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ABSTRACT

Like many aerial insectivores, Vaux's swift (*Chaetura vauxi*) populations are rapidly declining and therefore determining when and where populations are limited across the annual cycle is important for their conservation. Establishing the linkages between wintering and breeding sites and the strength of the connections between them is a necessary first step. In this study, we analyzed three stable isotopes (δ^{13} C, δ^{15} N, δ^{2} H) from feathers collected during spring migration from Vaux's swifts that perished during a stopover on Vancouver Island, British Columbia, Canada. We previously analyzed claw tissue (grown during winter) from the same individuals, revealing that the swifts likely wintered in two to three locations/habitats. Here, we used stable isotope analysis of flight feathers presumed to have been grown on, or near the breeding grounds to determine the likely previous breeding locations and presumed destinations for the swifts. Stable isotope values (δ^{13} C, δ^{15} N, δ^{2} H) showed no meaningful variation between age classes, sexes or with body size. Surprisingly, $\sim 26\%$ of the birds sampled had feather isotope values that were not consistent with growth on their breeding grounds. For the remaining birds, assigned breeding origins appeared most consistent with molt origins on Vancouver Island. Overall, migratory connectivity of this population was relatively weak ($r_{\rm M} = 0.07$). However, the degree of connectivity depended on how many winter clusters were analyzed; the two cluster solution suggested no significant connectivity, but the three cluster solution suggested weak connectivity. It is still unclear whether low migratory connectivity as observed for Vaux swift and other aerial insectivores may make their populations more or less vulnerable to habitat loss, therefore further efforts should be directed to assessing whether aerial insectivores may be habitat limited throughout the annual cycle.

INTRODUCTION

Migratory birds move hundreds to thousands of kilometres each year on their annual journey between breeding and wintering sites. While we have some understanding of species range-wide distribution on both the breeding and overwintering grounds for most migratory birds, connecting specific breeding and wintering populations (i.e., migratory connectivity) remains a major challenge. Strong connectivity occurs when individuals from specific breeding populations winter together in one or a few distinct locations; weak connectivity occurs when individuals from a specific breeding population disperse to multiple over-winter locations (Webster et al. 2002). If breeding and wintering populations are strongly linked, stochastic events (e.g., storms, disease) can be a serious conservation concern (Webster and Marra 2005). Migratory connectivity can also affect evolutionary processes, influencing the ability of species and populations to adapt to changing environmental conditions (Webster et al. 2002).

Delineating patterns of migratory connectivity has been constrained in large part by the inherent difficulty of tracking small birds throughout their annual cycle. Despite this challenge, several methods have been employed to establish patterns of migratory connectivity, most notably large-scale banding efforts for mark-recapture studies. Unfortunately, recapture rates are notoriously low, especially in tropical regions and for non-harvested species, and this method has thus been largely ineffective for connecting breeding and wintering populations of small bodied species, including many passerines (Webster et al. 2002, Van Wilgenburg and Hobson 2011). The advent of light-level geolocators and miniaturized GPS devices is revolutionizing our ability to track smaller birds throughout the annual cycle (Stutchbury et al. 2009). However, this approach is limited by high cost and the necessity to recapture individuals to retrieve data, which often limits samples sizes. In addition, extrinsic markers such as geolocators and GPS tags are

often not as useful as intrinsic markers for determining diet and habitat use during different phases of the annual cycle.

Stable isotope analyses provide an alternative to the use of extrinsic markers in the study of avian migratory connectivity. While the spatial resolution of inferred origins using stable isotope analyses tends to be lower than that obtained by using extrinsic markers, they have been used extensively to link breeding and wintering populations (Hobson and Norris 2008). In addition, stable isotope analyses have also been used to infer diet and habitat use (Bearhop et al. 2004, Hobson and Norris 2008). Stable isotopes are incorporated into growing tissues from the environment and by understanding the distribution of stable isotopes in the environment, one can infer information about the location of tissue growth (Wassenaar 2008). A further advantage is that this technique requires only a single capture event and can be applied broadly across many individuals relatively inexpensively, thus allowing for the large sample sizes necessary to ascertain population-level migratory connectivity. Furthermore, multiple intrinsic markers can be assayed from the same tissue sample, potentially allowing for improved precision and accuracy of inference (Haché et al. 2014).

Here, we employ a multiple stable isotope approach, using hydrogen (δ^2 H), carbon (δ^{13} C), and nitrogen (δ^{15} N) to examine patterns of migratory connectivity in a population of Vaux's swifts at a northern migratory roost site. Much like other aerial insectivores (Nebel et al. 2010), Vaux's swifts have experienced long-term (1970-2017) declines (-35%, 95% CI: -60.8 – 7.6%; Smith A.C. et al. unpublished, an update of Environment and Climate Change Canada 2017) and it is unclear which stage(s) of the annual cycle are most limiting for this species (Bull and Collins 2007). The severity of declines in aerial insectivores has been linked to migration distance, land-use change (Nebel et al. 2010) and may be related to a decline in food resources

(Nocera et al. 2012); declines appear to be more pronounced in populations that inhabit more northern areas of their range (Fraser et al. 2012). An improved understanding of migratory connectivity for this species is clearly needed (Reudink et al. 2015) and would facilitate where and how to allocate conservation actions (Hobson et al. 2014).

Here we analyze the stable isotope composition of flight feathers grown post breedingseason the previous year (Pyle 1997) from Vaux's swifts for which stable-isotope values of claw material grown on the wintering grounds were analyzed (Reudink et al. 2015). Our objectives were to estimate the approximate breeding distribution of this population, determine whether birds from the previously delineated wintering areas were linked to distinct breeding populations, and estimate the strength of migratory connectivity between breeding and wintering areas. Given the suggestion of large movements on the wintering grounds for species such as Black Swift (*Cypseloides niger borealis*; Beason et al. 2012) and other species of swift (Åkesson et al. 2012, Liechti et al. 2013), we hypothesized that Vaux's swifts would show relatively low migratory connectivity and that breeding origins would not likely be tightly linked to previously defined wintering clusters. In addition, we hypothesized that wing length would be negatively related to $\delta^2 H_f$ (i.e., the individuals that had the lowest $\delta^2 H_f$ values would have the longest wings) since migration distance should exert selective pressure on wing morphology and favor longer wings for populations migrating farther (Nowakowski et al. 2014).

METHODS

Field Methods

On 9 May 2012, approximately 1,350 Vaux's swifts became trapped and subsequently suffocated in a migratory roost in Cumberland, British Columbia. The swifts used this roost

annually during northward spring migration and this single event resulted in a loss of approximately 1.5-2.7% of the British Columbia population (Reudink et al. 2015). We analyzed feather tissue from 97 individuals previously sampled by Reudink et al. (2015) for stable isotope analysis of claw tips (used to infer winter habitat/location).

We sampled approximately 0.5 mg of the distal tip of the first primary (P1) feather from each individual, taking care to avoid the rachis. We sampled the P1 feather as it is generally the first flight feather replaced during molt in approximately late June (Bull and Collins 1993) and therefore is likely to reflect conditions on the breeding grounds.

Stable Isotope Analysis

To determine the approximate breeding locations from this sample of Vaux's swifts, we examined stable isotope values (δ^2 H, δ^{13} C, and δ^{15} N) in primary flight feathers, which should be grown on, or close to the breeding grounds. δ^2 H has been used frequently in studies of avian migration and connectivity because values vary with both latitude and elevation. At more northern latitudes and higher elevations, ²H is relatively less abundant (Hobson 2011), resulting in more negative isotope values in the growing feathers. δ^{13} C varies in plant tissues based on the photosynthetic system and water stress in the environment; individuals occupying habitats with higher proportions of C4 plants and plants that are under high water stress tend to exhibit less negative δ^{13} C values (Lajtha and Marshall 1994, Cerling et al. 1997; Still and Powell 2010). Nitrogen isotope ratios (δ^{15} N) offer a marker of trophic position because the heavier isotope (¹⁴N) and as a result, δ^{15} N values tend to increase with trophic level (Post 2002, Poupin et al. 2011). δ^{15} N

can also reflect the relative humidity of a biome, with δ^{15} N being negatively correlated with rainfall and positively correlated with temperature (Sealy et al. 1987, Craine et al. 2009).

Stable isotope analyses were conducted at the Smithsonian Institution OUSS/MCI Stable Isotope Mass Spectrometry Facility in Suitland, Maryland, USA. Feathers were first washed in a 2:1 chloroform:methanol solution, and allowed to acclimate to lab conditions for 72 hours in a fume hood prior to sample preparation. The samples were pyrolyzed in a Thermo TC/EA elemental analyzer (Thermo Scientific, Waltham, Massachusetts, USA) at 1,350 °C and analyzed using a Thermo Delta V Advantage isotope ratio mass spectrometer. We ran calibrated standards for every 10 samples, which included the hydrogen standard International Atomic Energy Agency CH-7 and three additional standards (Kudu Horn Standard (KHS): -54.1 \pm 2.3‰, Caribou Hoof Standard (CBS): -197.3 \pm 2.0‰, Spectrum keratin: -121.6 \pm 2.5‰). Using methods from Wassenaar and Hobson (2003), any non-exchangeable δ^2 H values were corrected to the keratin standard; these were then repeatable to within 3 \pm 2‰ (mean \pm SD, n = 10). Two in-house standards (acetanalide and urea) were run for every 10 samples of both stable carbon and nitrogen analysis. Stable isotope values are expressed in parts per thousand (‰) deviation from international standards Vienna standard mean ocean water (VSMOW; hydrogen), Pee Dee Belemnite (PDB; carbon), and air (nitrogen) using the following equation:

 $\delta \mathbf{X} = \{ [(\mathbf{R}_{sample} - \mathbf{R}_{standard}) - 1] \ge 1000 \}$

where X is the isotope ratio of interest (δ^2 H, δ^{13} C, or δ^{15} N) and R is the corresponding ratio (²H:¹H, ¹³C:¹²C or ¹⁵N:¹⁴N). Carbon and nitrogen samples were repeatable to within ± 0.2 ‰ based on repeated measurements of standards.

Statistical Analysis

We examined putative breeding origins of Vaux's swifts using previously described spatially explicit assignments to molt origin based on analysis of $\delta^2 H$ in feathers (Wunder 2010, Van Wilgenburg and Hobson 2011, Vander Zanden et al. 2014). While previous work suggests Vaux's Swifts molt P1 on their breeding grounds during the boreal summer (Bull and Collins 1993), preliminary examination of our data suggested that some individuals in our sample may not be isotopically consistent with the breeding season isoscape, even after accounting for measurement and assignment error. Some individuals molt on migration or display interrupted molt, which is completed on the non-breeding grounds (Howell 2010), may have had adventitious feather replacement, or may have originated from regions in which the food web has been altered by irrigation (see Hobson et al. 2012) and thus the isoscape may not accurately predict origins. Therefore, prior to assigning birds to their breeding grounds, we first used previously described, spatially-explicit approaches to assign birds to one of three potential molt origins (wintering grounds, migratory route or breeding grounds) using a Bayesian framework to compare observed feather δ^2 H values against predictions from calibrated feather isoscapes (Wunder 2010, Van Wilgenburg and Hobson 2011, Vander Zanden et al. 2014). To begin, we obtained δ^2 H in feathers from a subset of known-origin birds from data in Hobson et al. (2012). Specifically, we used a subset of known origin birds that were either aerial insectivores (Tree Swallow (*Tachycineta bicolor*; n=30) and Least Flycatcher (*Empidonax minimus*, n=4), and American Redstarts (Setophaga ruticilla, n=55), which also forage on the wing. For each capture location of the known-origin birds, we queried the predicted amount-weighted mean δ^2 H value growing-season precipitation ($\delta^2 H_p$) isoscape of Bowen et al. (2005). We then used 1000 nonparametric bootstrap regressions in which we randomly selected 25 known-source birds with

replacement to derive mean slope and intercept estimates relating $\delta^2 H_f$ to $\delta^2 H_p$. This resulted in a mean rescaling function of $\delta^2 H_f = -41.24$ (SD = 9.28) + 0.81 (SD = 0.10) * $\delta^2 H_p$. We derived a predicted mean feather isoscape via rescaling of the Bowen et al. (2005) isoscape using the aforementioned algorithm. The resulting feather isoscape had predicted $\delta^2 H_f$ values between -147.0 – -55.5 ‰ (Figure 1a). In order to derive a raster (pixel based) map depicting the variance ($\sigma^2_{rescale}$) of the rescaled $\delta^2 H_f$ isoscapes, we also saved separate calibrated isoscapes from each iteration of the bootstrap (separately applied each regression equation) and calculated the variance between the 1000 isoscapes on a pixel-by-pixel basis using the "cellStats" function of the raster package (Hijmans 2015) in the R statistical computing environment, version 3.4.3 (R Core Team 2017). We also calculated the mean variance of the residuals across the 1000 regressions and used this value to represent between individual variance ($\sigma^2_{individual}$). Finally, following Vander Zanden et al. (2014) we derived a spatially explicit prediction error surface by taking the square root of the sum of $\sigma^2_{rescale} + \sigma^2_{individual}$. The resulting prediction error surface ranged in values from 13.5 – 15.3 ‰ (Figure 1b) which we used to propagate assignment error (below).

We assigned the birds to origins by applying normal probability density functions to provide a spatially-explicit assessment of the likelihood that a given feather was grown at a given location within the predicted mean $\delta^2 H_f$ isoscape derived above. We parameterized the normal probability density function by treating isoscape-predicted $\delta^2 H_f$ values (within every pixel) as the mean values against which the $\delta^2 H_f$ was compared and by treating our spatially explicit prediction error surface (Figure 1b) as the variance estimate (Vander Zanden et al. 2014). This yielded one posterior probability density map per individual. To determine whether each individual had likely grown its feather on the breeding grounds versus on wintering range or on

migration, we summed the posterior probability densities of all pixels falling within polygons defining the breeding, migration and wintering ranges, respectively. To accomplish this, we used the 'zonal' function in the raster package (Hijmans 2015) to calculate the sum of the posterior probabilities of falling within polygons of the breeding, migratory and wintering ranges from a digital species distribution map (BirdLife International and Handbook of the Birds of the World 2016). Each bird was then assigned to molt origins within one of breeding, migratory or wintering ranges, based upon the region that had the highest cumulative likelihood of representing a molt origin.

To determine location of breeding grounds (in the year prior to collection) for each individual that was assessed as likely having molted on the breeding grounds (n = 72), we selected the upper 67% of the cumulative probability distribution (consistent with 2:1 odds of being correct versus incorrect) and recoded these as "likely" origins (1) and treated the lower 33% of the distribution as unlikely (0). We then summed the results of each of the individual assignments by addition of the predicted origin surfaces (Hobson et al. 2009, Van Wilgenburg and Hobson 2011).

We examined whether isotopic variation in breeding origin Vaux's swifts was associated with age, sex, wing length, and wintering ground cluster using a series of competing regression models. Preliminary modeling of variation in δ^{13} C, δ^{15} N, and δ^{2} H using linear models suggested heterogeneity of variance and convergence issues, and therefore we modeled the data using Bayesian robust regression to fit competing models to the data using the "brms" package (Bürkner 2017) by specifying the student family and an identity link function in the R statistical computing environment, version 3.4.3 (R Core Team 2017). Prior to analysis, we removed one individual from the sample due to a missing value for δ^{15} N and another for which the sex was undetermined, resulting in 70 individuals for which we had complete data to model. We treated each isotope ratio (δ^{13} C, δ^{15} N, δ^{2} H) as the response variable in a series of analyses in which we fit 11 candidate models to our data, with the least parameterized model containing only an intercept (null model) and the most heavily parameterized model containing factors for age, sex, wintering ground cluster and a linear covariate for wing length. Owing to sample size, we only considered models with additive effects. We ran four chains, each with 30,000 samples, a burn-in of 20,000, and thinning rate of 10, and assessed model convergence by inspecting trace plots and posterior predictive checks, and the Gelman-Rubin statistic (Gelman and Rubin 1992). Finally, we used the Widely Applicable Information Criterion (WAIC; Watanabe 2010) to rank our competing models, and considered models within 2 WAIC units as potentially competitive.

We assessed the strength of migratory connectivity by calculating the Mantel correlation coefficient (r_M , range -1 to 1; *sensu* Ambrosini et al. 2009). Unlike previous applications which have used the Mantel test between pairwise distance matrices of breeding and wintering sites, we constructed pairwise distance matrices based solely on isotopic variation in δ^{13} C, δ^{15} N and δ^{2} H of tissues grown on the wintering (claws) versus breeding (feathers) grounds. Prior to analyses, data were centered and standardized to zero mean and unit variance. Positive correlations between the distance matrices indicate that individuals that breed closely together also winter closely together (Ambrosini et al. 2009). We repeated this analysis for all individuals assessed as having molted on the breeding grounds, and on subsets based on their wintering ground clusters derived from Reudink et al. (2015).

RESULTS

Based on spatially explicit assignments to the $\delta^2 H_f$ isoscapes (Figure 2–4), 72 swifts were classified as having grown their feathers on the breeding ground. The cumulative likelihoods within the breeding ground portion of the isoscape were greater than the cumulative likelihoods in either the migratory portion of the range or on the wintering grounds for these individuals. The remaining 25 individuals were classified as molt migrants based on feather $\delta^2 H$ being most consistent (highest likelihoods) with portions of the isoscape associated with areas of the species range used on migration. None of the 97 Vaux's swifts were assigned molt origins within the species wintering range.

We detected substantial variation for the three stable isotopes (Table 1). Among the three isotopes, only $\delta^{13}C_f$ and δ^2H_f were correlated with each other (Table 2); however, there was no relationship between the feather and claw isotope values for the subset of 71 birds with complete isotope data that molted on the breeding grounds (Supplemental Material Table S1). Despite substantial variation in all three isotopes within feathers, there was little support for any of our covariates driving variation δ^2H_f , $\delta^{15}N_f$, or $\delta^{13}C_f$ as in all three cases the Null model (intercept only) received greater support than all other candidate models based on WAIC (Table 3). There was weak evidence (Δ WAIC = 0.06) for there being a possible median difference of almost 5‰ in δ^2H_f between males and females; however, both sexes had broad 95% credible intervals (Female median = -116.1‰, 95% CI= -123.4 - -108.9 ‰; Male median = -111.1‰, 95% CI= -118.0 - -105.7‰). Based on WAIC, we did not find strong support for an effect of wintering ground cluster (Δ WAIC relative to the null model of 1.01 and 1.37 respectively for the two and three cluster solutions), age, or wing length on δ^2H_f (Table 3). Similarly, WAIC model selection suggested weak support for sex and wing length contributing to variation in $\delta^{15}N$ (Δ WAIC for

the Sex + Wing model = 1.16 and 1.64 for the model including only Sex; Table 3). However, 95% credible intervals for the effect of sex (β = -0.01 and 95% CI = -0.49 – 0.46 for the Sex + Wing length model; β = 0.00 and 95% CI = -0.46 – 0.50 for the model including only Sex) and wing length (β = -0.02 and 95% CI = -0.11 – 0.07) suggested no biologically meaningful variation was associated with these parameters. Finally, models exploring variation in $\delta^{13}C_f$ within 2 WAIC units of the Null model included parameters for sex, wing length and age (Table 3); however, parameters from these models showed no biologically meaningful variation (Sex β = -0.25 and 95% CI = -0.69 – 0.20; Wing length β = 0.04 and 95% CI = -0.04 – 0.12; and Age β = -0.34 and 95% CI = -1.14 – 0.45).

Regardless of which wintering cluster individuals were associated with (as per Reudink et al. 2015), the vast majority of Vaux's swifts in our sample were assigned to breeding origins that overlapped the roost location where the birds were sampled (Figures 2–4). While assignment uncertainty precludes us from excluding other portions of the breeding range as possible origins (Figures 2–4), a local (Vancouver Island) origin is the most parsimonious assignment for the vast majority of birds in our sample.

Overall, Vaux's swifts displayed weak migratory connectivity ($r_{\rm M} = 0.07, P = 0.11$). The putative strength of migratory connectivity, however, differed between wintering ground clusters defined based on isotopic analysis of claws. In contrast with cluster 3, which displayed positive migratory connectivity ($r_{\rm M} = 0.20, P = 0.02$), neither cluster 1 ($r_{\rm M} = -0.11, P = 0.92$) nor cluster 2 ($r_{\rm M} = -0.02, P = 0.53$) showed any significant correlation between wintering and breeding ground distance matrices constructed using isotopic variation (δ^{13} C, δ^{15} N and δ^{2} H) between claws (wintering) versus feathers (breeding).

DISCUSSION

We examined the approximate breeding origins and patterns of migratory connectivity in Vaux's swifts recovered in spring from a migratory roost on Vancouver Island, Canada. Stable isotope analysis (δ^{13} C, δ^{15} N and δ^{2} H) revealed that the swifts were primarily migrating to local breeding locations, likely on Vancouver Island. Consistent with recent work by Pyle et al. (2018), we also determined that a substantial proportion of birds (27 out of 99 sampled) were isotopically consistent with being molt-migrants, exhibiting δ^{2} H_f values that were not consistent with the breeding season isoscape, or may have grown their feathers in otherwise isotopically enriched habitats. All three stable isotopes exhibited substantial isotopic variation, which likely reflects the diverse array of habitats (e.g., coastal, inland, mountain) in coastal British Columbia.

While new technologies have revolutionized the study of migratory connectivity, strength of migratory connectivity has been quantified for relatively few species (Table 4), mostly during stationary periods of the annual cycle. Although Vaux's swifts displayed some evidence of using isotopically similar sites between breeding and wintering grounds, the inferred strength of connectivity was weak ($r_{\rm M} = 0.07$; range: -0.11 - 0.20) when compared with most other species (see Table 4). For example, Swainson's thrush (*Catharus ustulatus*) exhibit high connectivity ($r_{\rm M} = 0.72$; Cormier et al. 2013), with individuals from the same breeding population wintering within the same general area of Mexico. On the other end of the spectrum, the barn swallow (*Hirundo rustica*) exhibits extremely weak migratory connectivity ($r_{\rm M} = 0.025 - 0.22$; Ambrosini et al. 2009); barn swallows in that population neither wintered nor bred together. The low connectivity we observed for Vaux's swift fit our *a priori* hypothesis, and may be generally true for aerial insectivores given the weak migratory connectivity estimated for other species (Ambrosini et al. 2009, Fraser et al. 2017), the generally low connectivity of long-distance

migrants in general (Finch et al. 2017), and the large-scale movements within the non-breeding season by some aerial insectivores (Åkesson et al. 2012, Beason et al. 2012, Liechti et al. 2013). The relatively weak connectivity we found for Vaux's swifts roosting together during spring migration suggests that factors (e.g., habitat loss) influencing populations on the wintering grounds should have relatively weak impacts spread over multiple breeding populations. Alternatively, the weaker connectivity we observed may in part owe to mixing of individuals on migration. Future efforts examining strength of connectivity of birds on stopover would provide useful insight as to whether population mixing is greater along migratory routes than during stationary periods of the annual cycle.

Although we found evidence for a connection between wintering and breeding grounds, the strength of migratory connectivity depended upon which wintering cluster the individuals were associated with. Our initial analysis (Reudink et al. 2015) revealed that the swifts likely originated from two or three clusters. When we examined connectivity using the two cluster solution, there was no evidence of connectivity between winter clusters and breeding origins. However, when we examined the three cluster solution, we did identify weak positive migratory connectivity. While it is possible the finding of connectivity in the three cluster solution is spurious, the fact that we found evidence of connectivity in the three cluster, but not two cluster solution, may lend support to the idea that these swifts originated from three, rather than two, distinct wintering locations/habitats. We cannot completely preclude the possibility that birds may have been panmictic and simply selecting isotopically distinct habitats within the same region; however, a lack of sex-based differences (see below) suggests this may be less probable. Calibration of wintering ground multi-isotope claw isoscapes would further increase our confidence in the strength of connectivity estimates for the analysis based on our three cluster

solution. Alternatively, future work could deploy miniaturized tracking devices such as archival GPS tags (Hallworth and Marra 2015) on Vaux's swift on the breeding grounds and multiisotope assays of claw material from recaptured individuals could be used to assess whether birds from differing wintering ground isotopic clusters were indeed spatially segregated.

Segregation of migratory birds during the non-breeding season by age, sex and breeding origins has previously been described for several species (Marra 2000; Valdez-Juárez et al. 2018). In some instances, competition amongst individuals may result in varying age, sex or body size ratios along gradients of habitat quality, some of which may be isotopically distinct (Marra et al. 1998). For example, older American redstart (*Setophaga ruticilla*) males hold territories in high quality mangrove habitats and competitively exclude females and young males, relegating them to neighboring, lower quality scrub habitat (Marra et al. 1993; Marra 2000). The Vaux's swift does not appear to exhibit sex-based segregation during winter (Reudink et al. 2015) and our results here also indicate that the sexes do not use isotopically distinct habitats or locations during the post-breeding molt. Along with a lack of sex-based segregation, we found no relationship between body size (wing or tail length) and all three stable isotopes. The lack of relationship between body size and $\delta^2 H_f$ in particular may indicate that body size does not affect migration distance; however, this relationship is unlikely to be apparent at such a fine spatial scale (localized) and may instead only be visible at a range-wide scale.

Assignment of individuals to a feather isoscape revealed that a large portion (25.8%) of the sample may have molted during migration, south of the breeding region, or were otherwise isotopically inconsistent with this portion of the isoscape, while the remaining individuals (74.2%) likely molted on or near the breeding grounds. While this result appears in stark contrast to work by Bull and Collins (1993) that suggests P1 feathers should reflect the breeding grounds,

our results do appear generally consistent with recent analyses by Pyle et al. (2018) and Tonra and Reudink (2018) that point to molt migration being more commonplace than previously described in the literature. Indeed, stable isotope analysis has previously revealed the apparent ubiquity of molt-migration and is proving indispensable for determining the location of feather growth for both small and large-bodied birds (Rohwer et al. 2015) and can be effectively used on species that migrate thousands of kilometers (Hobson et al. 2014). While it is possible that some individuals may have grown P1 in isotopically enriched food-webs within the breeding range (e.g. areas influenced by irrigation), it seems improbable that such a high proportion would derive from enriched food-webs. Here, we used a likelihood-based method to link the isotopic signatures of P1 feathers to the period of the annual cycle during which they were most likely grown. We suggest future work should employ similar methods to ours to assess whether molt may have occurred on versus off the breeding grounds given the apparent prevalence of molt migration (Pyle et al. 2018), and to filter out individuals for which it may be more conservative to not make isotopic assignments to breeding season origin using isoscapes.

Many studies have used stable isotope analysis as a method to determine either breeding location (from individuals caught on their wintering grounds; Hobson et al 2014) or wintering location or habitat (from individuals caught on breeding grounds; Bearhop et al. 2004, Marra et al. 1998). We took a novel approach, as we sampled birds traveling *en route* north to their breeding grounds and used stable isotopes to determine both the wintering clusters (Reudink et al. 2015) and approximate breeding locations. While stable isotope analysis has many benefits, one limitation is the uncertainty of the hydrogen isoclines (Hobson et al. 2014). With more complete sampling, especially on the wintering grounds, further studies will improve the resolution of feather and claw isoscapes and allow a better picture of connectivity. In particular,

improvement of the isoscapes that have been developed for central and South America would allow for better assignments of individuals to specific winter and breeding regions.

It has previously been established that spatial or habitat based segregation of birds from differing populations, ages or sexes has the potential to explain population trajectories and fluctuations on the breeding grounds (Marra et al. 2015; Rushing et al. 2016, Taylor and Stutchbury 2016). In addition, recent theoretical (Taylor and Norris 2010) and experimental (Betini et al. 2015) evidence suggests that the strength of migratory connectivity has the potential to moderate the effect of environmental perturbations on populations. The apparent weak migratory connectivity observed for Vaux's swift and other aerial insectivores might buffer aerial populations against climate driven shifts in habitat because more individuals will manage to reach suitable habitat if it shifts when the population disperses widely (Finch et al. 2017). Given the pervasive and persistent declines of aerial insectivores in North America (Nebel et al. 2010), this does not appear to be the case. Alternatively, Finch et al. (2017) suggest that weak connectivity might simultaneously increase susceptibility to habitat loss. In this light, the continued loss and degradation of habitat from deforestation, agricultural intensification, urbanization, and land use change (Paquette et al. 2014, Curtis et al. 2018) should be the focus of further research and conservation efforts for aerial insectivores. Clearly there is a need for continued work to determine factors limiting their populations across the annual cycle and to devise optimal strategies for their conservation (Martin et al. 2007).

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TABLE 1. Mean, SD, Min and Max of the $\delta^{13}C_f$, $\delta^{15}N_f$ and δ^2H_f feather isotope analysis of Vaux's swifts from a northern migratory roost.

Isotope	Mean	SD	Min	Max
$\delta^2 \mathrm{H_f}$	-107.6	23.0	-176.1	-41.1
$\delta^{13} \mathrm{C_{f}}$	-24.2	1.0	-26.3	-19.4
$\delta^{15} \mathrm{N_f}$	8.2	1.0	6.25	10.56

Isotope	$\delta^2 \mathrm{H_f}$	$\delta^{13}C_{\rm f}$	$\delta^{15}N_{\rm f}$
$\delta^2 \mathrm{H_f}$	-	0.29	0.06
$\delta^{13} C_{\mathrm{f}}$	<i>P</i> = 0.003	-	0.01
$\delta^{15} N_{\rm f}$	P=0.56	<i>P</i> =0.94	-

Model	WAIC	SE	AWAIC
$\frac{\delta^2 H_c}{\delta^2 H_c}$	witte	5L	
Null	610.88	17 41	0
Sev	610.00	16.85	0.06
Sex Cluster $(2)^1$	611.80	16.05	1.01
Cluster (2)	(12.25	10.45	1.01
Cluster (3)	612.25	18.38	1.3/
Age	612.45	1/.3/	1.5/
Wing	612.59	16.83	1./1
Sex + Wing	613.02	16.19	2.14
Age + Sex + Wing	614.46	16.08	3.58
Age + Wing	614.60	16.69	3.72
Age + Sex + Wing + Cluster (2)	616.04	15.12	5.16
Age + Sex + Wing + Cluster (3)	618.61	15.94	7.73
δ^{15} N			
Null	201.95	9.94	0
Sex + Wing	203.11	10.06	1.16
Sex	203.89	9.93	1.94
Cluster (2)	203.99	9.93	2.04
Age	204.01	10.32	2.06
Wing	204 23	10.08	2.28
Cluster (3)	204.25	9.81	23
$\Delta ge + Wing$	201.23	10.48	4 36
$\Lambda ge + Sev + Wing$	200.51	10.40	6.56
Age + Sex + Wing + Cluster (2)	208.51	10.57	0.50 8.66
Age + Sex + Wing + Cluster (2) Age + Sex + Wing + Cluster (2)	210.01	10.40	8.00
Age + Sex + w ling + Cluster (3)	210.80	10.40	0.91
\$ ¹³ C			
	196.07	10.02	0
INUII S	100.92	10.05	0 02
Sex	187.84	10.20	0.92
Wing	188.09	10.59	1.17
Age	188.62	9.70	1.70
Sex + Wing	189.02	10.64	2.10
Cluster (2)	189.1	10.17	2.18
Age + Wing	189.75	10.27	2.83
Cluster (3)	190.62	10.8	3.7
Age + Sex + Wing	190.81	10.19	3.89
Age + Sex + Wing + Cluster (2)	193.01	10.24	6.09
Age + Sex + Wing + Cluster (3)	194 63	10.59	7 71

TABLE 3. WAIC - based model selection for Bayesian robust regression models examining variation in $\delta^2 H_f$, $\delta^{15} N$, and $\delta^{13} C$ respectively of Vaux's swifts from a northern migratory roos tory roost.

¹Cluster (2) and Cluster (3) are 2 level and 3 level factors (respectively) representing the alternative wintering ground cluster solutions from Reudink et al. (2015)

Mantel Correlation		
Coefficient (r _M)	Species	Paper
0.84	Ovenbird (Seiurus aurocapilla)	Hallworth and Marra 2015
0.78	American Robin (Turdus migratorious)	Brown and Miller 2016
0.72	Swainson's Thrush (Catharus ustulatus)	Cormier et al. 2013
0.66	Golden-crowned Sparrow (Zonotrichia atricapilla)	Cormier et al. 2016
0.53 - 0.56	Great Reed Warbler (Acrocephalus arundinaceus)	Koleček et al. 2016
0.51 - 0.53	Tree swallow (<i>Tachycineta bicolor</i>)	Knight et al. 2018
0.50	Montagu's Harrier (Circus pygargus)	Trierweiler et al. 2014
0.50	European Roller (<i>Coracias garrulus</i>)	Finch et al. 2015
0.48	European Robin (Erithacus rubecula)	Ambrosini et al. 2016
0.42	American woodcock (Scolopax minor)	Moore and Krementz 2017
0.36	European Roller (Coracias garrulus) - eastern populations	Finch et al. 2015
0.33	Wood Thrush (Hylocichla mustelina)	Stanley et al. 2015
-0.30	European Roller (<i>Coracias garrulus</i>) - western populations	Finch et al. 2015
-0.11 - 0.22	Purple Martin (<i>Progne subis</i>)	Fraser et al. 2017
-0.12 - 0.22	Loggerhead Shrike (Lanius ludovicianus)	Chabot et al. 2018
-0.11 - 0.20	Vaux's swift	This study
-0.03 - 0.19	Common Tern (Sterna hirundo)	Bracey et al. 2018
0.025 - 0.22	Barn Swallow (Hirundo rustica)	Ambrosini et al. 2009
		van Wiik et al 2018

FIGURE LEGENDS

FIGURE 1. Predicted δ^2 H of feathers (δ^2 H_f) of Vaux's swifts from a northern migratory roost a) derived from 1000 bootstrap regressions relating δ^2 H_f to predicted δ^2 H_p from the isoscape of Bowen et al. (2005) and b) spatially explicit estimates of prediction error (SD); see Methods.

FIGURE 2. Predicted origins of 35 Vaux's swifts from a northern migratory roost that were isotopically consistent with a common wintering environment (cluster 1 in Reudink et al. 2015) based on spatially explicit assignment to a $\delta^2 H_f$ isoscape. Red dot depicts the sampling location on Vancouver Island, Canada.

FIGURE 3. Predicted origins of 11 Vaux's swifts from a northern migratory roost that were isotopically consistent with a common wintering environment (cluster 2 in Reudink et al. 2015) based on spatially explicit assignment to a $\delta^2 H_f$ isoscape. Red dot depicts the sampling location on Vancouver Island, Canada.

FIGURE 4. Predicted origins of 26 Vaux's swifts from a northern migratory roost that were isotopically consistent with a common wintering environment (cluster 3 in Reudink et al. 2015) based on spatially explicit assignment to a $\delta^2 H_f$ isoscape. Red dot depicts the sampling location on Vancouver Island, Canada.





FIGURE 2



FIGURE 3



FIGURE 4



- 2 3 4 5 6 7 8 9 10 11 12 13 16 17 18 19 20 21 22 23 24 25 26 27 28 33 34 35 36 37 38 39 40 41 42 43 44 45 49 50 51 52 53 54 55 57 58 59

- 64 65

SUPPLEMENTAL MATERIAL

Supplemental Material Table S1. Relationship between claw and feather isotopes (δ^{13} C, δ^{15} N and δ^{2} H), using only feathers identified as molted on the breeding ground (n = 71) of Vaux's swifts from a northern migratory roost.

		Feather	
	$\delta^2 \mathrm{H}$	$\delta^{13}C$	$\delta^{15}N$
Claw	r P	r P	r P
$\delta^2 \mathrm{H}$	-0.08 0.44	-0.03 0.80	0.00 0.40
$\delta^{13}C$	-0.01 0.89	-0.11 0.31	0.09 1.00
$\delta^{15}N$	0.01 0.91	-0.16 0.11	-0.08 0.41