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RESEARCH ARTICLE

Patterns of migratory connectivity in Vaux's Swifts at a northern migratory roost: A multi-isotope approach

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ABSTRACT

The strength of migratory connectivity between breeding, stopover, and wintering areas can have important implications for population dynamics, evolutionary processes, and conservation. For example, patterns of migratory connectivity may influence the vulnerability of species and populations to stochastic events. For many migratory songbirds, however, we are only beginning to understand patterns of migratory connectivity. We investigated the potential strength of migratory connectivity within a population of Vaux's Swifts (*Chaetura vauxi*). Like many aerial insectivores, this species is currently experiencing population declines. In 2012, a mass mortality event at a spring migratory roost on Vancouver Island, British Columbia, Canada, resulted in the deaths of >1,000 individuals (~2% of the British Columbia population). In these individuals, we examined variation in 3 stable isotopes (δ^2H, δ^{13}C, and δ^{15}N) from claw samples to determine whether spring migrants showed inherent isotopic similarity in the habitats they used on their Mexican and Central American wintering grounds. Our results indicated the presence of 2 or 3 broad isotopic clusters, which suggests that Vaux's Swifts that migrated through Vancouver Island most likely originated from 2 or 3 overwintering locales or habitat types. We found no evidence of sex- or morphology-based segregation, which suggests that these groups likely share a similar overwintering ecology and, thus, may be equally vulnerable to stochastic events or habitat loss on the wintering grounds. Our results highlight the need for more studies on the nonbreeding-season ecology and migratory connectivity of this species.

Keywords: cluster analysis, conservation, migratory connectivity, roost, stable isotope, Vaux's Swift

Patrones de conectividad migratoria en *Chaetura vauxii* en un dormidero migratorio del norte: un enfoque de isótopos múltiples

RESUMEN

La fuerza de la conectividad migratoria entre áreas de cría, parada e invernada puede tener implicancias importantes para la dinámica poblacional, los procesos evolutivos y la conservación. Por ejemplo, los patrones de conectividad migratoria pueden influenciar la vulnerabilidad de las especies y de las poblaciones a eventos estocásticos. Para muchas aves canoras migratorias, sin embargo, recién estamos comenzando a comprender los patrones de conectividad migratoria. Aquí investigamos la fuerza potencial de la conectividad migratoria dentro de una población de *Chaetura vauxii*. Esta especie, como muchas insectívoras aéreas, está experimentando actualmente disminuciones poblacionales y un evento de mortalidad masivo en un dormidero migratorio de primavera en la Isla Vancouver, Columbia Británica, Canadá, resultando en la muerte de más de 1,000 individuos, lo que representa cerca del 2% de la población de Columbia Británica. A partir de estos individuos, examinamos la variación en tres isótopos estables (δ^2H, δ^{13}C y δ^{15}N) de muestras de las garras para determinar si los migrantes de primavera mostraban una similitud isotópica inherente de los hábitats que usan en los sitios de invernada en México y América Central. Nuestros resultados indicaron la presencia de dos a tres agrupaciones isotópicas amplias, sugiriendo que los individuos de *C. vauxii* que migran a través de la Isla Vancouver probablemente provienen de dos o tres localidades o tipos de hábitat de invernada. No encontramos evidencia de segregación basada en el sexo o en la morfología, sugiriendo que estos grupos diferentes probablemente comparten una ecología de invernada similar y por lo tanto pueden ser igualmente vulnerables a los eventos estocásticos o a la pérdida de hábitat en los sitios de invernada. Nuestros resultados remarcan la necesidad de más estudios sobre la ecología de la estación no reproductiva y la conectividad migratoria de esta especie.

Palabras clave: análisis de agrupación, *Chaetura vauxii*, conectividad migratoria, conservación, dormidero, isótopos estables

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INTRODUCTION

Migratory birds move annually between breeding, wintering, and stopover sites that can be separated by hundreds or thousands of kilometers. Hence, they face an array of both natural and human-mediated environmental challenges. For their effective conservation, it is essential to take an annual-cycle approach that addresses factors that influence populations throughout the year and across broad geographic scales (Webster et al. 2002, Webster and Marra 2005). Stressors that occur during one phase of the annual cycle can have carryover effects to subsequent phases of the annual cycle, affecting both individual- and population-level dynamics (Marra et al. 1998, Sillett et al. 2000, Reudink et al. 2009a). Population-level carryover effects can be caused by density-dependent population regulation (Fretwell 1972, Ratikainen et al. 2008), large-scale climatic cycles (Sillett et al. 2000, Wilson et al. 2011), and habitat loss (Norris 2005). Examples of carryover effects that influence individual fitness include wintering-habitat-mediated differences in reproductive success (Reudink et al. 2009a) and natal dispersal (Studds et al. 2008). Understanding patterns of migratory connectivity, defined as the extent to which individuals from the same wintering site migrate to the same breeding site and vice versa (Marra et al. 2010), may be important for understanding species- or population-specific responses to anthropogenic disturbances (e.g., land-use change, agricultural development), as well as large-scale selective pressures such as climate change (Webster et al. 2002).

Migratory populations may be especially vulnerable to stochastic events when they display high migratory connectivity, particularly if population size is also small. For example, Kirtland's Warblers (*Setophaga kirtlandii*) exhibit extremely strong connectivity between breeding populations in Michigan, USA, and wintering populations in the Bahamas, Turks, and Caicos (Bocetti et al. 2014). As a consequence, the species experiences pronounced carryover effects, whereby drier winters delay arrival and nest initiation on the breeding grounds, ultimately resulting in fewer offspring fledged (Rockwell et al. 2012). Intensive management of the species on the breeding grounds has led to population increases, but continued long-term recovery likely depends on active management in the Bahamas as well (Wunderle et al. 2010), especially given that climate change is predicted to increase drought severity in the Caribbean (Rockwell et al. 2012).

For small migratory birds, making geographic connections for individuals and populations between different phases of their annual cycle can be exceedingly difficult. In recent years, information gleaned from traditional bird ringing has been greatly enhanced with the use of intrinsic markers such as genetic (e.g., Ruegg et al. 2014) and stable-isotope (Hobson 2011) techniques, as well as combinations of these techniques (Chabot et al. 2012, Rundel et al. 2013). Stable isotopes of hydrogen (δ^2H), in particular, have been instrumental in migratory-connectivity research, owing to geographically predictable patterns of isotopic variation that are reflected in animal tissue and thus provide "markers of origin" that indicate where the tissue was grown (Hobson et al. 2012a). Such intrinsic markers have the advantage that birds need only be captured once, and they may be especially useful as a first step to understanding patterns of migratory connectivity in poorly studied species or in remote areas (Hobson et al. 2014, Pekarsky et al. 2015). The advent of new extrinsic marker technologies such as geolocators and GPS loggers has led to higher-resolution information on the migratory behavior of certain species (Stutchbury et al. 2009). However, use of these extrinsic markers is complicated by the need to recover data loggers and remains impractical, and often prohibitively expensive, for large-scale studies (Arlt et al. 2013, Bridge et al. 2013, Hobson et al. 2014). In addition, extrinsic markers cannot be used to infer historical patterns of migratory connectivity. By contrast, intrinsic markers can be extremely useful in forensic studies, including dietary reconstruction (Nocera et al. 2012, Blight et al. 2015) and inference of migratory connectivity from historical specimens (Hobson et al. 2010). Given the paucity of information on population- or region-specific migratory connectivity for many species of conservation concern, there is a pressing need to apply intrinsic and/or extrinsic marker approaches to evaluate factors that limit populations throughout their annual cycle (Hobson et al. 2014).

Like many other aerial insectivores, breeding populations of Vaux's Swift (*Chaetura vauxi*) have undergone significant declines (Nebel et al. 2010). Recent estimates from the North American Breeding Bird Survey suggest a population decline of –2.2% yr^{-1} in Canada since the 1970s (Environment Canada 2014). Vaux's Swifts breed throughout western North America but exhibit an unusual roosting strategy during migratory journeys between their western North American breeding grounds and their southern Mexican and Central American wintering grounds (Bull and Collins 2007). During migration, groups of Vaux's Swifts roost communally in tree cavities or, more commonly, in abandoned industrial chimneys, where they can remain for several days to weeks (Bull and Collins 2007). Migratory roosts may contain hundreds to thousands of individuals. During winter, Vaux's Swifts also appear to occupy large roost sites (Bull and Collins 2007). However, little is known about migratory connectivity in Vaux's Swift, and it is unknown whether (1) individuals from particular wintering areas migrate north together and stop at the same roost sites (strong migratory connectivity) or (2) migratory roost sites comprise individuals arriving from multiple locations across their winter range (weaker migratory connectivity). The degree of connectivity can have important implications

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for conservation (e.g., Sheehy et al. 2011), and if large concentrations of individuals winter together and move together throughout migration, they may be particularly vulnerable to stochastic events. Here, we use intrinsic markers to study putative migratory connectivity in migrating Vaux's Swifts. We sampled claws (grown during the overwintering period) from a large group of communally roosting Vaux's Swifts that accidentally suffocated at a spring migratory roost site on Vancouver Island, British Columbia, Canada. We used cluster analyses based on multiple stable-isotope markers (δ^2H, δ^{13}C, and δ^{15}N) to examine support for the existence of a single versus multiple wintering origins within this population.

METHODS

Field Methods

On May 9, 2012, a mass mortality event occurred at a migratory roost in Cumberland, British Columbia, used annually by Vaux's Swifts during spring migration. Approximately 1,350 Vaux's Swifts died from suffocation after being trapped in the roost. That single event represented a loss of 1.5–2.7% of the published population-size estimates (Summers and Gebauer 1995, Partners in Flight Science Committee 2013) for Vaux's Swifts in British Columbia. From these mortalities, we randomly subsampled 98 individuals for analysis. On each individual, we measured wing length, tail length, and tail pin length, and we sexed each individual via laparoscopy. We then sampled 2 mm (0.30–0.40 mg) of tissue from the tip of the central claw, ensuring that we avoided the quick, of each foot from each individual for isotope analysis. Although claws grow continuously and, because of their conical growth pattern, incorporate materials grown at slightly different times, analysis of the claw tip should accurately reflect the isotopic environment over an extended period (weeks to months) preceding sampling (Mazerolle and Hobson 2005, Hahn et al. 2012). For instance, on the basis of changes in δ^2H after arrival on the breeding grounds, Fraser et al. (2008) estimated that isotopic values in claws of parulids may reflect the nonbreeding area for 3–7 wk after the birds arrive on the breeding grounds. Hahn et al. (2014) also provided empirical evidence demonstrating that in Palearctic–African migratory passerines, the distal claw tip should reflect isotopic environments over a few months prior to sampling, with typical claw-growth rates of 0.03–0.05 mm day^{-1}. Though data on the migration timing of Vaux's Swifts are sparse, major flight passages occur during mid-April to late May in California (Small 1994), with birds arriving in Oregon from late April to late May (Bull and Collins 2007, and references therein). Thus, claws sampled from birds that died during spring migration on May 9 should reflect wintering conditions, as has been demonstrated in passerines captured both on migration (Bearhop et al. 2004) and upon arrival on the breeding grounds (Reudink et al. 2009a, 2009b).

Stable Isotope Analysis

We analyzed the stable isotope ratios of 3 naturally occurring elements that are incorporated predictably into an animal's diet. First, we analyzed δ^2H, which has been used extensively in studies of avian migration and connectivity because it is linked to both latitude and elevation, ^{2}H being relatively less abundant at more northern latitudes and higher elevations (Hobson 2011). Second, we used δ^{13}C, which varies in animal tissues with habitat: Individuals that occupy habitats with a higher proportion of C_4 plants or under higher water stress exhibit less negative δ^{13}C signatures (Lajtha and Marshall 1994, Cerling et al. 1997, Still and Powell 2010). Finally, we used δ^{15}N, because ^{15}N is preferentially incorporated into the tissues of consumers and thus biomagnifies with increasing trophic levels, leading to an increase in δ^{15}N signatures (Post 2002, Poupin et al. 2011). In addition, δ^{15}N may reflect the relative aridity of a biome because it is negatively correlated with rainfall and positively correlated with temperature (Sealy et al. 1987, Craine et al. 2009). All stable isotope analyses were conducted at the Smithsonian Institution OUSS/MCI Stable Isotope Mass Spectrometry Facility in Suitland, Maryland, USA. Claws were washed in a 2:1 chloroform:methanol solution, then air dried and allowed to acclimate to lab atmospheric conditions in a fume hood for 72 hr prior to sample preparation. 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. For stable hydrogen isotope analysis, we ran 4 calibrated standards for every 10 samples, including the hydrogen standard International Atomic Energy Agency CH-7 and 3 additional standards (KHS: –54.1 ± 2.3‰; CBS: –197.3 ± 2.0‰; Spectrum keratin: –121.6 ± 2.5‰). Nonexchangeable δ^2H values were corrected to keratin standards following Wassenaar and Hobson (2000) and were repeatable to within 3 ± 2‰ (mean ± SD; $n = 10$). For stable carbon and nitrogen analysis, we ran 2 in-house standards (acetanalide and urea) for every 10 samples. Stable isotope values are expressed in parts per thousand (‰) deviations from international standards VSMOW (hydrogen), PDB (carbon), and air (nitrogen) by the following equation:

$$X = \{[(R_{\text{unknown}} - R_{\text{standard}}) - 1] \times 1,000\},$$

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

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Statistical Analysis

There are many different methods available for determining the optimal number of clusters in a dataset. For this reason, we made use of the package "NbClust" in program R (R Development Core Team 2013), which provides the user with results from 30 indices aimed at determining the number of clusters into which the data should be split (Charrad et al. 2014). Clustering validity indices combine information such as intracluster and intercluster variation, geometric or statistical properties of the data, and dissimilarity or similarity measurements. For a detailed description of all 30 indices, see Charrad et al. (2014). Two widely used clustering algorithms are available in the NbClust package: *k*-means and hierarchical agglomerative clustering. In *k*-means clustering, observations are assigned to initial cluster centers, which are then iteratively updated until the cluster centers no longer change and the within-cluster sum of squares is minimized (MacQueen 1967). In hierarchical agglomerative clustering, each observation begins in its own cluster, and pairs of clusters are joined on the basis of a distance measure and an agglomeration criterion (Székely and Rizzo 2005). Because of the differences in these clustering approaches and a lack of a priori reasons to hypothesize a set number of clusters in our data, we used both clustering algorithms. We used a Euclidean distance (square distance between 2 vectors; Seber 1984) in both clustering algorithms and examined the relative support for division of the data into 2–10 clusters based on the 3 isotopic markers (δ^2H, δ^{13}C, and δ^{15}N). For hierarchical agglomerative clustering, we used the Ward agglomeration method (Ward 1963), which minimizes the total within-cluster variance. We also repeated the above procedures after removing 6 multivariate outliers, assessed using the robust Mahalanobis distance (Varmuza and Filzmoser 2009).

After the optimal number of clusters was identified by each clustering approach, we examined the partitioning of observations (individual birds) into clusters. We performed multivariate analysis of variance (MANOVA) to verify significant differences among the selected clusters in δ^2H, δ^{13}C, and δ^{15}N ratios. We then used a Pearson's chi-square test to examine whether the proportion of claws from male and female birds differed among clusters, and we used a *t*-test or analysis of variance (ANOVA) to examine whether wing length and tail length varied among clusters.

Finally, we used a model-based hierarchical clustering procedure within the package "mclust" in R (Fraley et al. 2012) to determine whether the optimal number(s) of clusters selected by the above procedures was preferred over no clustering at all. Package "mclust" uses an expectation-maximization (EM) algorithm to estimate the finite mixture models that correspond to different numbers of clusters, and uses the Bayesian Information Criterion (BIC) to select the best number of clusters. Importantly, a single cluster can also be considered. We evaluated the support for 1–10 clusters.

The δ^2H, δ^{13}C, and δ^{15}N isotope ratios were standardized prior to analysis by subtracting by their mean and dividing by their standard deviation. Standardization is recommended in cluster analysis when variables are on different scales, to minimize the effects of outliers and so that cluster formation is not overly influenced by variables with greater absolute variation (Milligan and Cooper 1988). Although isotope ratios represent the ratio of heavy to light isotopes in a sample divided by the ratio of a standard and are always expressed in the same units (‰), differences in the natural abundances and fractionation of heavy and light isotopes among elements lead to differences in the magnitude of the range of typical δ values (Fry 2006). Thus, standardization was useful in giving equal weight to variation among the 3 isotope ratios. All analyses were performed in R version 3.1.1, and results are shown as means ± SD.

RESULTS

Stable isotopic values (δ^2H, δ^{13}C, and δ^{15}N) were available from claws of 98 individuals. All 3 elements showed considerable variation in all 3 isotopes (Table 1). Mean isotope ratios were –37.9 ± 12.4‰ for δ^2H, –21.6 ± 0.6‰ for δ^{13}C, and 7.3 ± 0.9‰ for δ^{15}N. Correlations among isotope ratios were $r = -0.09$ ($P = 0.37$) for δ^2H and δ^{13}C, $r = -0.14$ ($P = 0.17$) for δ^2H and δ^{15}N, and $r = 0.53$ ($P < 0.001$) for δ^{13}C and δ^{15}N. Of those 98 individuals with isotope data, we were unable to determine sex for 1 individual. There was a nearly even number of males and females in our sample ($n = 47$ females, $n = 50$ males). Males and females did not differ in δ^2H ($t_{95} = -0.02$, $P = 0.98$), δ^{13}C ($t_{95} = -0.98$, $P = 0.33$), or δ^{15}N ($t_{95} = -0.18$, $P = 0.86$). Mean wing length was 113.5 ± 2.8 mm and did not differ between males and females (males: 113.4 ± 2.7, females: 113.7 ± 2.8; $t_{95} = -0.46$, $P = 0.65$). Wing length was not correlated with δ^2H ($r = -0.06$, $P = 0.59$), δ^{13}C ($r = 0.16$, $P = 0.12$), or δ^{15}N ($r = 0.16$, $P = 0.12$). Mean tail length was 36.2 ± 2.3 mm and did not differ between males and females (males: 35.8 ± 1.8, females: 36.5 ± 2.7; $t_{95} = -1.53$, $P = 0.13$). Tail length was not correlated with δ^2H ($r = 0.00$, $P = 0.99$) or δ^{13}C ($r = -0.07$, $P = 0.49$), but it was negatively correlated with δ^{15}N ($r = -0.23$, $P = -0.02$).

When using the full dataset, 11 of 30 clustering validity indices (37%) proposed 2 as the optimal number of clusters in the *k*-means clustering procedure. The next highest-ranked numbers of clusters were 3 and 4, which received support from 6 (20%) and 5 (17%) clustering indices, respectively. Three was deemed the optimal number of clusters by the majority (10, or 33%) of indices in the hierarchical agglomerative procedure, but a large proportion of indices (9, or 30%) also supported 2 clusters. The only alternative clustering that received support was a 10-

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TABLE 1. Sex, age, morphometrics (mm), and stable isotope values (‰) for 98 Vaux's Swift claws from a roost site on Vancouver Island, British Columbia, Canada.

ID	Sex	Wing	Tail	δ^2H	δ^{15}N	δ^{13}C
0258	M	110	38.0	−76.9	5.9	−21.8
0175	F	116	39.0	−71.3	8.5	−21.4
0288	F	113	35.0	−66.0	8.4	−19.4
0259	F	113	37.0	−57.0	6.2	−22.3
0242	M	115	32.0	−56.9	6.2	−21.8
0306	M	121	35.0	−56.5	7.6	−21.7
0237	F	118	39.0	−56.5	6.6	−22.4
0291	F	118	29.0	−56.2	11.6	−20.2
0182	M	116	36.0	−56.1	7.7	−21.5
0276	M	116	39.0	−55.7	9.2	−20.3
0241	F	113	38.0	−54.8	7.3	−21.5
0173	F	115	37.0	−52.8	7.9	−21.4
0280	F	111	34.0	−52.1	7.2	−21.3
0304	F	116	38.0	−50.8	8.4	−21.6
0295	M	109	34.0	−50.8	6.5	−21.5
0271	F	111	38.0	−50.6	8.9	−21.2
0294	F	113	34.0	−50.3	9.0	−21.1
0256	M	114	35.0	−50.3	8.0	−22.1
0176	M	115	37.0	−50.2	6.8	−22.4
0164	F	119	39.0	−47.8	5.8	−22.0
0286	M	113	36.0	−47.6	6.6	−22.3
0178	F	112	37.0	−46.9	6.9	−21.9
0287	F	115	40.0	−46.8	7.5	−21.3
0063	M	118	35.0	−46.5	6.9	−21.4
0308	M	110	37.0	−46.2	6.9	−22.1
0165	M	114	35.0	−46.0	9.3	−21.0
0289	F	111	34.0	−45.6	6.3	−22.1
0257	M	115	36.0	−45.1	7.0	−22.0
0290	F	113	38.0	−43.5	7.4	−21.6
0064	M	114	37.5	−43.2	6.5	−22.0
0252	F	109	38.0	−42.5	6.4	−21.8
0174	M	115	37.0	−42.3	7.8	−21.8
0278	F	111	39.0	−42.2	7.3	−22.4
0269	M	111	38.0	−41.8	8.1	−20.9
0260	M	111	33.0	−41.1	7.3	−21.4
0293	F	115	32.0	−41.1	7.1	−21.3
0285	M	113	33.0	−41.0	8.6	−21.0
0303	M	112	37.0	−40.6	6.7	−21.6
0255	M	112	33.0	−40.5	7.8	−21.4
0281	M	116	36.0	−40.0	7.2	−21.6
0244	M	111	36.0	−39.7	6.5	−21.9
0079	M	105	33.5	−39.5	6.4	−22.9
0311	UK	114	37.0	−39.2	7.2	−22.1
0052	M	117	34.0	−39.2	7.5	−21.9
0177	F	113	38.0	−38.8	7.8	−21.6
0181	M	115	32.0	−38.8	7.5	−21.6
0251	F	111	39.0	−38.7	6.3	−22.1
0279	M	111	35.0	−38.2	6.5	−21.6
0292	F	111	29.0	−37.8	7.7	−22.3
0248	M	111	36.0	−37.4	6.7	−22.5
0297	F	119	33.0	−37.2	6.5	−21.8
0171	F	110	36.0	−37.1	6.3	−21.4
0302	F	109	35.0	−37.0	7.0	−21.8
0183	M	112	37.0	−35.6	6.5	−22.2
0179	M	113	36.0	−35.3	6.6	−21.5
0305	M	110	37.0	−34.6	6.5	−21.9
0243	F	115	38.0	−34.5	6.8	−21.0
0310	M	112	38.0	−33.9	7.4	−21.5
0275	F	112	35.0	−33.2	7.6	−20.9
0309	M	110	38.0	−33.2	9.0	−21.3

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TABLE 1. Continued.

ID	Sex	Wing	Tail	δ^2H	δ^{15}N	δ^{13}C
0135	F	116	38.0	−32.8	7.0	−21.1
0180	M	113	38.0	−31.1	7.1	−21.5
0236	F	112	37.0	−31.0	7.7	−21.3
0307	M	113	37.0	−30.9	7.5	−21.8
0270	M	114	36.0	−30.9	7.8	−20.1
0238	F	111	36.0	−30.9	7.2	−22.4
0268	F	115	39.0	−30.8	8.1	−22.2
0235	F	118	41.0	−30.6	7.0	−22.3
0234	F	112	38.0	−30.2	7.5	−21.7
0277	M	114	36.0	−30.1	7.5	−21.7
0272	M	114	32.0	−29.5	8.2	−22.0
0261	F	111	38.0	−28.6	6.7	−21.7
0296	F	112	32.0	−28.4	8.0	−20.4
0321	M	114	36.0	−27.9	7.6	−22.2
0313	M	115	33.0	−27.7	8.4	−21.6
0166	F	121	35.0	−27.6	7.0	−21.1
0263	F	117	39.0	−27.2	6.6	−21.5
0300	F	114	38.0	−27.2	7.7	−20.1
0264	M	114	34.0	−27.2	8.1	−21.2
0274	M	116	36.0	−27.0	6.6	−22.1
0262	M	112	37.0	−26.8	8.3	−20.6
0169	F	115	39.0	−26.2	6.2	−20.9
0066	F	115	35.0	−26.0	7.4	−21.7
0273	M	119	37.0	−25.8	6.7	−21.6
0240	M	115	37.0	−25.6	7.2	−21.7
0247	F	115	39.0	−24.4	8.2	−21.0
0312	M	110	37.0	−24.2	6.4	−21.7
0246	M	115	37.0	−24.0	8.0	−21.1
0184	F	114	37.0	−23.9	6.4	−22.0
0265	M	113	35.0	−23.0	6.7	−21.8
0163	M	113	36.0	−22.8	6.8	−22.0
0323	F	115	36.0	−20.9	7.4	−21.5
0067	M	114	38.0	−20.2	6.7	−21.5
0245	F	111	37.0	−20.1	7.3	−21.6
0239	M	115	36.0	−19.8	7.8	−22.1
0322	F	115	35.0	−16.1	6.1	−21.9
0253	F	111	38.0	−16.0	6.7	−22.3
0249	F	110	31.0	−10.8	7.6	−22.1

cluster solution with support from 5 (17%) indices. Results of the *k*-means clustering procedure were similar when outliers were removed, with 2 deemed the optimal number of clusters by the majority (9, or 30%) of indices. For the hierarchical agglomerative procedure, 2 was identified as the optimal number (8, or 27% of indices) and 3 received the second-most support (5, or 17% of indices). Overall, these results suggest that the isotope data grouped most naturally into 2 or 3 clusters, and thus we used the full dataset for the remainder of the analyses. Although the selection of the optimal number of clusters was not unanimous among indices, similar results are obtained from simulated datasets even when distinct, non-overlapping clusters are used (Milligan and Cooper 1985, Charrad et al. 2014). Furthermore, according to the BIC, the model-based clustering procedure suggested that the optimal number of clusters was 2 (Table 2).

We examined the classification of individual claws into 2 or 3 clusters using the results from *k*-means clustering or hierarchical agglomerative clustering, respectively. The clusters were significantly different from one another for all 3 isotope ratios simultaneously when partitioned into 2 (MANOVA, $F = 52.5$, df = 3 and 93, $P < 0.001$) or 3 clusters ($F = 36.4$, df = 3 and 93, $P < 0.001$). The 2-cluster solution resulted from a split between individuals with higher δ^{15}N and δ^{13}C ratios and those with lower δ^{15}N and δ^{13}C ratios, with little influence of δ^2H on clustering (Table 3). The 3-cluster solution suggested an additional division of the individuals with low δ^{15}N and δ^{13}C ratios into those with higher or lower δ^2H ratio (Figures 1 and 2). There was no association between sex and cluster membership when the claws were grouped in 2 ($\chi^2_1 = 0$, $P = 1$) or 3 ($\chi^2_2 = 1.70$, $P = 0.42$) clusters. There was no association between wing length and cluster membership for 2 ($t_{96} =$

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TABLE 2. Bayesian Information Criterion (BIC) from model-based hierarchical clustering procedure using the package "mclust" in R. BIC values are shown for 1–10 clusters for δ^2H, δ^{13}C, and δ^{15}N isotopes from Vaux's Swift claws.

Number of clusters	BIC
2	−823.6
3	−835.3
4	−845.3
1	−849.7
5	−859.2
6	−877.4
7	−880.8
8	−886.3
9	−901.2
10	−917.0

0.62, $P = 0.54$) or 3 (ANOVA, $F = 0.70$, df = 2 and 95, $P = 0.50$) clusters. Similarly, there was no association between tail length and cluster membership for 2 ($t_{96} = -0.48$, $P = 0.64$) or 3 (ANOVA, $F = 1.60$, df = 2 and 95, $P = 0.21$) clusters.

DISCUSSION

Patterns of migratory connectivity in long-distance migratory birds can have important implications for population dynamics, evolutionary processes, and effective conservation strategies (Webster and Marra 2005). Using multiple stable isotopes (δ^{13}C, δ^{15}N, and δ^2H) from claw samples of Vaux's Swifts at a spring migratory roost, our goal was not to assign individuals to a particular overwintering locality or localities, which would have been exceedingly difficult given the poor resolution in isoscapes of Mexico and Central America (Bowen et al. 2005) and our lack of known-origin tissues from these areas. Rather, we asked whether Vaux's Swifts at a single migratory roost likely came from a single winter location, which would indicate stronger migratory connectivity, or multiple winter locations, which would indicate weaker migratory connectivity. We found evidence in support of 2 or possibly 3 broad isotopic clusters on the overwintering grounds from the single migratory roost on Vancouver Island. While alternative explanations for our observations are possible (see below), we tentatively interpret our findings as likely demonstrating differences in overwintering locations used by Vaux's Swifts in our sample.

Understanding patterns of migratory connectivity in small, long-distance migratory birds has been exceedingly challenging, but the use of stable isotope analysis over the past 2 decades has revolutionized our ability to establish patterns of connectivity (Hobson 2005). Generally, this approach relies on the assignment of tissues to spatially explicit isoscapes generated from precipitation isoscapes (Bowen and West 2008) or known-origin individuals sampled across their range (e.g., Hobson et al. 2009b, 2012b). Recently, these methods have been enhanced through the use of Bayesian statistical methods and GIS-based models of precipitation isoscapes, as well as additional information such as band recoveries, to improve assignments by creating probabilistic regions of origin (Hobson et al. 2009a, 2009c, Van Wilgenburg and Hobson 2011). However, most studies have been focused on assigning breeding origins to winter-captured individuals, rather than vice versa, because breeding-ground isoscapes, particularly in North America, are better delineated than wintering-ground isoscapes (Bowen et al. 2005). This poses a problem for assigning winter origins to individuals sampled within breeding or migratory populations, as in our study. Furthermore, the particular tissue chosen for sampling must reflect the area of origin that is of interest to the researcher. This too poses difficulties for assigning winter origins because many North American bird species, including Vaux's Swifts, molt their feathers on or near the breeding grounds (Pyle 1997; but see, e.g., Kelly et al. 2008, Quinlan and Green 2011). Thus, we chose to sample claws because they reflect conditions several weeks prior to sampling, a time during which the birds should have been present on the wintering grounds (Bearhop et al. 2004, Reudink et al. 2009a, 2009b).

Despite the relatively high variation in all 3 isotopic signatures (δ^2H range: 66‰; δ^{15}N range: 5.8‰; δ^{13}C range: 3.5‰; Table 1), our analysis provides support for Vaux's Swift claws fitting into 2 or 3 isotopically distinct clusters (Figure 2), with strongest support for 2 clusters when outliers were removed. When partitioned into 2 clusters, the claws separated into those with higher δ^{13}C and δ^{15}N and those with lower δ^{13}C and δ^{15}N. Variation in δ^{13}C and δ^{15}N is most likely related to broad-scale habitat differences, given that food-web δ^{13}C signatures are strongly related to the distribution of C_3 and C_4 vegetation (Lajtha and Marshall 1994), and food-web δ^{15}N signatures

TABLE 3. Mean (± SD) stable isotope ratios of Vaux's Swift claws partitioned into 2 or 3 clusters based on *k*-means or hierarchical agglomerative clustering, respectively. Cluster numbers (1–3) corresponds to those shown in Figures 1 and 2.

	2 clusters			3 clusters		
Cluster no.	δ^2H	δ^{13}C	δ^{15}N	δ^2H	δ^{13}C	δ^{15}N
1	−36.5 (11.6)	−21.8 (0.4)	7.0 (0.5)	−45.6 (8.9)	−21.8 (0.4)	7.0 (0.6)
2	−42.0 (13.8)	−20.9 (0.6)	8.4 (0.9)	−38.7 (12.3)	−20.7 (0.6)	8.6 (0.9)
3	–	–	–	−26.3 (5.6)	−21.7 (0.4)	7.1 (0.5)

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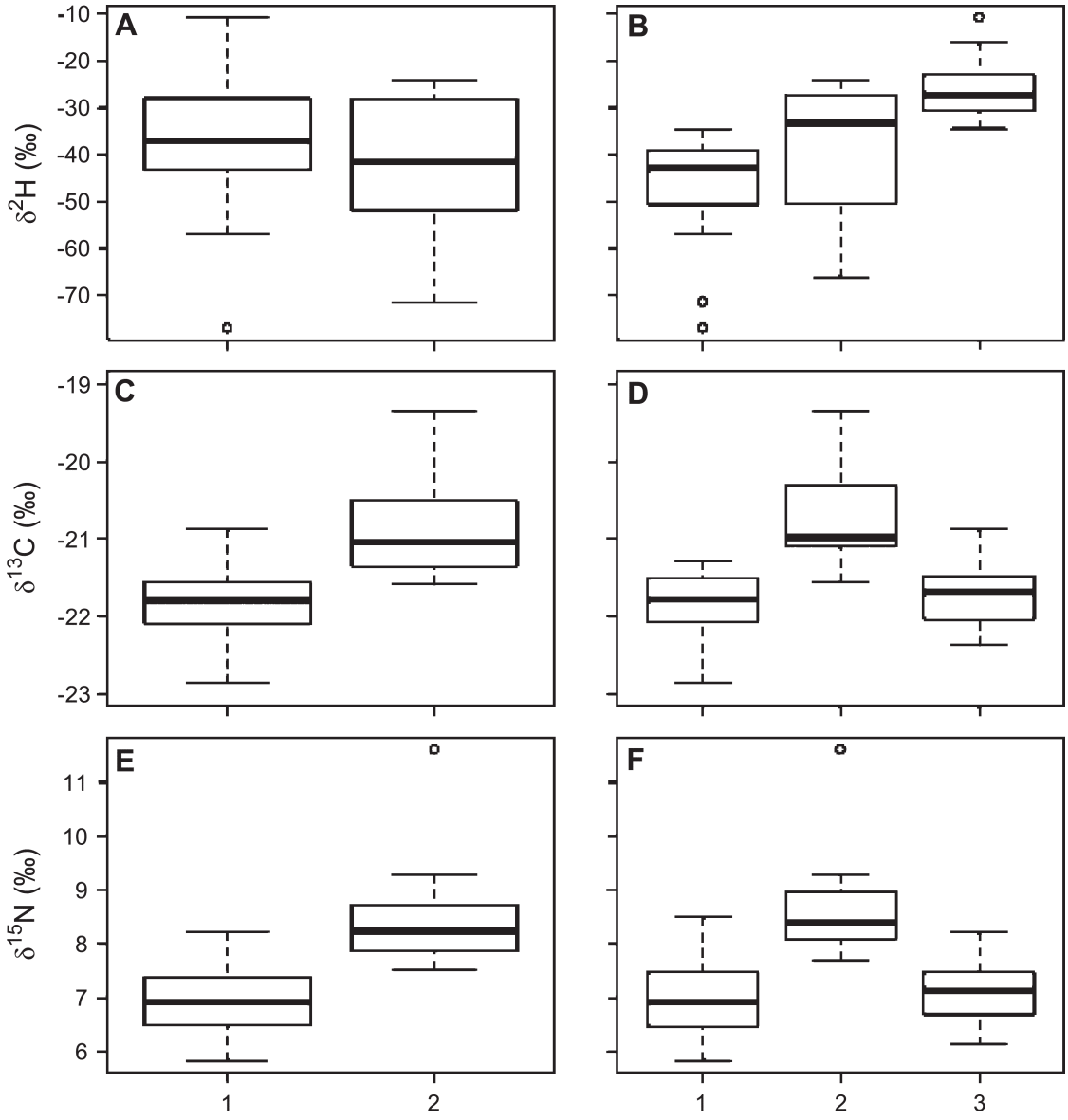


FIGURE 1. Variation in claw stable isotopes of hydrogen (δ^2H: **A**, **B**), carbon (δ^{13}C: **C**, **D**), and nitrogen (δ^{15}N: **E**, **F**) in Vaux's Swifts from a roost site on Vancouver Island, British Columbia, Canada. Claws were clustered into 2 (**A**, **C**, **E**) or 3 (**B**, **D**, **F**) clusters. The median, interquartile range (IQR), and outliers ($>1.5 \times$ IQR) are shown.

are associated with soil exposure and climate (Nadelhoffer and Fry 1994). Although we cannot exclude the possibility that birds were separated, in part, on the basis of dietary shifts and niche specialization, broad-scale differences in δ^{13}C, δ^{15}N, and δ^2H appear to be consistent with Vaux's Swift using habitats that follow climatic–moisture gradients. Regardless of the clustering algorithm, birds associated with cluster 2 were enriched in ^{13}C by ~0.9‰ over individuals from cluster 1. Simultaneously, birds associated with cluster 2 were also enriched in ^{15}N by ~1.6 ‰ compared with birds from cluster 1 (Table 3). Assuming that δ^{13}C follows gradients similar to those reported elsewhere (e.g., Marra et al. 1998), these data appear to suggest that birds in cluster 2 originated from hotter and drier habitats than birds in cluster 1.

The agglomerative clustering approach suggested that birds could be further partitioned into a third cluster on the basis of splitting claws that had both low δ^{13}C and δ^{15}N values, based on those with higher (cluster 3) and lower (cluster 1) δ^2H values (see Table 3). Latitudinal and altitudinal gradients in δ^2H are well established and among the strongest of isotopic gradients (Hobson 2005), and our results thus suggest that individuals that had low δ^{13}C and δ^{15}N were likely further segregated along a latitudinal or,

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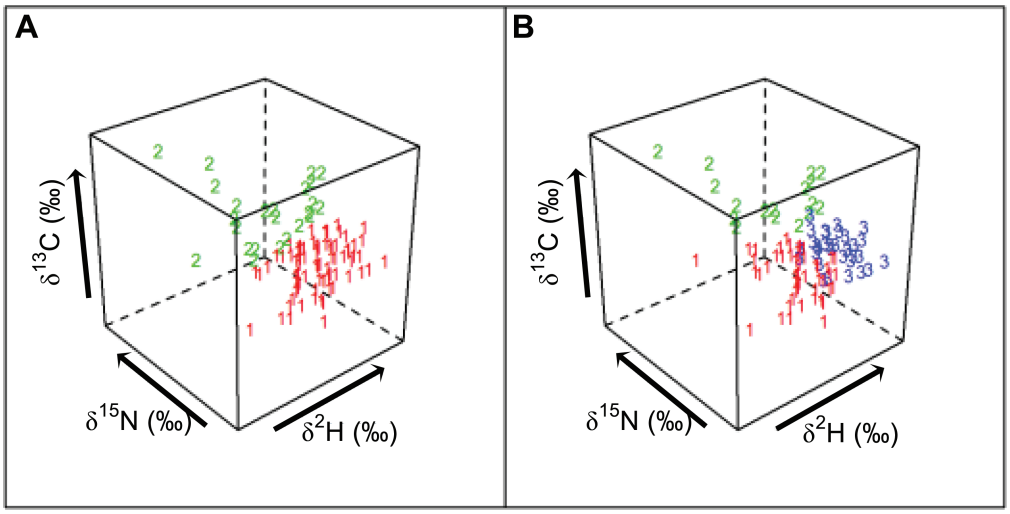


FIGURE 2. Clustering of stable isotope ratios of Vaux's Swift claws from a roost site on Vancouver Island, British Columbia, Canada, into (**A**) 2 clusters or (**B**) 3 clusters based on *k*-means or hierarchical agglomerative clustering, respectively.

possibly, an altitudinal gradient. Although a species-specific δ^2H claw-tissue isoscape is lacking for the Vaux's Swift overwintering range, a δ^2H feather isoscape developed for House Sparrows (*Passer domesticus*) in Mexico showed more positive δ^2H signatures in the northeast of the country and more negative signatures in the south and in high-altitude regions (Hobson et al. 2009b). Overall, our results indicate that individuals from the migratory population of Vaux's Swifts on Vancouver Island may have originated from a small number of different latitudes and/or habitats.

Breeding populations that are more strongly connected to specific wintering areas, particularly those experiencing degradation, may be most vulnerable to population declines (Dolman and Sutherland 1995, Webster and Marra 2005), although a recent study found that the strength of connectivity in breeding populations of Barn Swallows (*Hirundo rustica*) in North America was unrelated to their population trend (García-Pérez and Hobson 2014). Our data suggest that further research to estimate the strength of connectivity across breeding populations of Vaux's Swifts is now warranted and might help explain patterns of decline if extrinsic markers could be deployed along a gradient of declining versus increasing populations (*sensu* Fraser et al. 2012, Hobson et al. 2015).

We also asked whether individuals in our sample showed evidence of segregation based on sex or morphology during the overwintering period, as has been observed in several other passerines, such as Hooded Warblers (*Setophaga citrina*; Morton 1990), Prairie Warblers (*S. discolor*; Latta and Faaborg 2001), and American Redstarts (*S. ruticilla*), which segregate on the basis of habitat; and White-throated Sparrows (*Zonotrichia albicollis*; Mazerolle and Hobson 2007) and Hermit Thrushes (*Catharus guttatus*; Stouffer and Dwyer 2003), which segregate on the basis of latitude. For example, American Redstarts exhibit marked age- and sex-biased habitat segregation, with older males disproportionately inhabiting high-quality mangrove forests (Parrish and Sherry 1994, Marra 2000)—a characteristic also easily discerned via stable isotope analysis of muscle (Marra et al. 1998), blood (Norris et al. 2004), and claw samples (Reudink et al. 2009a, 2009b). Furthermore, larger females were more likely to inhabit high-quality mangrove territories because of dominance-mediated habitat segregation (Marra 2000). Latitudinal segregation, on the other hand, may be related to trade-offs between body size or wing size/shape and migration distance (García Peiró 2003, Mazerolle and Hobson 2007). Our results suggest no evidence for sex- or morphology-based segregation, at least when considering wing and tail length, and indeed there was no evidence of differences in wing size between males and females, which suggests that male and female Vaux's Swifts likely share a similar overwintering ecology and, thus, may be equally vulnerable to stochastic events or habitat loss.

The utility of triple-isotope isoscapes for assigning origins to South American and African wintering birds has recently been demonstrated (Hobson et al. 2012b, García-Pérez and Hobson 2014), and our results indicate that the approach has potential for identifying Mexican and Central American wintering clusters as well. Taken together, our results highlight the need for additional research on the overwintering ecology and behavior of this poorly studied long-distance migrant and the need for calibrating tissue-specific isoscapes to better assign Nearctic–Neotropical migratory birds to wintering localities. Our data suggest that birds migrating through Vancouver Island likely overwinter in 2 or 3 isotopically similar

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regions or habitat types, and these predictions should now be validated. Wintering-ground sampling would facilitate nominal assignment (*sensu* Wunder 2012) to 2 or 3 spatially delineated geographic regions or, alternatively, might facilitate spatially explicit, multivariate assignment approaches (e.g., García-Pérez and Hobson 2014, Veen et al. 2014).

Recent work has highlighted the potential for keratinous tissues to vary isotopically with diet (Fraser et al. 2011, Soto et al. 2013, Voigt et al. 2013, 2015) and microhabitat (Fraser et al. 2011). Thus, although we interpret our results primarily in the context of migratory connectivity, we cannot preclude the possibility that multivariate differences in the isotopic composition of claws could stem from variation in microhabitat, behavior, or dietary preferences among individuals. Given the high motility of Vaux's Swifts while foraging on the wing (Bull and Collins 2007), it is plausible that our results could also stem from variation in the degree of foraging over aquatic versus terrestrial habitats, or over forested versus grassland or agricultural habitats. Like other aerial insectivores, Vaux's Swifts forage broadly over forest canopy, meadows, and open water (Bull and Collins 2007), and their diets likely reflect the composition of aerial plankton from major insect emergences from both the aquatic and terrestrial environments. Within their wintering grounds, these major habitat types should be relatively isotopically distinct, owing to major isotopic differences in $\delta^{13}C$ and $\delta^{15}N$ between forest canopy, which primarily uses a C_3 phytosynthetic pathway, and grasslands–pastures, which are dominated by C_4 plants (Still and Powell 2010). It is important to note that the distribution of forest versus grassland, pasture, and agricultural lands displays a great deal of geographic structure (Ellis and Ramankutty 2008, Dixon et al. 2014) and, thus, it is probable that isotopic differences due to differences in habitat selection would also covary with any spatial segregation. Regardless of whether the patterns we observed are attributable solely to differences in migratory connectivity or to variation in local habitat selection, our results point to relatively limited variation in overwintering niches of Vaux's Swifts. Thus, a better understanding of the overwintering ecology of Vaux's Swifts is necessary to inform conservation. Wintering-ground work on habitat use and diets of Vaux's Swifts or multi-isotope assays on claws from birds fitted with miniaturized GPS tags (Hallworth and Marra 2015) would shed light on the mechanistic explanations for our observations.

Like most migratory aerial insectivores (Nebel et al. 2010), Vaux's Swifts are in decline. Given the unique roosting ecology of Vaux's Swifts, they are particularly susceptible to stochastic events as exemplified by this 1 mass mortality, which may represent a loss of about 1.5–2.7% of the British Columbia population of Vaux's Swifts in a single evening. This exceptional vulnerability, coupled with increasing habitat loss and alteration in the tropics (Hansen et al. 2013), indicates a crucial need for further research to determine patterns of migratory connectivity and identify critical winter and migratory roost sites for future conservation planning.

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