Final report to the Nova Scotia Habitat Conservation Fund
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Determining the role of wintering conditions on swallow population declines

Background

Aerial insectivores, especially swallows, are experiencing the most severe and widespread population declines among any group of passerines in North America (Nebel et al. 2010). These declines are most severe for populations in northeastern North America, including the Maritime provinces (Nebel et al. 2010, Shutler et al. 2012). Long-distance migrants (birds that overwinter in Central and South America) are also experiencing steeper population declines than short-distance migrants (birds that overwinter in the US) suggesting that conditions on the wintering grounds and/or migration routes are impacting overwintering survival leading to population declines (Nebel et al. 2010). Understanding the impact of conditions on the wintering grounds and during migration on population dynamics is necessary for determining the cause(s) of population declines observed on the breeding range.

There are a variety of ecological factors that can affect wintering ground conditions, including habitat quality, drought, predation, competition and disease (Sherry and Holmes 1996, Sillett et al. 2000, Sherry et al. 2005). Ultimately, poor wintering conditions result in negative effects on non-breeding populations through poor body condition and lower survival rates (Sherry and Holmes 1996, Marra and Holberton 1998, Sherry et al. 2005). In addition, the effects of poor wintering ground conditions can carry-over and affect other life cycle stages through lower survival rates during migration, delayed initiation of migration and lower reproductive success (e.g., smaller clutches, fewer young and second clutches) on the breeding grounds (review: Harrison et al. 2011). Determining overwintering locations and conditions at these sites is the first step in determining if overwintering conditions are impacting these species.

Stable isotopes are often used to determine overwintering locations for migratory birds (reviews: Inger and Bearhop 2008, Hobson 2011). Tissue samples, usually feathers grown on the wintering grounds, are analysed to determine ratios of the isotopes (e.g., $^{2}H/^{1}H$, $^{13}C/^{12}C$ and $^{15}N/^{14}N$). These ratios are compared to known patterns of isotope abundance across the landscape to determine where the feathers were grown, and ultimately the location of the individual at that time.

Once overwintering locations have been identified, then biomarkers (i.e., corticosterone [CORT] and telomere length) can be used to determine the effect of overwintering conditions on individuals. CORT is a hormone released in response to stressful conditions and allows the individual to mobilize energy resources (Astheimer et al. 1992, Holberton 1999). High levels of CORT in the blood plasma and feathers ($CORT_{f}$) have been associated with poor winter conditions (Marra and Holberton 1998) and decreased overwintering survival (Koren et al. 2012)

(Koren et al. 2012). Telomeres, which are non-coding sections of DNA that play a role in aging and disease (Monaghan and Haussmann 2006), have also been used to examine the impact of overwintering conditions on survival of migratory birds (Haussmann et al. 2005, Angelier et al. 2009). Specifically, greater rates of telomere shortening over a year were observed for individuals wintering in poor conditions (i.e., low food availability) when compared to the rates of shortening for individuals wintering in good conditions (Angelier et al. 2013). In addition, shorter telomeres were correlated with lower return rates to the breeding grounds (Angelier et al. 2013) and lower overwintering survival (Haussmann et al. 2005). These relationships demonstrate that increased telomere shortening associated with poor wintering ground conditions could impact the life span and total reproductive success of migratory birds. Measuring $CORT_f$ and telomere length can provide a method for determining if overwintering conditions impact apparent survival (based on annual return rates) and reproductive success.

Before conservation efforts can be directed to mitigate the potential impact of wintering conditions on populations that breed in the maritimes, it is necessary to identify overwintering locations and determine the potential effects of overwintering conditions on survival and subsequent reproductive success. The goal of this project was to address these knowledge gaps by first identifying where breeding populations of swallows overwintering and then determine if wintering conditions (i.e., high levels of $CORT_f$, large changes in telomere length), lead to impacts on individuals through low survival and carry-over effects on the breeding season (i.e., breeding phenology, reproductive success and adult mass).

Methods

Field methods

From 2014-2016, we monitored the reproductive success of Bank, Barn, Cliff and Tree Swallows from May to August. During this time, we will visit nests every 2-3 days to document the clutch initiation date (i.e., date the first egg was laid), number of eggs laid, hatching dates, number of eggs hatched and number of young to survive to day 12. We weighed and banded nestling Barn, Cliff and Tree Swallows at 9, 10 and 12 days of age, respectively; due to nest structure, it was not possible to access Bank Swallow nestlings.

We captured adult swallows throughout the breeding season using mist-nets (Bank, Barn and Cliff Swallows), tube-traps (Bank Swallows), and in nest boxes (Tree Swallows). Newly captured birds received a numbered aluminum band and the band number of previously captured birds was recorded. We collected five flank (or contour) feathers from Barn and Cliff Swallows for stable isotope and $CORT_f$ analysis. Unlike Bank, Barn and Cliff Swallows that molt during wintering, Tree Swallows molt during migration, therefore we are unable to use feathers to determine wintering locations/conditions for this species (Stutchbury and Rohwer 1990). We also collected a small (< 70 uL) blood sample from all recaptured adults (i.e., those that had been first banded in previous years) to determine telomere length.

Laboratory methods

Following the completion of fieldwork, we prepared feather samples for stable isotope analysis by washing them in a 2:1 solution of chloroform:methanol to remove preening oils and dirt and sent them to the University of Saskatchewan for stable isotope analysis.

We sent unwashed feather samples to the Toronto Zoo for $CORT_f$ analysis using an enzyme-immune assay.

We sent blood samples to the Chize Centre for Biological Studies (France) for telomere analysis using a quantitative PCR. Due to unforeseen issues with the primers for telomere analysis, only data on telomere length for Barn Swallows have been received to date.

Statistical analysis

To determine the number of overwintering locations for Bank, Barn and Cliff Swallows, we used a k-means cluster analysis to determine if individuals from each species can be grouped into overwintering locations based on stable isotope values for δ^2H, $\delta^{13}C$ and $\delta^{15}N$. The number of clusters for each species was determined using two methods. First, we used the elbow method to determine the fewest number of clusters to minimize the total within-cluster variation. Then we confirmed the number of clusters with the gap statistic which uses a null reference distribution to minimize within-cluster variation (Tibshirani et al. 2001).

To determine overwintering locations for Bank, Barn and Cliff Swallows, we used δ^2H and $\delta^{13}C$ isoscapes for South America to compare the distribution of isotopes across the landscape with isotopes in the feathers (Bowen et al. 2005, Powell et al. 2012). Then we used a normal probability density function to determine the likelihood that feathers were grown in each raster pixel of the isoscapes within the South American wintering range of each species (BirdLife International and Handbook of the Birds of the World 2016). The results of this process assume that all feathers used were molted in South America.

To determine if conditions vary with overwintering locations for each species, we determined if stable isotopes values (i.e., δ^2H, $\delta^{13}C$ and $\delta^{15}N$) were related to $CORT_f$, telomere length and changes in telomere length. Since there were many feather samples where the $CORT_f$ concentration was too low (< 0.02 pg/mm) to determine an exact value (Bank: n = 284 of 316; Barn: n = 69 of 223; Cliff: n = 29 of 156), we binned $CORT_f$ values (e.g., Bank: A = < 0.02, B = > 0.02 pg/mm; Barn and Cliff: A = < 0.02, B = 0.02-0.09, C = 0.10-0.99, D = > 1.00 pg/mm). Then we used a MANOVA to related stable isotope values to binned $CORT_f$ for all species, and a Pearson's r correlation to relate each stable isotope to telomere length and delta telomere length (i.e., difference in telomere length between two consecutive years) for Barn Swallows. To determine if binned $CORT_f$ values were related to telomere length and delta telomere length for Barn Swallows we also used an ANOVA. To determine if binned $CORT_f$ values, telomere length and delta telomere length differed by year, we used a Fisher's exact test ($CORT_f$) and an ANOVA (telomeres).

To determine if telomere length was related to subsequent survival, we used an ANOVA to compare telomere length for individuals that were recaptured in subsequent years (survivors) and those that were not recaptured (presumed dead).

Finally, to determine if wintering locations/conditions resulted in carry-over effects, we determined if there were relationships between stable isotope values, $CORT_f$, telomere length and delta telomere length, and swallow breeding phenology, reproductive success and adult mass. Since there were strong relationships between clutch initiation and hatching dates (Bank: $r = 0.97$; Barn: r: 0.99; Cliff: $r = 0.97$), and brood size and nestling survival (Bank: $r = 0.85$; Barn: $r = 0.94$; Cliff: $r = 0.71$); we used clutch initiation dates, clutch size, nestling survival to day 12 and whether adults fledged at least one young (termed fledging success) in these analyses. For all species, we used Pearson's correlation analysis to relate each stable isotope to clutch initiation date, clutch size, nestling survival to day 12 and adult mass; we also used a MANOVA to relate all stable isotopes to fledgling success. We also used an ANOVA to relate $CORT_f$ to clutch initiation date, clutch size, nestling survival to day 12 and adult mass and a chi-square test to relate $CORT_f$ to fledgling success. For Barn Swallows, we used a Pearson's correlation analysis to relate telomere length and delta telomere length to clutch initiation date, clutch size, nestling survival to day 12 and adult mass, and an ANOVA to relate telomere length and delta telomere length to fledging success.

Results

Overwintering locations

For all three species, there was little variation in stable isotope values (δ^2H, $\delta^{13}C$ and $\delta^{15}N$) that would indicate individuals were wintering in different locations. Therefore, we only identified one cluster for each species (Table 1).

Our assignment to potential wintering locations in South America suggests that all three species winter in different locations. Bank Swallows likely winter in Uruguay, northeastern Argentina, southern Brazil and/or Paraguay (Figure 1). However, there were also a few small areas with potential wintering origins along the coast of Ecuador and Venezuela. Barn Swallows likely winter in northern Venezuela and Columbia, western Ecuador, south-central Brazil, central Bolivia, southeastern Paraguay and/or northern Argentina (Figure 2). Cliff Swallows likely winter in southwestern and southern Brazil, northern Bolivia, southern Paraguay and/or northern Argentina (Figure 3).

Wintering conditions

We did not find any differences in stable isotope values (i.e., δ^2H, $\delta^{13}C$ and $\delta^{15}N$) and binned $CORT_f$ (MANOVA: Bank: $p = 0.69$; Barn: $p = 0.97$; Cliff: $p = 0.48$), indicating that wintering locations were not related to $CORT_f$.

We also did not find any relationships between δ^2H, $\delta^{13}C$ and $\delta^{15}N$ and telomere length or delta telomere length for Barn Swallows (Pearson's correlation: length: $r = -0.02$; $r = -0.01$; r =

0.03; delta length: r = 0.25; r = -0.27; r = -0.06, respectively), indicating that wintering locations were not related to telomere length or dynamics for this species.

There was a significant relationship between binned $CORT_f$ values and telomere length and delta telomere length for Barn Swallows (ANOVA: $p = 0.002$ and 0.04, respectively; Figure 4). Barn Swallows with higher levels of $CORT_f$ had shorter telomeres. Both high (C and D) and low (A) values of $CORT_f$ were associated with telomere shortening, and intermediate values (B) of $CORT_f$ were associated with telomere elongation for Barn Swallows.

There were significant differences between the number of samples in each bin for $CORT_f$ and the year for all species (Fisher's exact test: Bank: $p < 0.001$; Barn: $p < 0.001$; Cliff: $p < 0.001$). For all three species, these differences were driven by a larger number of samples in the bin containing higher $CORT_f$ values in 2016 (Bank B: 2014 = 2.6%, 2015 = 8.5%, 2016 = 42.9%; Barn D: 2014 = 11.1%, 2015 = 3.8%, 2016 = 77.5%; Cliff D: 2014 = 2.4%, 2015 = 1.2%, 2016 = 55.8%).

There were also significant differences in telomere length and delta telomere length, and year for Barn Swallows (ANOVA: $p < 0.001$ and < 0.001, respectively; Figure 5). Telomere length was shortest in 2016, followed by 2015 and 2014. For individuals captured in both 2014 and 2015, 16 of 37 (43.2%) elongated their telomeres (delta telomere length < 0; Figure 5). In contrast, for individuals captured in both 2015 and 2016, only two of 41 (4.9%) elongated their telomeres; and one individual experienced no change in telomere length. All other individuals had shorter telomeres in the year they were recaptured.

Survival

We did not find a difference in the telomere length of Barn Swallows that were recaptured in subsequent years (i.e., survivors) and those that were not recaptured (i.e., presumed dead) (ANOVA: $p = 0.87$), indicating that telomere length was not related to future wintering survival.

Carry-over effects

We did not find any relationships between δ^2H, $\delta^{13}C$ and $\delta^{15}N$, and clutch initiation dates [CID], clutch size [CS], nestling survival [NS] and adult mass for any species (Pearson correlation: Bank: CID: r = -0.24 to 0.11; CS: r = -0.04 to 0.18; NS: r = -0.12 to 0.10; mass: r = 0.05 to 0.14; Barn: CID: r = -0.05 to 0.02; CS: r = -0.02 to 0.12; NS: r = 0.02 to 0.20; mass: r = -0.10 to – 0.06; Cliff: CID: r = -0.12 to 0.17; CS: r = 0.01 to 0.18; NS: r = 0.07 to 0.11; mass: r = -0.13 to 0.02). We also did not find any relationships between all stable isotopes and fledgling success for Bank and Cliff Swallows (MANOVA: Bank: $p = 0.49$; Cliff: $p = 0.82$); however, there was a significant relationship for Barn Swallows ($p = 0.04$; Figure 6). For Bank and Cliff Swallows these results indicate indicating that wintering locations were not related to subsequent breeding phenology, reproductive success or adult mass. However, for Barn Swallows, while wintering locations were not related to subsequent breeding phenology, clutch size or nestling survival (i.e., number of young raised), there was a relationship between wintering locations and whether or not nests fledged young.

We did not find any relationships between $CORT_f$ and clutch initiation dates, clutch sizes, nestling survival and adult mass for Bank and Barn Swallows (ANOVA: Bank: CID: $p = 0.55$; CS: $p = 0.50$; NS: $p = 0.14$; mass: $p = 0.29$; Barn: CID: $p = 0.75$; CS: $p = 0.76$; NS: $p = 0.76$; mass: $p = 0.38$); $CORT_f$ was also unrelated to fledgling success for these species (Fisher's exact test: Bank: $p = 0.20$; Barn: $p = 0.71$). For Cliff Swallows, $CORT_f$ was unrelated to clutch initiation dates (CID: $p = 0.17$). However, for Cliff Swallows, there were relationship between $CORT_f$ and clutch size, nestling survival, adult mass (ANOVA: CS: $p = 0.01$; NS: $p < 0.001$; mass: $p = 0.003$; Figure 7, 8) and fledgling success (Fisher's exact test: $p = 0.03$; Figure 9). Intermediate levels (B) of $CORT_f$ were associated with larger clutches, and high levels (D) of $CORT_f$ were associated with lower nestling survival, lower fledging success and reduced adult body mass. These results indicate that wintering conditions (measured by $CORT_f$) did not have carry-over effects on Bank or Barn Swallows, and did not impact breeding phenology of Cliff Swallows. However, there were carryover effects of wintering conditions (measured by $CORT_f$) on the reproductive success and body mass of adult Cliff Swallows.

We did not find any relationships between telomere length and clutch initiation dates, clutch sizes, nestling survival, adult mass (Pearson correlation: CID: $r = 0.08$; CS: $r = -0.17$; NS: $r = -0.07$; mass: $r = 0.13$), or fledgling success (ANOVA: $p = 0.06$) for Barn Swallows. We also did not find any relationships between delta telomere length and clutch initiation dates, clutch sizes, nestling survival or adult mass (CID: $r = -0.06$; CS: $r = 0.18$; NS: $r = 0.27$; mass: $r = -0.11$). However, there was a significant relationship between delta telomere length and fledgling success ($p < 0.001$; Figure 10). These results indicate that wintering conditions (measured by telomere dynamics) did not have carry-over effects on Barn Swallow breeding phenology, clutch size, nestling survival and adult body mass. However, there may be carry-over effects from wintering to fledgling success for Barn Swallows.

Discussion

Our results indicate that breeding populations of Bank, Barn and Cliff Swallows from New Brunswick and Nova Scotia likely winter in different locations in South America. While little is known about wintering locations for different populations of Bank and Cliff Swallows, there is more information for Barn Swallows from stable isotopes and geolocators (Garcia-Perez and Hobson 2014, Hobson et al. 2015, Hobson and Kardynal 2016). The likely wintering origins in central South America from our sampling for Barn Swallows are very similar to those identified using geolocators deployed on birds at the same breeding sites (Hobson et al. 2015, Hobson and Kardynal 2016). No Barn Swallows equipped with geolocators from these breeding sites overwintered in northern South America, suggesting that it is less likely that barn swallows from the maritimes wintered in this region.

Wintering locations were not related to and wintering conditions ($CORT_f$ and telomeres [Barn Swallows only]) for all species. Wintering locations were also not related to carry-over effects for Bank and Cliff Swallows, but Barn Swallows that successfully fledged at least one young were found in isotopically different (driven by δ^2H) locations than those that did not fledge young. The lack of relationships between wintering locations and wintering conditions and/or carry-over effects may be due to the large scale at which wintering locations were defined.

Wintering conditions showed a consistent pattern for all three species. All three species, experienced higher levels of $CORT_f$ in feathers molted during the non-breeding season of 2015-2016 (i.e., collected in 2016). For Barn Swallows, telomere length was shorter and rates of telomere shortening were higher during the non-breeding season of 2015-2016. This suggests that during our study, swallows experienced two vastly different wintering periods.

Telomere length and changes in telomere length were strongly related to $CORT_f$ with shorter telomeres and higher rates of telomere shortening when they experienced high levels of $CORT_f$; high rates of telomere shortening also occurred during the lowest values of $CORT_f$. This suggests that both $CORT_f$ and telomere provide some measure of an individual's response to stress. Surprisingly, almost half of the individuals captured before and after the 2014-2015 non-breeding season experience telomere elongation, suggesting that conditions allowed individuals to invest in telomere repair. While elongation has been observed in long-live seabirds (e.g., Young et al. 2013); we are only aware of one example where telomere length elongated for a passerine (e.g., nestling Barn Swallows; Parolini et al. 2015).

Wintering conditions were related to carryover effects for Barn and Cliff Swallows. For Barn Swallows, telomere shortening was related to fledgling success. Perhaps conversely than anticipated, Barn Swallows with greater rates of telomere shortening were more likely to fledge at least one young. This may be explained by differential investment in breeding for adults; those that experienced greater changes in telomere length invested more in breeding as they perceived they were unlikely to survive to the following year. However, telomere length was unrelated to subsequent survival.

For Cliff Swallows, $CORT_f$ was related to reproductive success (i.e., clutch size, nestling survival and fledgling success) and adult body mass. High levels of $CORT_f$ were related to smaller clutches, lower nestling survival, higher rates of nest failure and reduced adult body mass; low levels of $CORT_f$ were also related to smaller clutches. These results suggest that Cliff Swallows wintering in poor conditions continue to breed at the same time as those in good conditions, but invest less in reproduction, resulting in lower success.

<u>Future analysis</u>

Future analysis of our data will focus on multi-variate analyses that account for non-independence of data collected from the same individuals in multiple years and for adults of both sexes contributing to a single nest.

We will also examine the relationships between telomere length, wintering locations, $CORT_f$ and carry-over effects for Bank and Cliff Swallows. We will also determine if there are carry-over effects on nestling body condition.

To date, our results for both $CORT_f$ for all species and telomere length for Barn Swallows suggest striking differences in wintering conditions between 2014-2015 and 2015-2016. We will examine weather data and other landscape-level variables for all three species between these years to determine why conditions varied so substantially between these years.

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Tables

Table 1. Stable isotope values (δ^2H, $\delta^{13}C$ and $\delta^{15}N$) for clusters from k-means analysis for each species.

			Stable isotope values		
Species	Cluster	n	δ^2H	$\delta^{13}C$	$\delta^{15}N$
Bank	1	157	-40.11	-20.29	9.93
Barn	1	134	-46.32	-16.90	11.17
Cliff	1	133	-53.61	-17.87	11.14

Figures

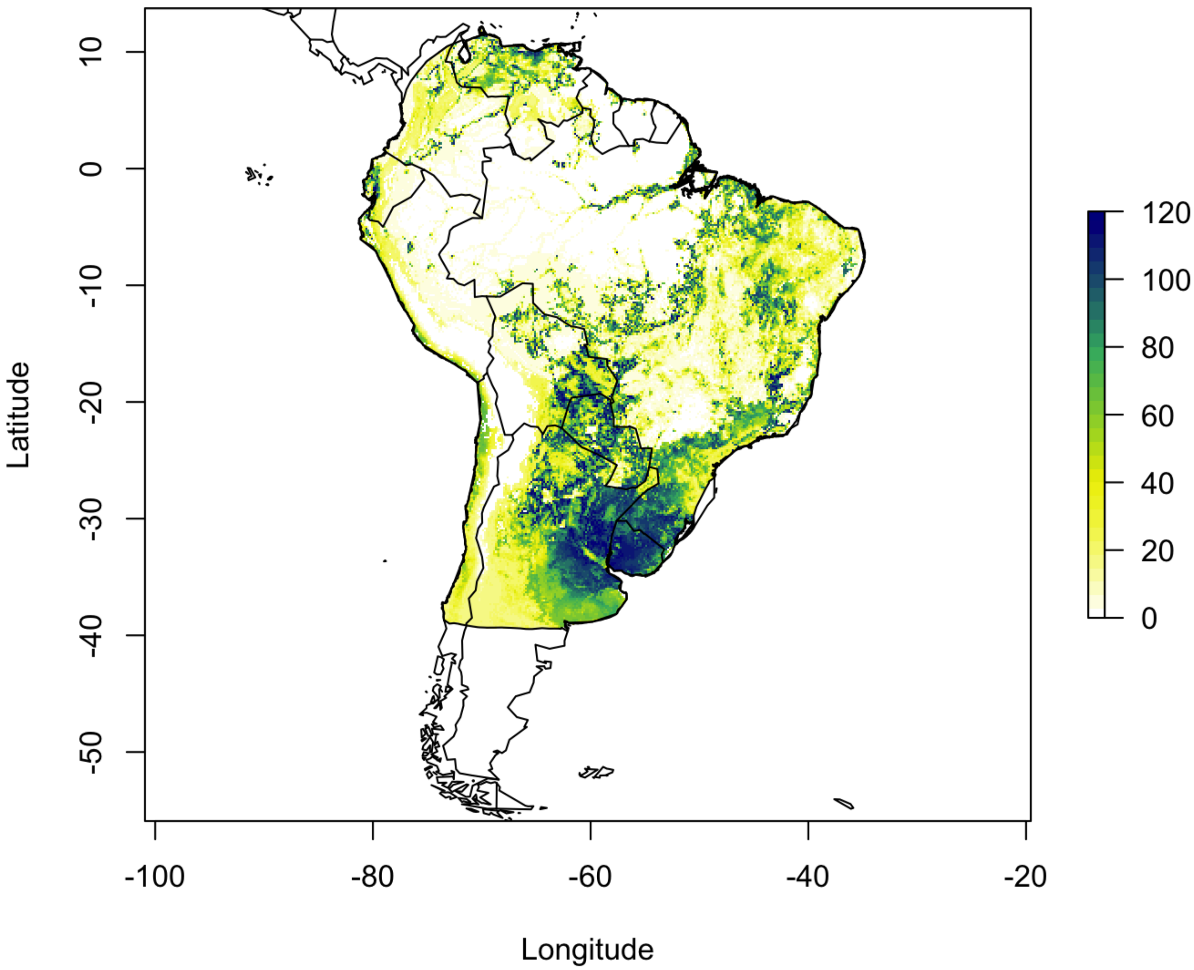

Figure 1. Likely winter origins for Bank Swallows based on flank feathers collected on the breeding grounds and compared to stable isotope icescapes (δ^2H, $\delta^{13}C$) for South America (values are the number of birds assigned to each raster pixel; maximum: 157).

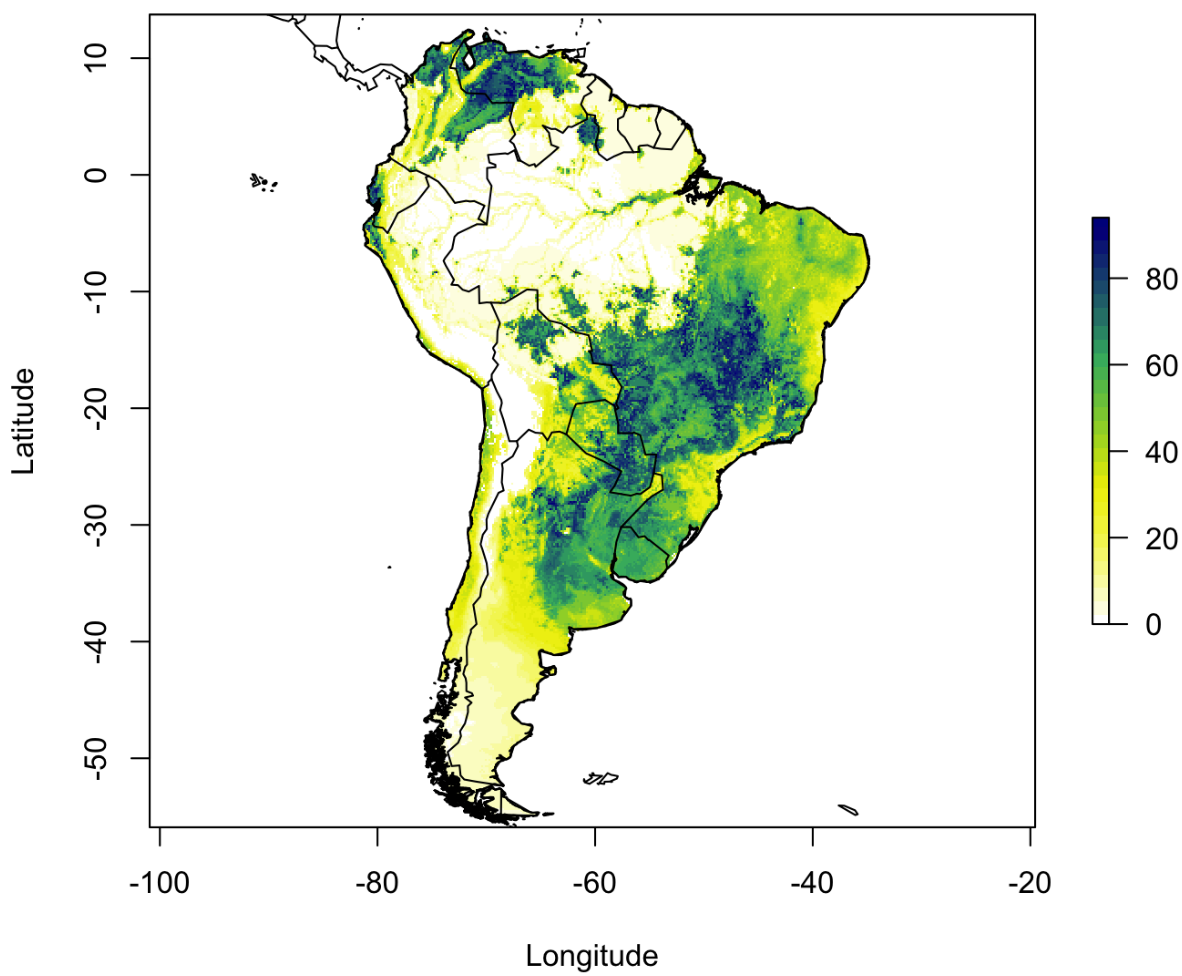

Figure 2. Likely winter origins for Barn Swallows based on flank feathers collected on the breeding grounds and compared to stable isotope icescapes ($\delta^2 H$, $\delta^{13} C$) for South America (values are the number of birds assigned to each raster pixel; maximum: 135).

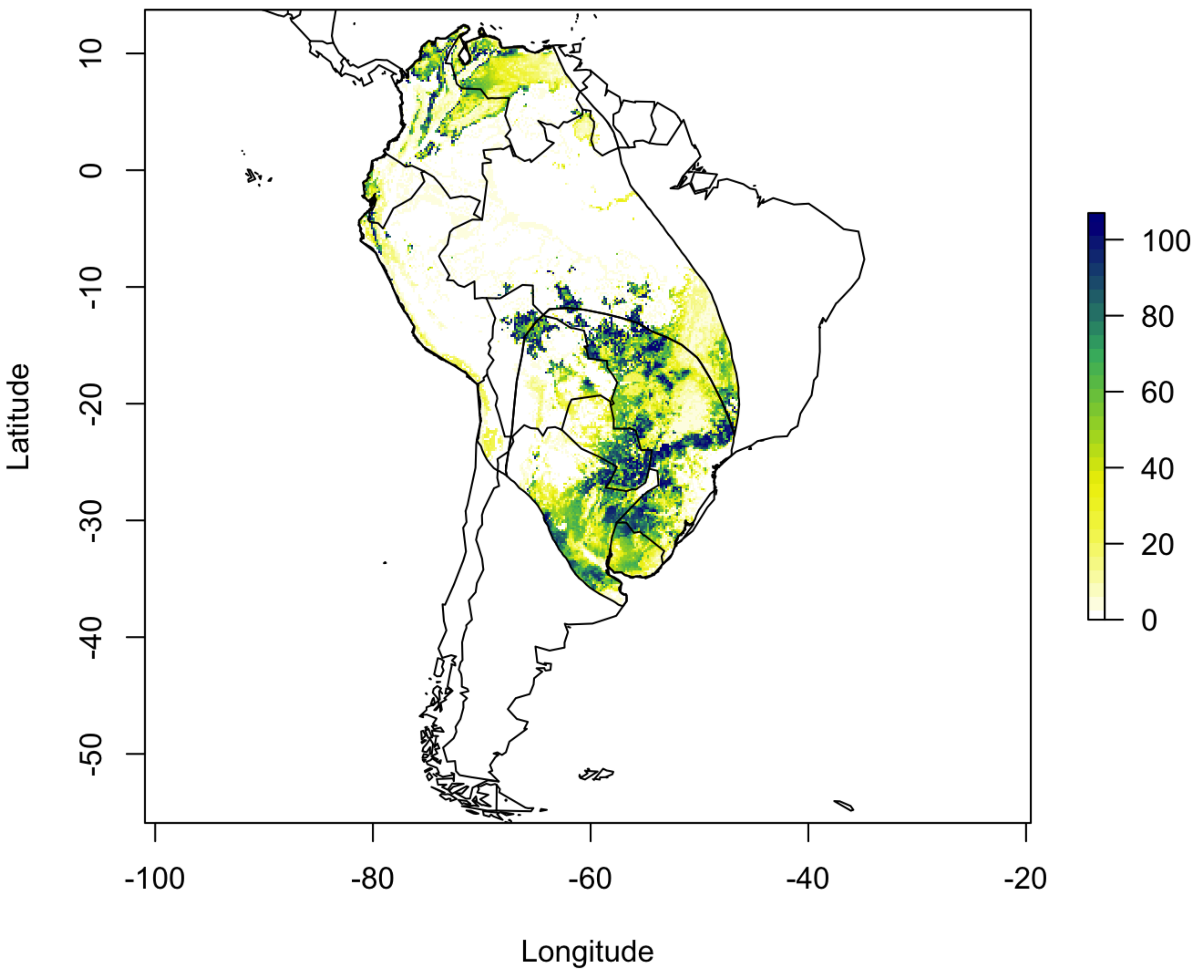

Figure 3. Likely winter origins for Cliff Swallows based on flank feathers collected on the breeding grounds and compared to stable isotope icescapes (δ^2H, $\delta^{13}C$) for South America (values are the number of birds assigned to each raster pixel; maximum: 134).

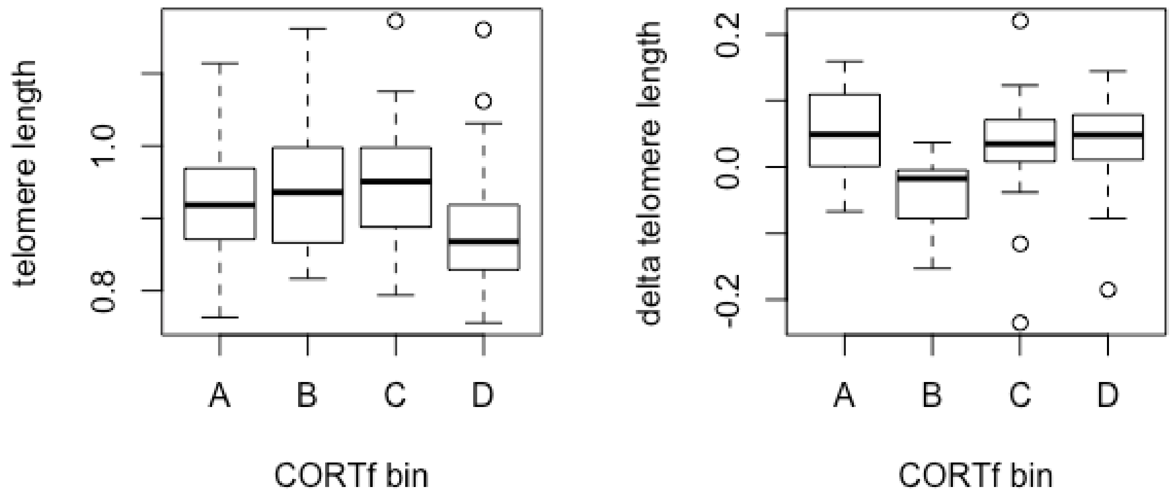

Figure 4. There were significant relationships between binned $CORT_f$ values and telomere length (left) and delta telomere length (right) for Barn Swallows. Barn Swallows with higher binned $CORT_f$ values (D) had significantly shorter telomeres than lower binned $CORT_f$ values. Barn Swallows also experienced telomere shortening (delta telomere length > 0) when binned $CORT_f$ values were low (A) and high (C and D), and telomere elongation (delta telomere length < 0) when binned $CORT_f$ values were at an intermediate value (B).

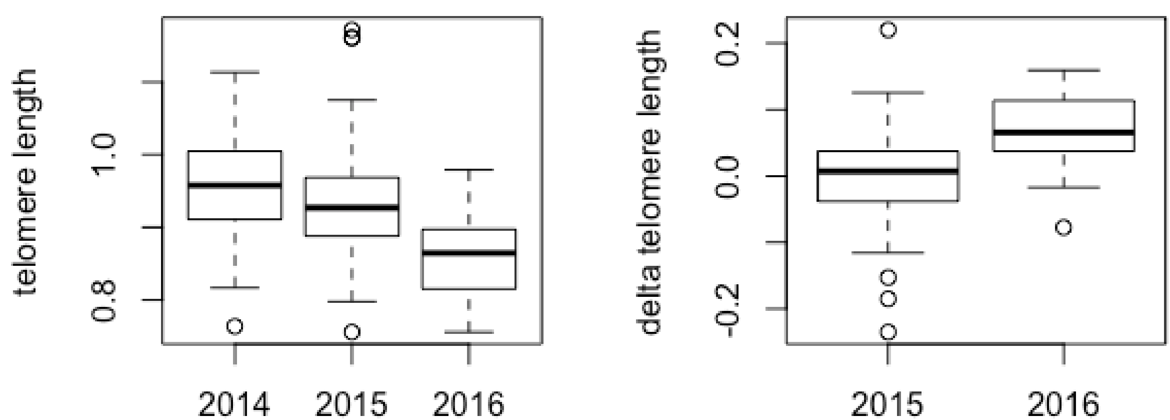

Figure 5. There were significant differences in telomere length (left) and delta telomere length (right) in the years that individual Barn Swallows were subsequently recaptured. In general,

telomeres were longer in 2014, followed by 2015 and 2016. Also, more individuals experienced telomere shortening (delta telomere length > 0) between 2015 and 2016 (2016 on graph).

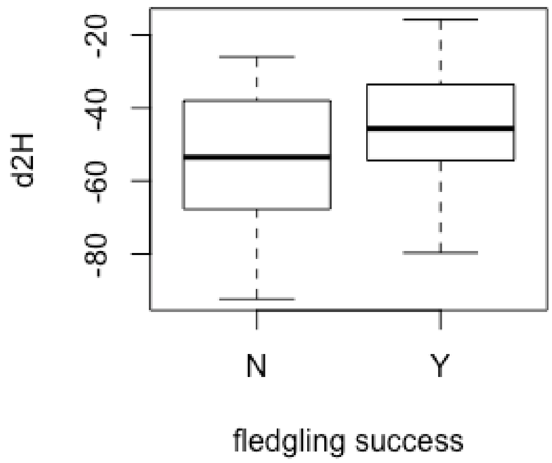

Figure 6. There was a significant relationship between wintering locations (specifically δ^2H) and fledgling success for Barn Swallows. In general, swallows that wintered in areas with higher δ^2H were more likely to raise at least one young (Y).

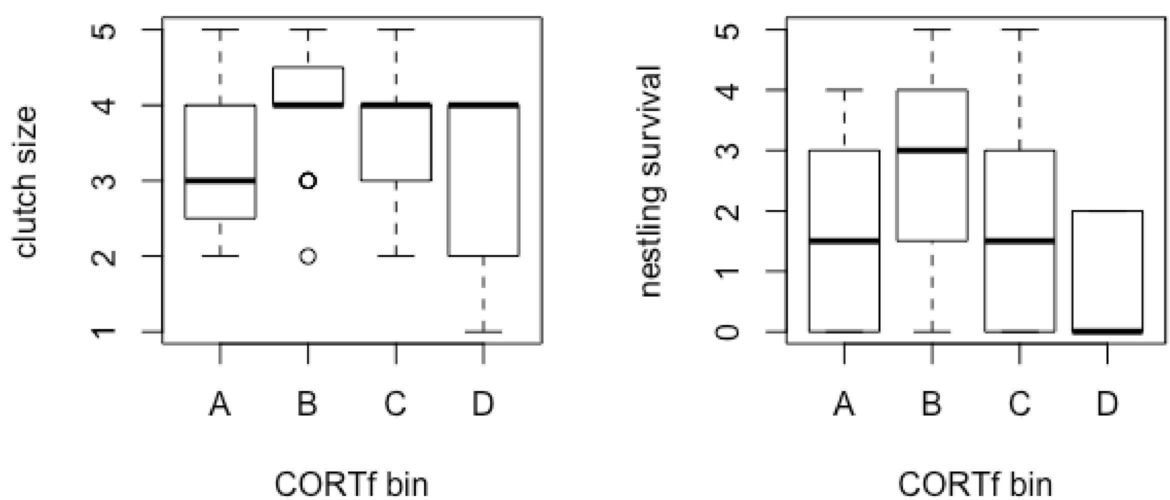

Figure 7. There were significant differences in clutch size (left) and nestling survival (right) for Cliff Swallows with different levels of $CORT_f$. Clutch size was significantly higher for adult Cliff Swallows with intermediate levels of $CORT_f$ (B) and nestling survival was significantly lower for adult Cliff Swallows with high levels of $CORT_f$ (D).

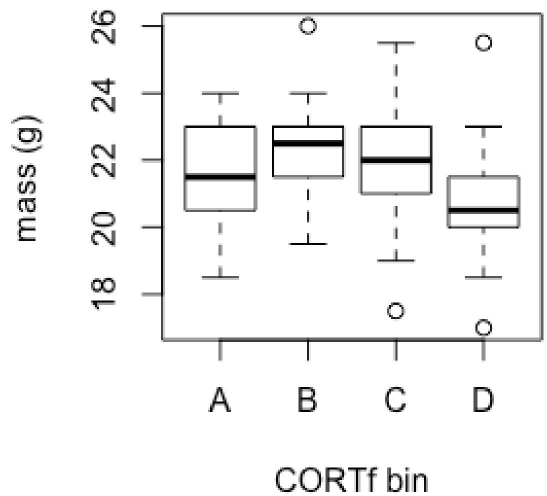

Figure 8. There were significant differences in adult body mass for Cliff Swallows with different levels of $CORT_f$. Mass was lower for adults with the highest levels of $CORT_f$ (D).

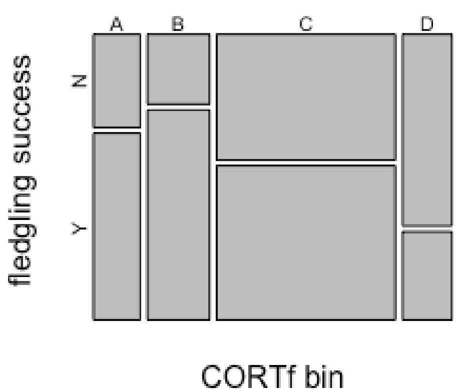

Figure 9. There was a significant difference in the fledging success of Cliff Swallows with different levels of $CORT_f$. Fledgling success was lower for adults with the highest levels of $CORT_f$ (D)

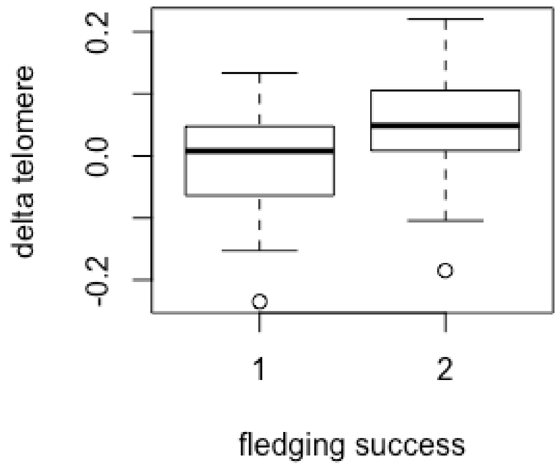

Figure 10. There was a significant difference in the fledgling success of Barn Swallows and delta telomere length. Fledgling success increased when adults experienced greater rates of telomere shortening.

Appendix I. Outreach and Communication

This project generated several opportunities for public outreach and stewardship in 2016-2017. In addition, project results were presented at several working group meetings. All outreach, stewardship and communication activities are listed below. Support from the Nova Scotia Habitat Conservation Fund was indicated at these activities.

Conference Presentations

Saldanha S, Leonard M, Taylor P. 2016. Communal roosting in breeding and pre-migratory Ban Swallows in New Brunswick.   North American Ornithological Conference, Washington DC.

Saldanha S, Leonard M, Taylor P. 2016. Foraging habitat selection on Breeding Bank Swallows in New Brunswick, Canada. North American Ornithological Conference, Washington DC.

Presentation to community group

Nova Scotia Bird Society (February 23, 2017).

Stewardship

Six landowners and families engaged in swallow monitoring.

Appendix II. Sources of in-kind funds

Dalhousie University	$7,460
Wildlife Preservation Canada	$16,933