, July and August (Paynter 1995). Possibly, birds from this disjunct breeding population winter in areas that are available following the departure of North American migrants to their breeding grounds. This change of migratory strategy may have involved a complete change in molt strategy motivated by an adaptation to the new annual cycle particular to the southern hemisphere. The adoption of an austral migration and molt strategy by a founder

population established in the opposite hemisphere clearly represents an extreme case of rapid adaptation which has been previously shown in a few species such as the Leach's Storm Petrel (*Oceanodroma leucorhoa*), a European long-distance migrant which has founded a new breeding population within its wintering range in South Africa (Underhill et al. 2002).

Table A1. Mean and SD of $\delta^2\text{H}$, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (‰) in feathers of Barn Swallows captured on their breeding grounds in Buenos Aires province. (A), feathers sampled once. (B), feathers forced to grow in known breeding grounds. (C), feathers initially plucked from birds sampled in (B).

Growing location		n	mean	SD
$\delta^2\text{H}$				
Wintering grounds	(A)	84	-52.3	20.7
Breeding grounds	(B)	16	-31.7	5.0
Wintering grounds	(C)	16	-57.2	20.6
$\delta^{13}\text{C}$				
Wintering grounds	(A)	84	-20.9	2.8
Breeding grounds	(B)	16	-22.2	0.2
Wintering grounds	(C)	16	-22.0	3.2
$\delta^{15}\text{N}$				
Wintering grounds	(A)	84	11.0	2.0
Breeding grounds	(B)	16	15.0	0.2
Wintering grounds	(C)	16	10.5	2.4

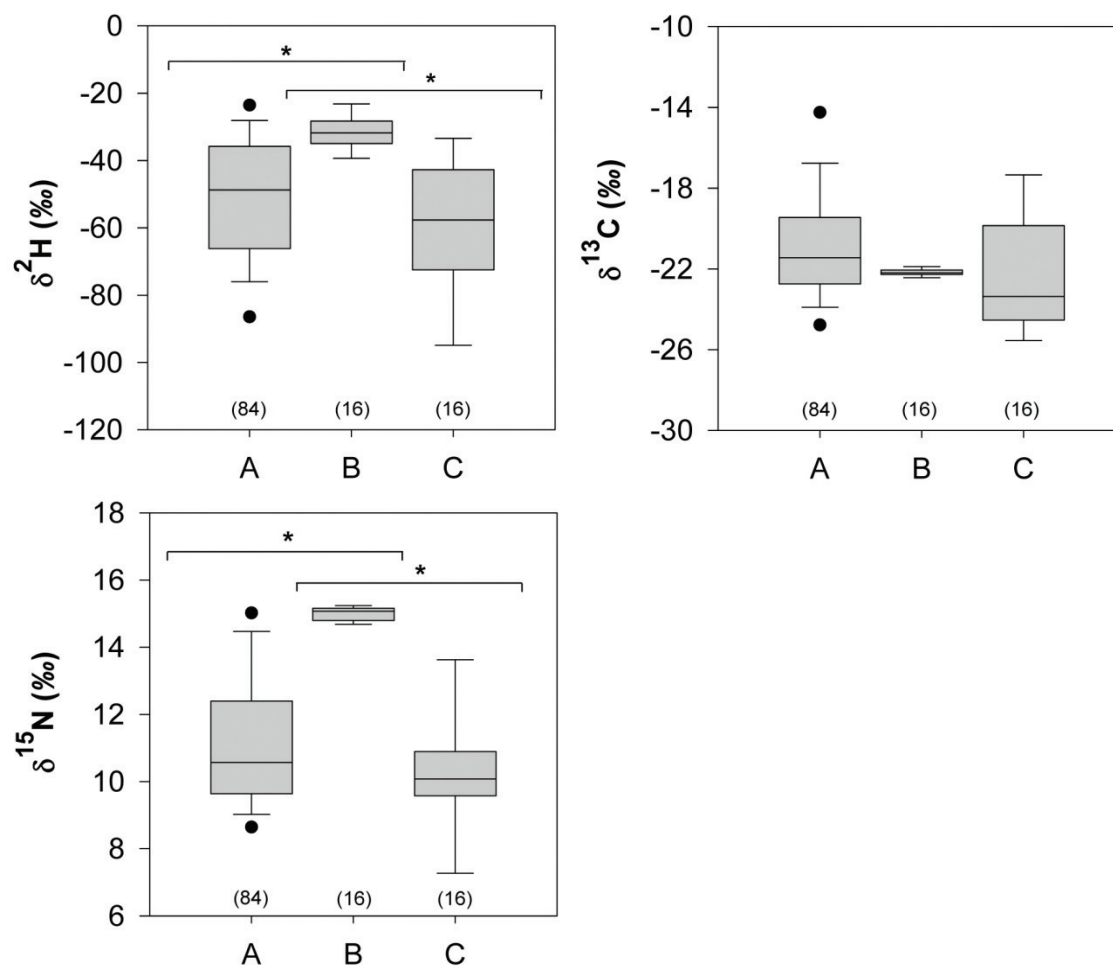


Figure A1. Boxplots of $\delta^2\text{H}$, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (‰) of Barn Swallow feathers. Letter A represents a sample of birds whose feathers were sampled once and were grown on unknown austral wintering grounds. Letters B and C represent feathers forced to grow on the breeding grounds in Argentina and those initially plucked (grown on unknown austral wintering grounds), respectively. Star symbol denotes significant differences in mean using independent (A vs C) or paired (B vs C) t-tests as appropriate ($p < 0.05$). Numbers in brackets represent sample sizes. Results indicate that feathers grown on the breeding grounds were isotopically different from those grown on the austral wintering grounds for $\delta^2\text{H}$ and $\delta^{15}\text{N}$ values.

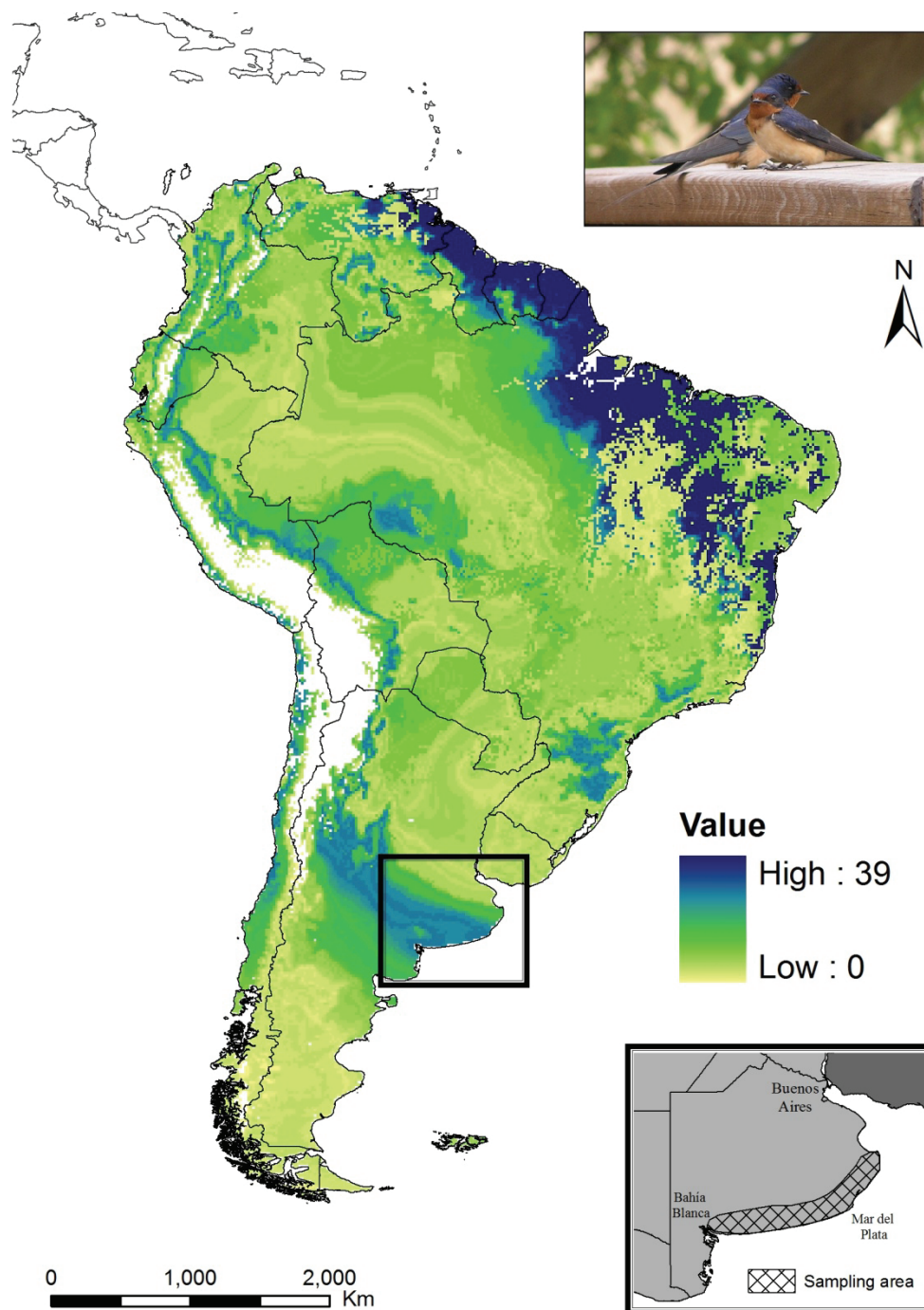


Figure A2. Potential wintering origins of Barn Swallows breeding in the Atlantic coast of Buenos Aires province (Argentina). Maps were created using $\delta^2\text{H}$ and $\delta^{13}\text{C}$ values of winter-grown feathers. Values depicted on maps represent the number of individuals in the total sample that were assigned to each cell in the map, representing a potential molting origin according to a 3:1 odds ratio.

The broad range of feather isotope values representing the austral wintering period of swallows breeding in Argentina suggest a number of possible molting areas in the southern portion of their breeding range. Indeed, we cannot rule out the possibility that some of the individuals we examined were in fact new arrivals from North America (Billerman et al. 2011) or represented an extreme case of double breeding (Rohwer et al. 2011). However, the most parsimonious explanation is the adoption of an austral migratory system that has Argentinean breeders wintering and molting over a broad range of northeastern South America. We recognize the ambiguity of assignment of birds to regions of South America using stable isotope methods. Indeed, little ground truthing of our multi-isotope feather isoscape for South America has been conducted and so ours represents only the most parsimonious of several possible explanations. Nonetheless, ours is a falsifiable hypothesis that can now be investigated further using isotopic tools and also the use of light-sensitive geolocators that are now small enough to be used on this species (Bächler et al. 2010, Bairlein et al. 2012).

APPENDIX B: MOLT OF BARN AND CLIFF SWALLOWS AT A WINTER ROOST SITE IN ARGENTINA

B.1. Introduction

Swallows are among the minority of Neotropical migrants breeding in North America that do not molt their body and flight feathers prior to departure to their wintering grounds (Pyle 1997). A likely reason for this delay is that, as aerial foragers, they are forced to replace flight feathers as slowly as possible to maintain aerial efficiency prior to and during migration. A complete molt (including the sequential replacement of all body and flight feathers) during the breeding season would require high energy costs that could affect their reproduction and migration (Rohwer et al. 2005). Of the eight species of migratory swallows that breed in North America, four of them; Tree (*Tachycineta bicolor*), Violet-green (*Tachycineta thalassina*), Cave (*Petrochelidon fulva*) and Northern Rough-winged (*Stelgidopteryx serripennis*) swallows, are short-distance migrants that initiate molt on the breeding grounds and finish on their wintering areas (Stutchbury and Rohwer 1990, Brown et al. 1992, Rohwer et al. 2011). In contrast, long-distance migratory swallows such as Barn (*Hirundo rustica*), Bank (*Riparia riparia*), Cliff (*Petrochelidon pyrrhonota*) swallows and Purple Martin (*Progne subis*) delay their molt until arrival on their winter areas with only few if any flight feathers molted before arriving (Freer and Belanger 1981, Brown and Brown 1995, Brown 1997, Pyle 1997, Brown and Brown 1999a).

During the non-breeding season, both Barn and Cliff swallows roost communally in marshes often involving millions of individuals (Winkler 2006). However, little is known about the winter distribution and phenology of molt on the wintering grounds of these species in Central and South America. As part of another study involving sampling swallows on their wintering grounds, we opportunistically recorded molt stages on birds captured. Here, we report an

important wintering site for migratory swallows in Argentina and provide the first description of molt of Barn and Cliff Swallows in the early austral summer.

B.2. Methods

Birds were captured from 22 November to 2 December 2010, at Colonia Carlos Pellegrini, Corrientes, Argentina (28° 32' 34" S, 57° 11' 27" W), located in the Natural Reserve of Iberá. This is an extensive (1,300,000 ha) shallow marsh surrounding *Laguna del Iberá* (Ibera Lake). Swallows foraged over open grassland and above water where high densities of flying insects were seen. Reed beds on the lake were used for roosting.

Swallows were captured passively using mist nets (6 and 12 m, 30 mm mesh) operated from 30 min before sunrise for five hrs and for four hrs before sunset. For all captured swallows, molt stages for flight feathers, wing coverts, head, and body feathers were scored and individuals were aged when molt stage permitted. For primaries, secondaries, and rectrices, the sequence of molt was recorded following the system developed by the British Trust for Ornithology (Ginn and Melville 1983) and the North American Banding Council guidelines (NABC 2001). Body feathers were scored as molting or not and the percentage of contour feathers that were molting was recorded at the time of capture. Different types of wing coverts that were molting or already replaced were additionally identified. All birds were weighed to the nearest 0.5 g, measurements of unflattened wing chord were also obtained to the nearest 0.1 mm and photographs taken for Barn Swallows.

B.3. Results

All Barn (16 hatching-year [HY], 1 after-hatch-year [AHY]) and Cliff (n = 5) Swallows were actively molting at the time of capture (Table B1 and Table B2). Four HY Barn Swallows (24%) were in an early stage of molt (Figure. A1). P1, P2 and P3 had started to grow, but they did not

Table B1. Qualitative assessment of molt for Barn Swallows (n = 17) captured in Colonia Carlos Pellegrini (Corrientes, Argentina) in late November and early December 2010 sorted and grouped from less to more advance stage of molt. Molt stage was scored for primaries (new and molting), secondaries, rectrices and wing coverts (Gr=Greater, Md=Medium and Ls=Lesser).

Ind. ID	Date	Age	Primaries (new)	Primaries (molting)	Secondaries	Rectrices	Coverts (molting)
1	22 Nov	HY	None	P1,P2,P3	Old	Old	Gr
2	24 Nov	HY	None	P1,P2,P3	Old	Old	Gr, Md
3	24 Nov	HY	None	P1,P2,P3	Old	Old	Gr, Md
15	1 Dec	HY	None	P1,P2,P3	Old	Old	Gr
4	25 Nov	HY	P1,P2,P3	P4	Old	Asymmetric molt	Gr
6	29 Nov	HY	P1,P2	P3,P4	Old	Old	Gr, Md, Ls
9	29 Nov	HY	P1,P2	P3,P4	Old	Old	Gr, Ls
10	29 Nov	HY	P1,P2	P3,P4	Old	Old	Gr, Ls
13	1 Dec	HY	P1,P2	P3,P4	Old	Old	Gr, Md, Ls
16	1 Dec	HY	P1,P2	P3	Old	Old	Gr, Ls
5	25 Nov	HY	P1,P2,P3	P4,P5	S1 molting	R1 molting	Gr, Md, Ls
7	29 Nov	HY	P1,P2,P3,P4	P5	Old	R1 molting	Gr, Md, Ls
8	29 Nov	AHY	P1,P2,P3,P4	P5	S1 molting	R1 molting	Gr, Md, Ls
11	29 Nov	HY	P1,P2,P3	P4	S1 molting	Old	Gr, Ls
17	2 Dec	HY	P1,P2,P3	P4,P5	S1 molting	R1 molting	Gr, Md, Ls
12	30 Nov	HY	P1,P2,P3,P4,P5	P6	S1, S2 molting	R1 molting	Gr, Md, Ls
14	1 Dec	HY	P1,P2,P3,P4,P5	P6	S1, S2 molting	R1, R2, R3 molting	Gr, Md, Ls

Table B2. Qualitative assessment of molt for Cliff Swallows (n = 5) captured in Colonia Carlos Pellegrini (Corrientes, Argentina) in 2010. Molt stage was scored for primaries (new and molting), secondaries, rectrices and wing coverts (Gr=Greater, Md=Medium and Ls=Lesser).

Ind. ID	Date	Primaries (new)	Primaries (molting)	Secondaries	Rectrices	Coverts (molting)
3	29 Nov	None	P1, P2	Old	Old	Gr.
2	29 Nov	None	P1, P2	Old	Old	Gr.
4	29 Nov	P1	P2, P3	Old	Old	Gr., Md.
5	30 Nov	P1, P2	P3, P4	Old	Old	Gr., Ls.
1	29 Nov	P1, P2, P3	P4, P5	Old	R1 molting	Gr, Md, Ls



Figure B1. Barn Swallow individuals actively molting captured during November-December 2010 in a winter site in Argentina. Upper left: P1, P2, P3 actively molting. Upper right: bird in an advance stage of molt with most primaries already replaced and secondaries and wing coverts actively growing. Lower left: Rectrices molting. Lower right: Dorsal body contour feathers molting and some already replaced. Arrows indicate replaced and replacing feathers.

present any replaced primaries, secondaries or rectrices. Six HY individuals (35%) had replaced P1 and P2, while P3 and P4 were still in molt, and rectrices and secondaries had not started to be replaced.

Of the remaining individuals, four HY and one AHY (29%) had replaced the first three or four primaries and were simultaneously molting P4 and P5, secondaries and rectrices. Two individuals were in an advanced stage of molt; their first five primaries were new and P6, secondaries and rectrices were actively molting (Figure A1). Symmetric molt of rectrices had started in 35% of all Barn Swallows (five HY and one AHY) (Figure A1). Body feathers and wing coverts were actively molting for all individuals (Figure A1). All Cliff Swallows were molting primaries at the time of capture. Two individuals (40%) were actively molting P1 and P2 but did not have any flight feathers completely replaced. The remaining 60% were more advanced in their molt and had already replaced some of the inner primaries (P1, P2 and P3) and were sequentially molting the rest of them. No secondary molt had started and only one individual, in the most advanced stage of molt, was growing its inner rectrices (R1). Body molt on Cliff Swallows was not very extensive since only a 5-10% of body feathers were observed growing in all Cliff Swallows but 100% were actively molting coverts.

B.4. Discussion

Molt in Barn and Cliff Swallows clearly occurred shortly after arrival on the wintering grounds. For primary feathers of both species, a sequential replacement occurred consecutively starting with P1 and was synchronized with the molt of secondaries which was also sequential. For Barn Swallows, it was evident that secondaries started to grow from S1 to S6 following replacement of P1, P2 and P3, and molt of rectrices was underway. For Cliff Swallows, the same sequential molt pattern for primary feathers was found, but secondary molt was not recorded and

only one individual was molting rectrices. Both species were actively molting body contour feathers and wing coverts at the time of capture, but Barn Swallows were more advanced.

Molt in Barn Swallows was consistent with previous descriptions of molt in this species at wintering locations in Africa. However, our study showed that 100% of individuals captured were molting primary feathers by the end of November, while other studies in southern Africa suggested that at least a 20% of individuals had not started molting primaries at that time (Broekhuysen and Brown 1963, Francis 1980). Barn and Cliff Swallows molted flight feathers gradually and in sequence presumably to maintain flight efficiency (Rohwer et al. 2005), since primary replacement only commenced when the previous feather had grown at least three-fourths of the total length. In addition, Barn Swallows were more advanced in molt than Cliff Swallows and overall molt period appeared protracted.

APPENDIX C. RELATIONSHIP BETWEEN $\delta^2\text{H}$ VALUES ON TAIL AND CONTOUR
FEATHERS OF BARN SWALLOWS SAMPLED FROM SAME INDIVIDUAL

