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RESEARCH ARTICLE

An isotope ($\delta^{34}S$) filter and geolocator results constrain a dual feather isoscape (δ^2H, $\delta^{13}C$) to identify the wintering grounds of North American Barn Swallows

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ABSTRACT

The discovery of spatial patterns in naturally occurring isotopes (e.g., δ^2H, $\delta^{13}C$) at continental scales has been tremendously important in providing a method to infer potential breeding and wintering origins of migratory animals through assignment to tissue-specific isoscapes. Single-isotope (i.e. δ^2H) assignments of birds to molting origins in South America have been limited by the lack of strong spatial gradients in precipitation δ^2H there. We integrated an mvnpdf (multivariate normal probability density function) approach using δ^2H and $\delta^{13}C$ values in tail feathers to determine wintering origins of adult Barn Swallows (*Hirundo rustica*) breeding in eastern Canada ($n = 208$). Spatial assignments were conducted using precipitation (δ^2H) and theoretical plant-based ($\delta^{13}C$) isoscapes for South America calibrated for feathers of Nearctic–Neotropical migrant songbirds. We also measured feather $\delta^{34}S$ values of Barn Swallows equipped with geolocators ($n = 9$) and of a larger group of Barn Swallows ($n = 121$) of unknown molt origin to assess the possibility of using this isotope to identify birds molting in coastal habitats and for which the terrestrial δ^2H isoscapes would potentially be invalid. We constrained the mvnpdf assignment to areas generally south of the Amazon basin, based on data retrieved from Barn Swallows fitted with archival light-level geolocators from Ontario ($n = 3$) and New Brunswick ($n = 11$), Canada, which showed consistent overwintering fidelity to south-central South America. The majority of birds from our breeding populations were assigned to south-central Brazil. Results from the $\delta^{34}S$ analysis indicate that a threshold of 11‰ may be appropriate to constrain the use of terrestrial δ^2H isoscapes in South America. Our results refine the toolbox available to examine migratory connectivity in species that molt on their South American wintering grounds and underline the value of using multiple proxies for assignments of animals to spatial origin.

Keywords: carbon-13, deuterium, geolocators, isoscape, isotopic assignment, migratory connectivity, multivariate normal probability density function, sulfur-34

Una combinación de isopaisaje dual (δ^2H, $\delta^{13}C$) de las plumas, filtro de isótopos ($\delta^{34}S$) costeros y localizador geográfico permite identificar las áreas de invernada de *Hirundo rustica*

RESUMEN

El descubrimiento de patrones espaciales en isótopos de presencia natural (e.g., δ^2H, $\delta^{13}C$) a la escala continental ha sido enormemente importante para contar con un método que permita inferir los orígenes potenciales de cría e invernada de los animales migratorios mediante la asignación específica de isótopos en los tejidos. La determinación del origen de la muda de las aves en América del Sur en base a la asignación de un único isótopo (i.e. δ^2H) ha sido limitada debido a la falta de fuertes gradientes espaciales de precipitación δ^2H. Nosotros integramos una función de densidad de probabilidad normal multivariada (fdpnmv) usando los valores de δ^2H y $\delta^{13}C$ en las plumas de la cola para determinar los orígenes de invernada de individuos adultos de *Hirundo rustica* criando en el este de Canadá ($n = 208$). La determinación espacial se realizó usando isopaisajes basados en la precipitación (δ^2H) e isopaisajes teóricos basados en las plantas ($\delta^{13}C$) para América del Sur, calibrados para plumas de aves canoras migratorias Neárticas-Neotropicales. También medimos los valores de $\delta^{34}S$ de plumas de golondrinas equipadas con localizadores geográficos ($n = 9$) y de un grupo más grande de golondrinas ($n = 121$) cuyo lugar de la muda era desconocido para evaluar la probabilidad de usar este isótopo para identificar a las aves que mudan en hábitats costeros y para las cuales el isopaisaje terrestre de δ^2H podría ser potencialmente inválido. Restringimos la determinación de la fdpnmv a áreas generalmente al sur de la cuenca amazónica, usando como base datos tomados de golondrinas equipadas con localizadores geográficos de archivo de nivel de luz de Ontario ($n = 3$) y New Brunswick ($n = 11$), los cuales mostraron de modo consistente una fidelidad a lo largo del invierno con el sur-centro de América del Sur. La mayoría de las aves de nuestras poblaciones reproductivas fueron asignadas al sur-centro de Brasil. Los resultados de los análisis de $\delta^{34}S$ indicaron que un umbral de 11‰ puede ser apropiado para restringir el uso de los isopaisajes δ^2H terrestres en

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América del Sur. Nuestros resultados refinan las herramientas disponibles para examinar la conectividad migratoria de las especias que mudan en sus áreas de invernada en América del Sur y subraya el valor de usar múltiples indicadores para asignar el origen espacial de los animales.

Palabras clave: azufre-34, asignación isotópica, conectividad migratoria, carbono-13, deuterio, función de densidad de probabilidad normal multivariada, isopaisaje, localizador geográfico

INTRODUCTION

It is now widely recognized that the conservation of migratory birds requires knowledge of population-level connectivity between breeding, wintering, and stopover locations (Webster and Marra 2005, Faaborg et al. 2010, Hostetler et al. 2015). By establishing spatial connections among sites used by populations throughout their annual cycle, conservation efforts can be made more strategic (Martin et al. 2007, Taylor and Norris 2009). Establishing migratory connectivity can also assist in deciphering causes of population trends and fluctuations, since it allows researchers to query a host of factors that may be operating in different regions. Species showing overall population declines at national or continental scales often reveal heterogeneous trends at finer scales, with populations in some regions being stable or increasing (Nebel et al. 2010, Michel et al. 2015, Smith et al. 2015). Such patterns may be driven by factors operating on the breeding grounds but may also be operating hundreds or thousands of kilometers distant and to varying degrees, depending on where a particular breeding population winters and the strength of migratory connectivity (Sillett and Holmes 2002, Hostetler et al. 2015). For example, climatic cycles such as the El Niño–Southern Oscillation have been shown to differentially affect survival of Nearctic–Neotropical migrants that winter in the Caribbean basin compared with those in other areas, primarily because of changes in precipitation that, in turn, influence winter habitat quality (Nott et al. 2002, Paxton et al. 2014).

Like many aerial insectivores, Barn Swallows (*Hirundo rustica*) in North America have shown considerable population declines, especially in the northern portion of their range (Nebel et al. 2010, Smith et al. 2015). However, in other regions, notably the southern United States, the species is stable or increasing. Michel et al. (2015) recently examined breeding-population trends in this and other aerial insectivore species in North America, and Barn Swallows exhibited some of the most spatially heterogeneous population trends. Barn Swallows winter over an extensive range throughout most of Central America, the Caribbean, and South America, so there is considerable potential for coarse-scale wintering-ground factors such as climate or habitat change to operate differentially among breeding areas and thus drive differential population responses. Unfortunately, as with most migratory passerines, migratory connectivity is poorly understood for this species, but recent investigations using stable isotopes and light-sensitive geolocators have provided valuable new insights into wintering areas, migration routes, and phenology (García-Pérez and Hobson 2014, Liechti et al. 2014, Hobson et al. 2015).

Increasingly, researchers are recognizing that continental-scale patterns in naturally occurring stable isotopes in food webs can be used to delineate origins and movements of migratory organisms (Hobson and Wassenaar 2008, West et al. 2010, Hobson et al. 2014b). In particular, deuterium (^{2}H) concentrations in precipitation vary according to well-described kinetic processes and continental patterns of hydrogen isotopes (δ^2H) in precipitation and surface waters, which are transferred to metabolically inert animal tissues (e.g., feathers or hair). These tissue isotope values become signatures of origin that can be delineated using probabilistic models (Wunder 2010, Hobson et al. 2014b). Stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotopes can also show spatial patterns in food webs based on a variety of plant physiological mechanisms that are, in turn, linked to climate, photosynthetic pathway, nitrogen fixation mechanisms, and even land-use practices (Still et al. 2003, West et al. 2006, Craine et al. 2009). Hobson et al. (2012b) combined precipitation (δ^2H) and plant-based (δ^{13}C, δ^{15}N) isoscapes to identify multiple isotope clusters in Africa to which birds could be assigned on the basis of their African-grown feather isotope values. García-Pérez and Hobson (2014) used a similar cluster-analysis approach to identify potential South American wintering areas of Barn Swallows migrating from North America. That study generally confirmed weak migratory connectivity in this species but also described several potential isotopic regions that could inform further investigation and hypothesis testing. The cluster approach to assigning migratory wildlife to potential regions of origin has since been advanced to a more spatially explicit method that assigns migratory animals to a single probability surface. The latter method has been used to assign monarch butterflies (*Danaus plexippus*) to breeding origins in North America (Flockhart et al. 2013), and Wood Warblers (*Phylloscopus sibilatrix*) breeding in Europe to their winter grounds in Africa (Hobson et al. 2014a). That approach requires the assumption that each isotope is independent over the spatial scales of interest.

Regardless of the multiple-isotope approach used, the forensic assignment of individuals or populations of migratory birds to origins where tissues were grown can be advanced by combining information based on other, nonisotopic, data. For example, the Bayesian assignment approach allows the use of priors that describe the spatial distribution of expected breeding density or expected movement trajectories based on band returns (Royle and Rubenstein 2004, Van Wilgenburg and Hobson 2011). However, actual ground-truthing of predictions made by isotopic models is extremely difficult because of the general paucity of data on individual movements (i.e. the basic impetus for the use of isotopes in the first place). The recent development of light-sensitive geolocators for use on small ($\sim$10 g) birds has provided an important tool that can complement the isotope approach. Geolocators provide reasonable estimates of movements but require marked individuals to be recaptured and are generally too expensive to apply at large scales (e.g., hundreds of individuals). Nonetheless, sampling of tissues from individuals of known location, or the possibility of excluding areas predicted by the isotope approach on the basis of cumulative evidence (e.g., geolocator, band return, genetic marker), makes the combination of isotopes with other tools particularly powerful.

Values of several stable isotopes (e.g., δ^{13}C, δ^{34}S) provide a useful means of distinguishing between environments in which these elements were derived (Hobson 1999, Hebert et al. 2008, Cross et al. 2014). For example, stable sulfur and carbon isotopes are more enriched in marine than in terrestrial habitats, and sulfur is especially useful because discrimination between diet source and tissue is negligible (Arneson and MacAvoy 2005, Haché et al. 2014). Transportation of oceanic ^{34}S into continental regions via aerosols can also increase food-web δ^{34}S values up to 100 km inland in some areas (Zazzo et al. 2011), and feathers of birds foraging and molting in these environments can exhibit correspondingly higher δ^{34}S values. Previous studies have used a threshold of $\delta^{34}\text{S} \geq 10‰$ to delineate marine provenance (Lott et al. 2003, Hebert et al. 2008), but δ^{34}S has not been used widely for determining coastal origins of landbirds (but see Haché et al. 2014). The complexity of continental patterns of δ^{2}H in precipitation and of δ^{13}C in food webs in coastal regions can confound isotopic assignment of birds to origin. Identifying and removing individual birds likely wintering in coastal habitats, using δ^{34}S thresholds, can potentially improve spatial assignments using δ^{2}H and δ^{13}C values (Lott et al. 2003, Ofukany et al. 2012), in addition to providing insights into the importance of coastal habitats as foraging areas.

The overall goal of the present study was to provide a general template for combining multiple tools (i.e. isotopes and geolocators) to describe migratory connectivity for Nearctic–Neotropical migrant landbirds wintering in South America. First, we tested for differences in isotope composition (δ^{2}H, δ^{13}C) of Barn Swallow feathers between sexes and sampling locations in 3 eastern Canadian provinces to determine whether these samples could be combined for further analyses. We then used a dual-isotope assignment-to-origin model constrained to the potential wintering areas of Barn Swallows, based on recent geolocator results (Hobson et al. 2015), to create the most parsimonious model for migratory connectivity in this species. Finally, we used birds fitted with geolocators for which we had feather δ^{34}S measurements to test whether this isotope could be used to differentiate between Barn Swallows wintering in coastal versus inland areas; and we also examined a larger, continent-wide feather δ^{34}S dataset for Barn Swallows breeding in North America.

METHODS

Study Areas and Field Methods

Barn Swallows were captured using mist nets at nesting sites (e.g., barns and bridges) in Canada and the United States during the breeding season (May–July) in 2009–2014. The sex of individual birds was determined by evidence of a cloacal protuberance (male) or brood patch (female), and each bird was fitted with a uniquely numbered U.S. Geological Survey metal leg band. One inner tail feather, representing assumed wintering (i.e. molting) location (Pyle 1997), was collected from each bird for stable isotope analysis. Feathers collected for the mvnpdf (multivariate normal probability density function) assignment to isoscape ($\delta^{2}H_{f}$ and $\delta^{13}C_{f}$) were sampled in Ontario ($n = 154$), Quebec ($n = 10$), and New Brunswick ($n = 44$), Canada (hereafter referred to collectively as "eastern Canada"; Table 1). We measured δ^{34}S values in feathers ($\delta^{34}S_{f}$) from Barn Swallows equipped with geolocators ($n = 9$; see below) from New Brunswick to assess the possibility of using this isotope to differentiate between coastal- and inland-molting birds and to potentially filter out birds wintering (i.e. molting) in coastal habitats (e.g., marshes). Individuals of unknown winter molt origin sampled at breeding areas across North America were also used in an analysis of $\delta^{34}S_{f}$ in New Brunswick ($n = 51$) and Saskatchewan ($n = 20$), Canada, and in Washington ($n = 16$) and Alabama ($n = 34$), USA, to determine marine or coastal dietary inputs for these populations on their wintering grounds. Isotope values ($\delta^{34}S_{f}$) for birds fitted with geolocators were analyzed from feathers sampled after birds were recaptured to match geolocation data (see below). We used feathers from García-Pérez and Hobson (2014) and supplemented them with feathers collected in 2012–2014. García-Pérez and Hobson (2014) examined wintering origins of breeding populations of Barn Swallows across North America during 2009–2012 by assigning birds to isotopically distinct spatial clusters in South America.

TABLE 1. Locations, years, and sample sizes (*n*) of tail feathers collected from North American Barn Swallows for stable isotope analysis at breeding locations in Canada and the United States.

Location	Latitude (N) [a]	Longitude (W) [a]	*n* (δ^2H, $\delta^{13}C$)	*n* (δ^2H, $\delta^{34}S$)	Years
New Brunswick	45.93	65.26	44	51	2012–2014
Ontario	43.66	80.23	154	–	2009–2010
Quebec	47.87	70.09	10	–	2009
Saskatchewan	53.71	106.05	–	20	2012–2014
Washington	47.67	122.35	–	16	2012–2013
Alabama	32.57	85.36	–	34	2012

[a] Approximate coordinates.

As part of another study examining migratory connectivity, we attached light-level archival geolocators to adult Barn Swallows from Ontario ($n = 13$) and New Brunswick ($n = 16$) in 2011–2013 (Hobson et al. 2015). Thirteen geolocators were recovered after 1 migration cycle (i.e. breeding grounds to wintering grounds and return; Ontario, $n = 3$; New Brunswick, $n = 10$). Data from an additional geolocator recovered in 2015 (attached in 2013) in New Brunswick are also presented. We used a Kalman filter state-space model to estimate movement parameters and "most probable tracks" (Kalman 1960, Sibert et al. 2003) from raw geolocations in the R package "kftrack" (Sibert and Nielsen 2002). The mean estimated wintering (i.e. molting) area was calculated from geolocation data where no large (≥150 km) movements were detected for >2 consecutive days and where a bird remained for the longest period during the nonbreeding season (Hobson et al. 2015). Directional standard deviational ellipses (± SD) were constructed from geolocations during the estimated wintering period. For a detailed overview of the geolocator component of the present study, see Hobson et al. (2015). Information from the recovered geolocators was used to constrain potential spatial origins for our eastern Canadian Barn Swallow study population to southern South America (approximately south of the Amazon River).

Stable Isotope Analyses of Feathers

Feathers were stored in paper envelopes and kept dry prior to isotope analysis. All feathers were cleaned of surface oils in a 2:1 chloroform:methanol solvent soak overnight and subsequently rinsed before being dried for 72 hr in a fume hood. Samples were stored in equilibration with ambient (laboratory) water vapor for several months prior to further preparation. Samples were assayed for δ^2H, $\delta^{13}C$, and $\delta^{34}S$ analyses at the Stable Isotope Laboratory of Environment Canada, Saskatoon, Saskatchewan. We determined the nonexchangeable δ^2H value of feathers by the comparative equilibration method described by Wassenaar and Hobson (2003), using 3 calibrated keratin hydrogen-isotope reference materials (CBS: −197‰; KHS: −54.1‰; SPK: −121.6‰). Hydrogen isotopic measurements were performed on H_2 gas derived from high-temperature (1,350°C) flash pyrolysis of 350 ± 20 μg feather and keratin standard subsamples loaded into silver capsules using continuous-flow isotope-ratio mass spectrometry (IRMS; Isoprime, Manchester, UK). Measurement of the keratin laboratory reference materials corrected for linear instrumental drift were both accurate and precise, with typical within-run SD values <2‰ ($n = 5$). We report all results for nonexchangeable H using the typical delta (δ) notation, in units of per mil (‰) normalized on the Vienna Standard Mean Ocean Water–Standard Light Antarctic Precipitation (VSMOW–SLAP) standard scale.

We used 0.5–1.0 mg of feather material for $\delta^{13}C$ analyses, which were combusted online using a EuroVector 3000 (EuroVector, Milan, Italy; http://www.eurovector.it) elemental analyzer. The resulting CO_2 was separated by gas chromatography and introduced into a Nu Horizon (Nu Instruments, Wrexham, UK; http://www.nu-ins.com) triple-collector isotope-ratio mass spectrometer via an open split and compared with a CO_2 reference gas. Stable carbon ($^{13}C/^{12}C$) isotope ratios were expressed in delta notation, as deviation in parts per thousand (‰) from the primary standard Vienna Pee Dee Belemnite. Using previously calibrated internal laboratory C standards (powdered Bowhead Whale Baleen keratin [BWB-3, $\delta^{13}C = -20.0‰$] and gelatin [PRGEL $\delta^{13}C = -13.6‰$]), within-run precision for $\delta^{13}C_f$ assays was ±0.15‰ ($n = 5$). For $\delta^{34}S_f$ analyses, 3,500 ± 100 μg of feather material was combusted in a Vario Pyro Cube elemental analyzer, and the resulting SO_2 gas was introduced into Isoprime IRMS. Our laboratory standard was BWB-3 keratin ($\delta^{34}S$ = 13.2‰), and δ values were reported in relation to the Canyon Diablo Triolite standard. Measurement precision, based on within-run replicate measurements of the lab standard, was ±0.3‰.

Statistical Analysis and Assignment to Origin

We tested for differences in δ^2H_f and $\delta^{13}C_f$ values of eastern Canadian Barn Swallows by applying a multivariate analysis of variance (MANOVA) based on Pillai's trace statistic. An initial MANOVA that tested for location-specific differences in feather isotope values indicated that the 3 Canadian sampling locations could be pooled into 1 group representing a single eastern population. Sex, year, and their interaction terms were then included as explanatory variables in further analyses using MANOVA. We also contrasted $\delta^{2}H_{f}$ and $\delta^{34}S_{f}$ composition and $\delta^{34}S_{f}$ separately using MANOVA and analysis of variance (ANOVA), respectively, to test for differences in these values among populations, potentially indicating differences in marine dietary inputs. We had sex and age information for a limited number of individuals; therefore, we only tested for differences between populations for the continent-wide $\delta^{34}S_{f}$ dataset. We used ANOVA to test for differences in $\delta^{34}S_{f}$ values for geolocator birds with mean wintering positions <100 km from a coast and those farther inland. Our dataset contained birds captured in multiple years and had missing information (i.e. sex) for some individuals. Only data from first captures were included in the analyses (except for comparison with geolocation data; $n = 208$). Results of statistical tests were considered significant at $P < 0.05$ and are reported as means ± SD.

We adapted an mvnpdf method for assigning birds to winter origins that was originally applied in Africa, where a 3-isotope approach was used (Hobson et al. 2014b). However, we avoided using $\delta^{15}N_{f}$ values because of potential anthropogenic inputs from agriculture that are challenging to model spatially, and used $\delta^{2}H_{f}$ and $\delta^{13}C_{f}$ data only for South America. The mvnpdf method calculates the probability that a particular spatially referenced cell could represent a possible origin in calibrated raster feather isoscape space ($\delta^{2}H_{f}$, $\delta^{13}C_{f}$) as modified from Hobson et al. (2014b):

$$fx(x^{i}y^{i}|\ \mu_{HC}, \sigma_{HC}, \rho_{HC}) \\ = 2\pi^{-1/2k}|\Sigma|^{-1/2k}e^{[-1/2(y-\mu_{x}i)/\Sigma-1(y-\mu_{x}i)]}$$

where the spatially explicit probability density function for a potential location of origin (x^{i}), given a feather of unknown origin (y^{i}) having known $\delta^{2}H_{f}$, $\delta^{13}C_{f}$ isotopic composition, is denoted by *fx*. Subscripted HC represents the predicted mean (μ), standard deviation (σ), and correlation (ρ) of the $\delta^{2}H$ (H) and $\delta^{13}C$ (C) values for a feather grown at a particular location (i.e. raster cell), and *k* indicates the number of isotopes. Mean isotopic composition for an individual location (x^{i}) was derived from raster cells in the calibrated isoscapes, and $\mu_{x}{}^{i}$ represents a vector of means for individual locations. The variance–covariance matrix (| Σ |) of the isoscapes using the 2-isotope scenario is represented as

$$\Sigma = \begin{bmatrix} \sigma^{2}_{\delta^{2}H} & \sigma^{2}_{\delta^{2}H,\delta^{13}C} \\ \sigma^{2}_{\delta^{2}H,\delta^{13}C} & \sigma^{2}_{\delta^{13}C} \end{bmatrix}$$

We applied a conservative odds ratio to assign feathers to potential molt origin using the spatially explicit probability densities for individual samples where georeferenced locations (i.e. raster cells) of ≥66.7% probability were coded as possible origins (1) and values below this threshold were not considered possible origins (0) (Hobson et al. 2009, 2014b). Individual assignments conducted for each feather sample therefore resulted in a spatially referenced binary raster file, which was then summed across assignments for all other individuals to represent potential origins for the eastern Canadian Barn Swallow population. The mvnpdf assignment to isoscape analysis was conducted using the "mvnlme" (Gross and Bates 2012) and "raster" (Hijmans 2015) packages in R version 3.1.1 (R Development Core Team 2014).

We used a regionalized cluster-based water isotope prediction (RCWIP) raster surface derived from the Global Network of Isotopes in Precipitation (GNIP) to represent global amount-weighted growing-season precipitation $\delta^{2}H_{p}$ (Terzer et al. 2013, IAEA/WMO 2015, International Atomic Energy Agency 2015). This surface provides improved predictive accuracy and precision, particularly in areas where there are few or no sampling stations compared with other available $\delta^{2}H_{p}$ isoscapes (Terzer et al. 2013). To account for discrimination between $\delta^{2}H_{p}$ and $\delta^{2}H_{f}$, we converted the $\delta^{2}H_{p}$ surface to an equivalent feather isoscape using the equation for non-ground-foraging Nearctic–Neotropical migrants from Hobson et al. (2012a): $\delta^{2}H_{f} = -17.57 + 0.95\ \delta^{2}H_{p}$ (Figure 1A).

We used a $\delta^{13}C$ isoscape developed by Powell et al. (2012) that reflects a theoretical spatial distribution of $\delta^{13}C$ values in plants in South America. This isoscape is based on annual plant $\delta^{13}C$ composition approximately corresponding to mean annual conditions in the year 2000 and incorporates intra-annual and interannual variability in vegetation distribution and productivity (Powell et al. 2012). Plant-based isoscapes are expected to exhibit minimal annual changes in $\delta^{13}C$, so this isoscape provides the most current and accurate approximation of plant $\delta^{13}C$ composition available for South America (Powell et al. 2012). We subsequently applied +2‰ to the plant $\delta^{13}C$ isoscape to account for descrimination between plants and herbivorous insects in feather isotopes, thus obtaining a $\delta^{13}C_{f}$ isoscape (Figure 1B; see Hobson et al. 2012b). The spatial assignment was constrained to areas <3,000 m above sea level (Brown and Bomberger Brown 1999) in the known South American wintering range of Barn Swallows that breed in eastern Canada (BirdLife International and NatureServe 2011, Hobson et al. 2015). Additionally, we removed the northwestern region of South America from potential molt origins on the basis of geolocator results from Hobson et al. (2015), in which study all birds from eastern breeding populations wintered south of the Amazon basin (see Figure 3).

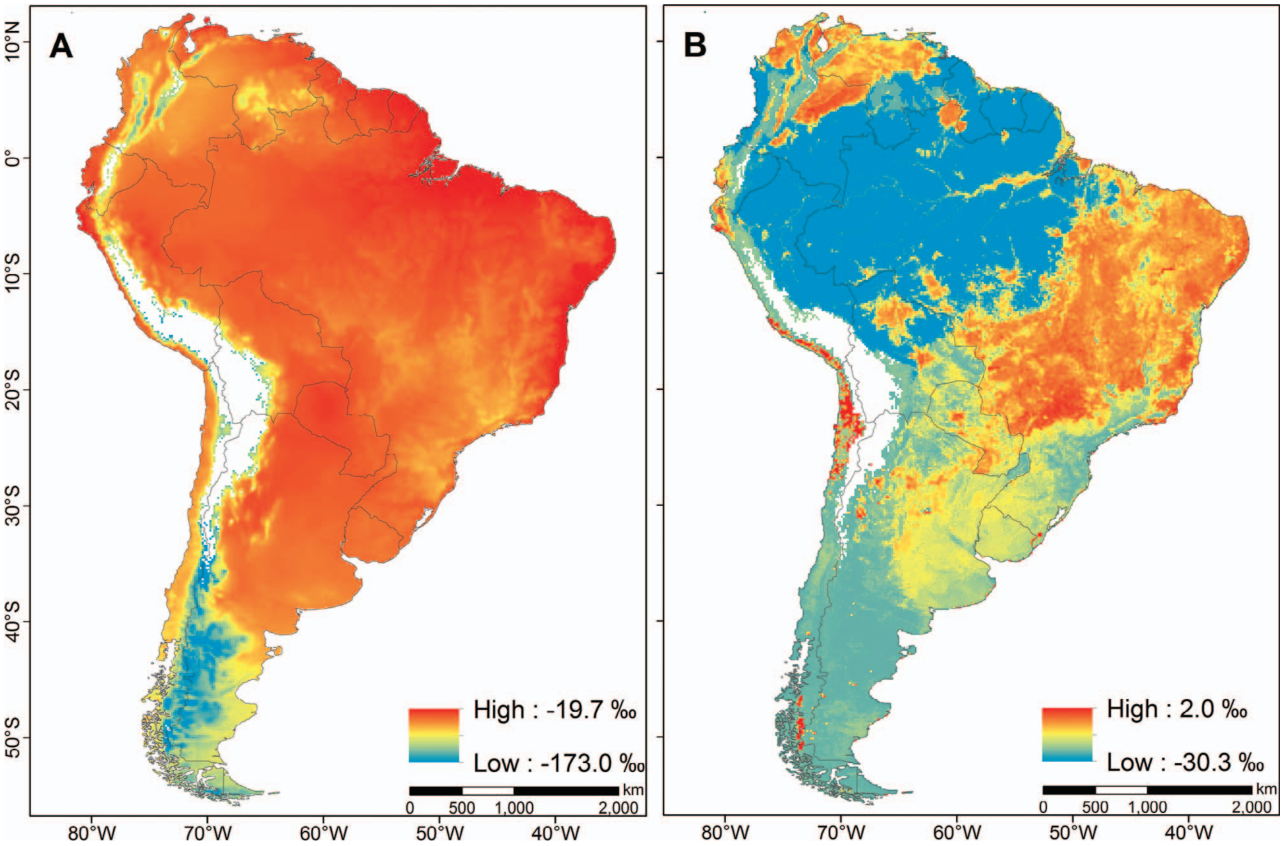

FIGURE 1. Calibrated (**A**) hydrogen (δ^2H_f) and (**B**) carbon ($\delta^{13}C_f$) feather isoscapes based on the theoretical isotopic distribution of mean-weighted growing-season precipitation (Terzer et al. 2013) and mean annual plant $\delta^{13}C$ (Powell et al. 2012), respectively, for the Barn Swallow's winter range in South America.

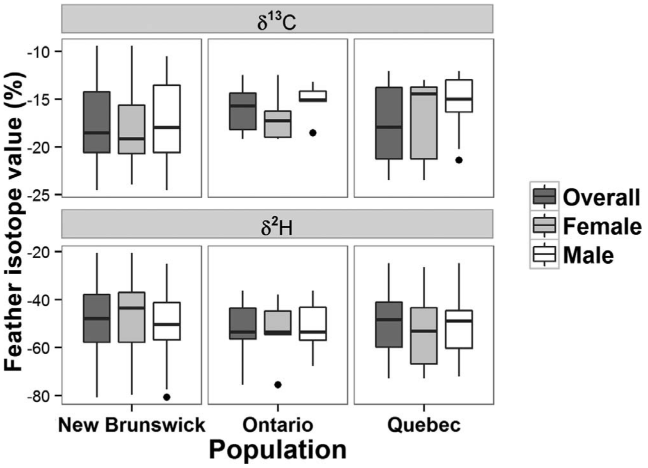

FIGURE 2. Box plots representing variation in feather $\delta^{13}C$ and δ^2H (‰) isotope values from both sexes (overall, $n = 208$) and from female ($n = 99$) and male ($n = 83$) adult Barn Swallows sampled at 3 locations in eastern Canada, 2009–2014. Midlines within the boxes denote the median isotope value, whiskers extend 1.5× beyond the interquartile range, and dots indicate outliers.

RESULTS

The MANOVA of Barn Swallow feather isotopic (δ^2H_f, $\delta^{13}C_f$) composition indicated nonsignificant differences among sampling locations in eastern Canada (approximate $F = 1.5$, df = 2 and 205, $P = 0.2$; Figure 2); therefore, data were combined for all further analyses. Isotope (δ^2H_f, $\delta^{13}C_f$) differences among years were also nonsignificant (approximate $F = 1.7$, df = 2 and 203, $P = 0.10$); however, interannual differences in δ^2H_f were significant ($F = 2.5$, df = 4 and 203, $P < 0.05$; Table 2). The sexes did not differ significantly ($F = 1.3$, df = 2 and 204, $P = 0.08$) in $\delta^{13}C_f$ values (females: $\bar{x} = -17.9 \pm 3.7$‰, $n = 99$; males: $\bar{x} = -16.6 \pm 3.7$‰, $n = 83$) or δ^2H_f values (females: $\bar{x} = -48.8 \pm 14.3$‰, $n = 99$; males: $\bar{x} = -50.5 \pm 12.2$‰, $n = 83$), and the interaction between sex and year was not significant ($F = 0.8$, df = 4 and 196, $P = 0.64$). Therefore, we grouped all birds in our mvndpf analysis to provide an overall depiction of wintering origins for our eastern Canadian breeding locations.

Overwintering areas of our sample of Barn Swallows, as determined by geolocation, ranged across much of south-central South America, with 12 of 14 individuals settling south of 10°S and 11 of 14 individuals wintering south of

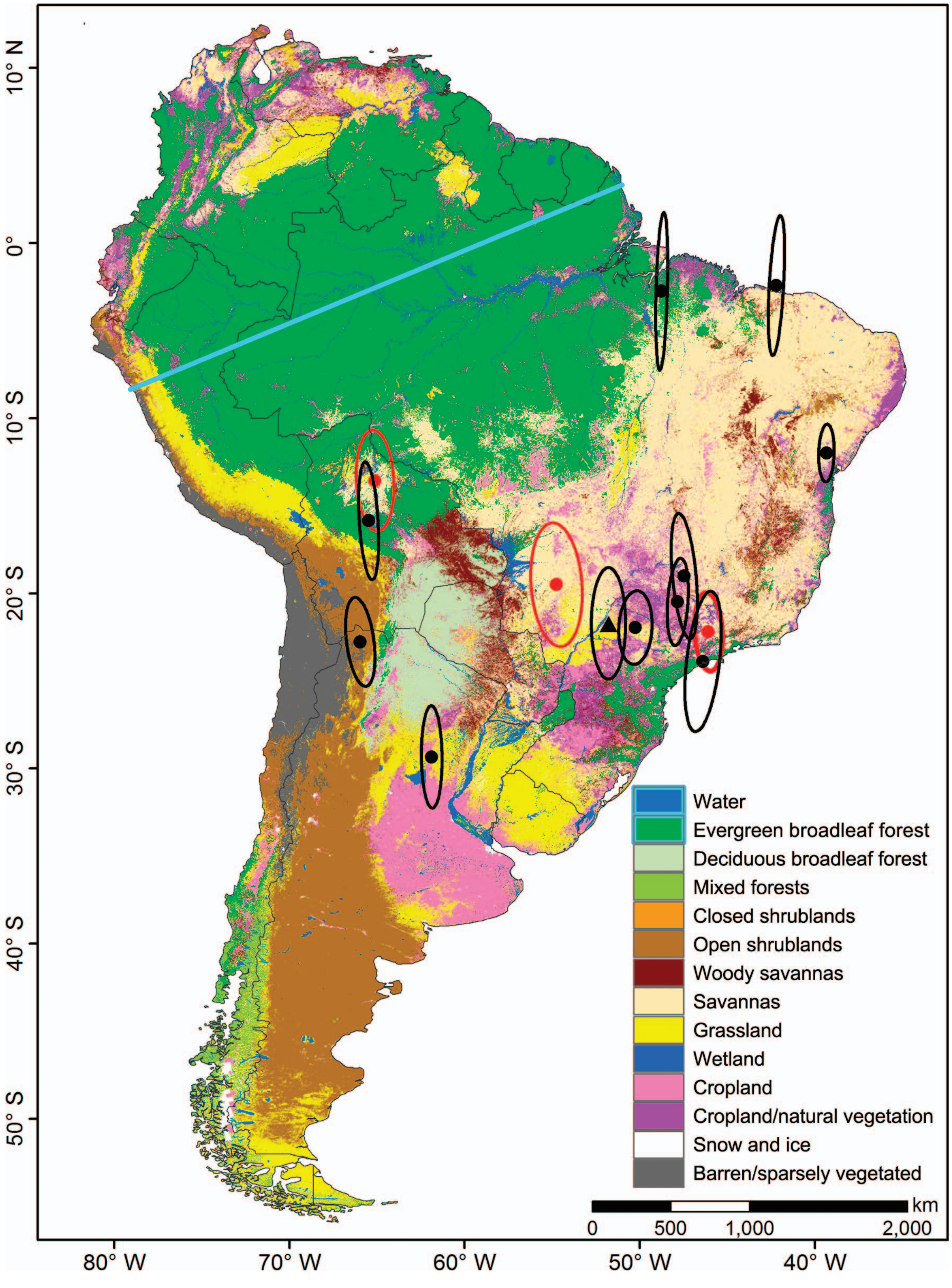

FIGURE 3. Predicted mean wintering locations (dots) and directional standard deviational ellipses (± SD) of Barn Swallows fitted with archival light-level geolocators from breeding populations in Ontario (red, $n = 3$) and New Brunswick (black, $n = 11$), Canada. An additional wintering location of a bird fitted with a geolocator recaptured in 2015 from New Brunswick, not shown in Hobson et al. (2015), is indicated by a triangle. The diagonal blue line represents the cutoff where areas to the south were considered as possible origins used for spatially explicit assignment to isoscape for Barn Swallows breeding in eastern Canada, based on geolocation data. Land cover data are from Broxton et al. (2014).

TABLE 2. Summary of isotopic composition (‰; δ^2H, δ^{13}C) of Barn Swallow feathers used for mvnpdf assignment to isoscape, from females ($n = 99$), males ($n = 83$), and individuals of unknown sex ($n = 26$), molted on the wintering grounds in South America and captured at 3 breeding sites in eastern Canada, 2009–2014.

		δ^2H (‰)			δ^{13}C (‰)		
Year	*n*	Mean	SD	Range	Mean	SD	Range
2009	139	−47.7	14.3	−80.7 to −20.6	−17.5	3.7	−23.9 to −9.4
2010	25	−55.2	7.5	−65.2 to −38.2	−17.4	3.8	−24.6 to −10.5
2012	34	−53.7	12.1	−72.0 to −26.5	−16.5	3.7	−23.5 to −12.5
2013	4	−49.8	17.1	−72.8 to −34.3	−19.6	3.8	−22.4 to −14.2
2014	6	−48.8	9.1	−63.1 to −36.1	−17.5	5.1	−23.0 to −12.1

the Amazon basin (Figure 3). Wintering sites were in Brazil ($n = 10$), Argentina ($n = 2$), and Bolivia ($n = 2$), and 2 of these sites were within 100 km of the Brazilian coast. On the basis of estimated wintering locations from geolocators, we removed the northern part of South America from our spatial assignment, from ~6.5°S (northern Peru) to ~4.4°N (north of the Amazon delta in Brazil; diagonal blue line in Figure 3). Feather δ^{34}S was significantly higher for the 2 birds wintering within 100 km of the northeastern (11.4‰) and southern (12.0‰) Brazilian coast than for birds that wintered farther inland ($\bar{x} = 6.1 \pm 3.0$‰; $F = 6.46$, df = 1 and 7, $P < 0.05$, $n = 7$) for which we also had geolocation data. We did not apply a filter based on feather sulfur (δ^{34}S) values to differentiate between coastal and inland foraging birds in our assignment to dual $\delta^{13}C_f$, δ^2H_f isoscape because of low sample sizes of birds for which we had both sulfur and geolocation information, and we did not have sulfur isotope values for all birds used in the assignment to isoscape.

The spatial assignment to isoscape that grouped all sampling locations, sexes, and years revealed a high proportion of individuals that potentially originated from areas concentrated in southern Brazil, northern Bolivia, east-central Argentina, southern Paraguay, and coastal Chile (Figure 4). Our survey of δ^2H_f and $\delta^{34}S_f$ values for breeding birds showed significant differences in isotopic composition between breeding populations (Pillai's trace statistic, approximate $F = 8.94$, df = 3 and 117, $P < 0.001$). Feather δ^{34}S values were highest in New Brunswick ($\bar{x} = 7.8 \pm 4.3$‰) and Alabama ($\bar{x} = 7.6 \pm 4.8$‰) populations, but only Saskatchewan birds had significantly lower $\delta^{34}S_f$ values than other populations ($\bar{x} = 1.6 \pm 4.5$; $F = 11.4$, df = 3 and 117, $P < 0.001$). Overall, relatively few individuals showed evidence of growing feathers in areas influenced by marine aerosols (Figure 5), with only birds from New Brunswick ($n = 13$; 25.5%) and Alabama ($n = 6$; 17.6%) exceeding our proposed $\delta^{34}S_f$ threshold of 11‰.

DISCUSSION

By combining information from both geolocator-based locations and a spatially explicit dual stable-isotope model, we provide evidence that eastern Canadian populations of Barn Swallows migrate to sub-Amazonia to winter. In addition, we present, for the first time, an evaluation of the potential for using a modeled dual-isotope (δ^2H, δ^{13}C) feather isoscape to infer molt origins of Nearctic–Neotropical migrant birds in South America and provide a first estimate of the feather δ^{34}S threshold that can potentially be applied there to filter out individuals molting near coastal areas. Taken together, these results refine the toolbox available for examining migratory connectivity in this and other declining species that molt on their wintering grounds in South America and, more generally, underline the value of using multiple proxies for any assignment of animals to spatial origin (Hallworth et al. 2013, Rundel et al. 2013, Hobson et al. 2014a).

Unlike those for North America, δ^2H precipitation patterns for South America lack a strong latitudinal gradient, except for the southernmost regions. Nevertheless, these broad patterns can be informative in geographically vast multiple-isotope assignments to origin. Large areas such as the Amazon basin are relatively constant in δ^2H_p, which results in considerable ambiguity in assignment based on that isotope alone. As we demonstrated for Africa (Hobson et al. 2014b), the inclusion of a modeled δ^{13}C plant-based isoscape as a combined probability surface allowed for greater refinement of the isotope approach, because C4 grasslands and savannas of the north, northeast, and central regions of the continent could be distinguished against an otherwise largely C3 continent. Nonetheless, even with this refinement, there are still large areas of South America that are isotopically homogeneous for δ^2H and δ^{13}C, and this necessarily limits assignment possibilities based on these isotopes alone. However, as with all probabilistic assignments of animals based on tissue isotope data, ambiguity can be reduced through the use of Bayesian priors, such as known patterns of population density (Royle and Rubenstein 2004) or knowledge of the winter distribution of the species of interest. In the present study, prior information based on light-sensitive geolocators allowed us to constrain possible wintering areas of Barn Swallows breeding in eastern Canada to areas generally south of the Amazon and

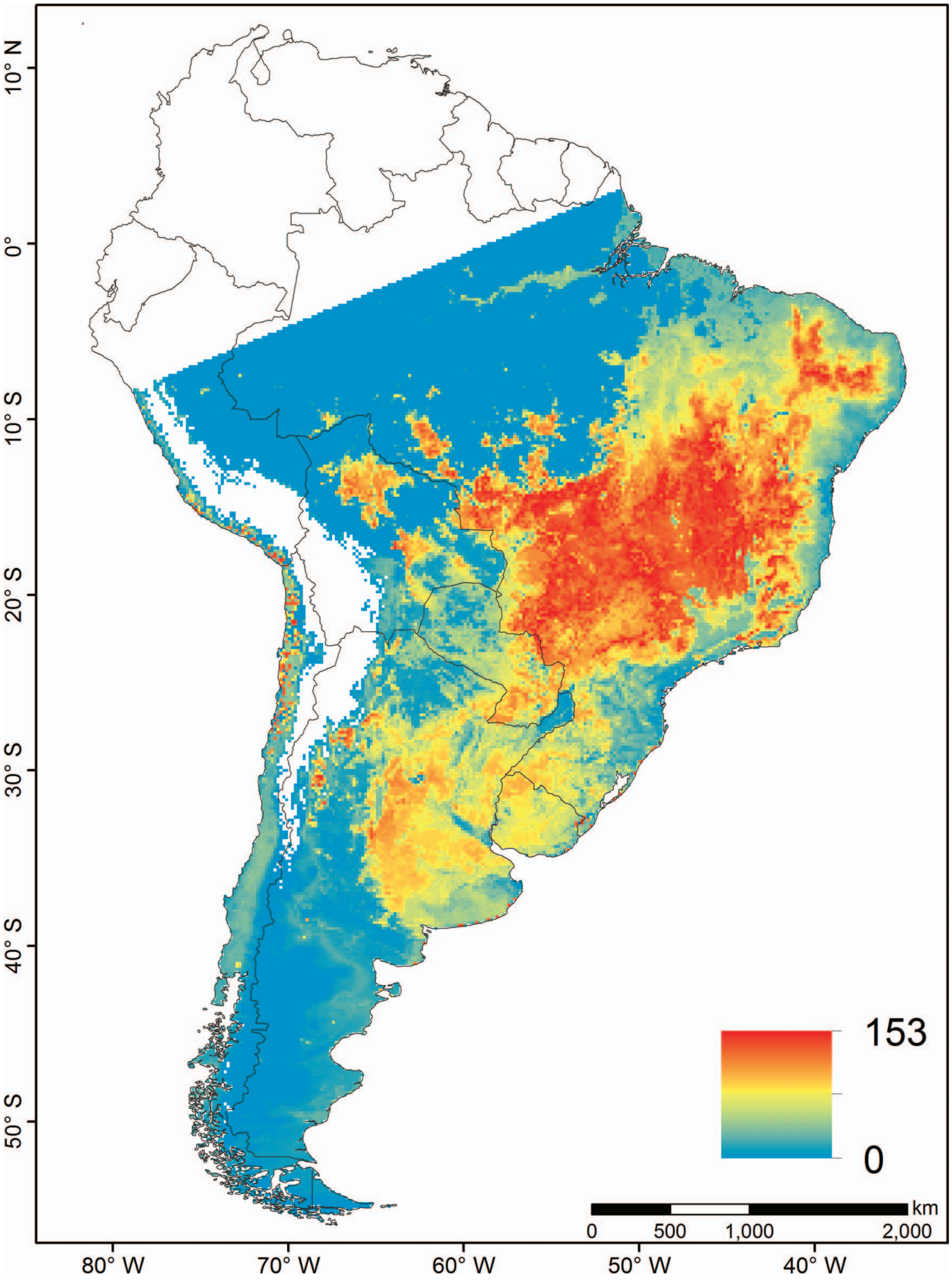

FIGURE 4. Predicted winter origins of Barn Swallows from a geospatial assignment based on a multivariate normal probability density function using $\delta^{13}C_f$ and δ^2H_f assays (values are the number of birds assigned to each raster cell).

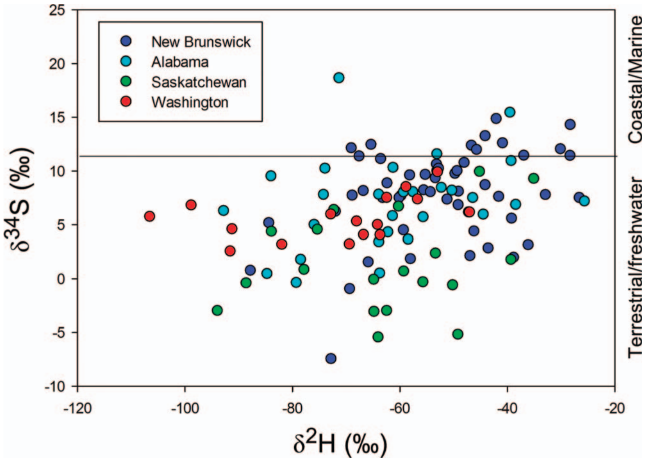

FIGURE 5. Relationship between δ^{34}S and δ^{2}H of winter-grown tail feathers of Barn Swallows ($n = 121$) sampled at breeding sites across North America. The horizontal line indicates the coastal–marine versus terrestrial–freshwater threshold of 11‰, based on feather isotope data from geolocator-equipped birds of known locations and on the literature.

strengthened our contention that although birds exhibited weak connectivity, they nonetheless used open savanna regions of the east-central part of the continent. Information at this scale will still be useful in examining how land-use practices and winter climate in that part of South America may influence population trajectories compared with those of Barn Swallow populations that winter elsewhere (Hobson et al. 2015). Interestingly, geolocator ($n = 9$) returns from the disjunct breeding population in Argentina (García-Pérez et al. 2013) showed that these birds also wintered primarily, but not exclusively, in areas outside of the Amazon Basin (K. A. Hobson and K. J. Kardynal personal observation).Thus, open savannas may be preferred by this species during migration and the nonbreeding period (see also Sanaiotti and Cintra 2001). We are encouraged by the development of predictive plant δ^{13}C isoscapes based on modeled C3 and C4 plant distributions (Powell et al. 2012) and await the development of such an isoscape for Central America and the Caribbean (C. Still personal communication). This isoscape would be particularly valuable because the majority of Nearctic–Neotropical migrants winter in that region (Newton 2008), including Barn Swallows from western North America (Hobson et al. 2015). These modeled isoscapes can also include spatial correction for agricultural crops, although it is unclear to what degree carbon from C4 agriculture in a modeled C3 biome, or from C3 agriculture in a modeled C4 biome, enters food webs that lead to wintering birds. This is an area that requires further research and ground-truthing, but potentially it could further refine assignment to origins using stable isotopes. Indeed, for Barn Swallows and other aerial insectivores, it is currently unknown how much carbon in their wintering diet may be derived from agricultural crops versus natural terrestrial and wetland habitats. Nonetheless, assignment of individuals on the basis of multiple isotopes is anticipated to be more informative than assignment based on single isotopes (Sellick et al. 2009, Hobson et al. 2014b).

There is interest in contrasting the results of assignments based on light-sensitive geolocators with those from stable isotope models (Hallworth et al. 2013). The degree to which these methods "agree" will depend on the structure of underlying isoscapes for the areas of interest and the accuracy of the geolocator assignments, so it is impossible to generalize. The occurrence of large, isotopically homogeneous regions will typically result in poorer assignment accuracy with the dual-isotope approach than with geolocator tracks. However, it is possible to sample many more individuals for stable isotopes than with geolocators, because only a single capture is required, analyses are relatively inexpensive (approximately one-tenth the cost of a geolocator), and isotopic sampling is not biased to the regions of initial capture. As such, the isotope approach for South America is best suited to describing coarse-scale patterns that can ultimately be modified or constrained by a smaller subset of geolocator data. In this way, the isotope data can also be used to guide efforts using geolocators or other tracking technologies (Hobson et al. 2014b). Geolocation of Nearctic–Neotropical migrant birds is a relatively new technique that requires further development to reduce inherently large errors (e.g., via shading) and issues with equinox and to ground-truth data on the wintering grounds. Also, birds fitted with geolocators may behave differently than those without geolocators, and hence these data may not be entirely unbiased (Arlt et al. 2013, Costantini and Møller 2013). As we have demonstrated for South America and expect to find for other continents, stable-isotope and geolocator approaches are entirely complementary, and their combined use is especially suited to investigating migratory connectivity in birds with broad breeding and wintering distributions.

Although our geolocator sample of birds was relatively low, our examination of $\delta^{34}S_f$ values for birds of known wintering area suggests that a threshold of 11‰ may be appropriate to distinguish between those individuals molting feathers in coastal regions and those molting farther inland or away from a marine influence. This value is similar to previous estimates of 9–10‰ suggested by others (Lott et al. 2003, Haché et al. 2014). We recognize that there can be cases of inland-molting birds with $\delta^{34}S_f$ values higher than this value—for example, in birds using food webs based on ^{34}S-enriched volcanic soils and in those using freshwater-marsh food webs where sulfate reduction occurs under anaerobic conditions (Thode 1991). However, in general, we think that (1) those situations will be quite rare, as indicated by our survey of feathers from 121 Barn Swallows across North America (Figure 5); and (2) a conservative approach that uses this $\delta^{34}S_f$ threshold will generally prevent erroneous assignments based only on δ^2H_f and $\delta^{13}C_f$ measurements. Our broader survey (Figure 5) suggests that Barn Swallows from colonies in eastern Canada and Alabama are more likely to winter in coastal habitats on their wintering grounds, compared with western populations. Using geolocators, Hobson et al. (2015) determined that western-breeding Barn Swallows winter in Central America, the Caribbean, and north coastal South America. The overall lower $\delta^{34}S_f$ values of those western-breeding birds suggest that coastal marshes in wintering grounds are probably not being used as roosting or foraging areas, and this may reflect the lack of, the quality of, or the loss of such habitat in the region compared with coastal areas of eastern South America (Bildstein et al. 1991, Lehner and Döll 2004, Davidson 2014). We encourage the use of $\delta^{34}S$ tissue measurements in similar studies and for species that potentially winter in coastal areas, to refine thresholds in using sulfur isotopes to distinguish between marine and inland wintering areas and foraging areas. This information could also provide cues for determining the potential importance of coastal habitats for overwintering birds.

Most Nearctic–Neotropical migrant bird species molt on the breeding grounds, and our method of determining wintering origins of birds in South America is therefore limited to a small suite of species (mostly aerial insectivores) that molt on that continent. However, our work serves as an important advancement, both theoretical and practical, in the use of multiple proxies for assignments of animals to spatial origin, for several reasons. Many bird species that breed in North America and molt in South America are declining (Michel et al. 2015, Smith et al. 2015), and methods for determining their wintering origins and connectivity are urgently needed for the conservation of these species. Tags fitted to aerial insectivores can have negative effects on their survival, nest success, and fitness (Scandolara et al. 2014) and are costly to apply at large scales. Additionally, there are many austral and intratropical migrant species for which our method provides a potential template for determining origins. Finally, all birds wintering in South America, regardless of molt schedules, acquire isotopic values in their claws that reflect isotopic signatures of areas where they were grown. Therefore, our method will assist in assignments using claw isotopes, and presumably for a much larger number of species, provided that claws are sampled early enough in the breeding season.

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LITERATURE CITED

Arlt, D., M. Low, and T. Pärt (2013). Effect of geolocators on migration and subsequent breeding performance of a long-distance passerine migrant. PLOS One 8:e82316.

Arneson, L. S., and S. E. MacAvoy (2005). Carbon, nitrogen, and sulfur diet–tissue discrimination in mouse tissues. Canadian Journal of Zoology 83:989–995.

Bildstein, K. L., G. T. Bancroft, P. J. Dugan, D. H. Gordon, R. M. Erwin, E. Nol, L. X. Payne, and S. E. Senner (1991). Approaches to the conservation of coastal wetlands in the Western Hemisphere. Wilson Bulletin 103:218–254.

BirdLife International and NatureServe (2011). Bird Species Distribution Maps of the World. BirdLife International, Cambridge, UK, and NatureServe, Arlington, VA, USA.

Brown, C. R., and M. Bomberger Brown (1999). Barn Swallow (*Hirundo rustica*). In Birds of North America Online (A. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. http://bna.birds.cornell.edu/bna/species/452

Broxton, P. D., X. Zeng, D. Sulla-Menashe, and P. A. Troch (2014). A global land cover climatology using MODIS data. Journal of Applied Meteorology and Climatology 53:1593–1605.

Costantini, D., and A. P. Møller (2013). A meta-analysis of the effects of geolocator application on birds. Current Zoology 59:697–706.

Craine, J. M., A. J. Elmore, M. P. M. Aidar, M. Bustamante, T. E. Dawson, E. A. Hobbie, A. Kahmen, M. C. Mack, K. K. McLauchlan, A. Michelsen, G. B. Nardoto, L. H. Pardo, et al. (2009). Global patterns of foliar nitrogen isotopes and their relationships with climate, mycorrhizal fungi, foliar nutrient concentrations, and nitrogen availability. New Phytologist 183:980–992.

Cross, A. D. P., J. Hentati-Sundberg, H. Österblom, R. A. R. McGill, and R. W. Furness (2014). Isotopic analysis of island House Martins *Delichon urbica* indicates marine provenance of nutrients. Ibis 156:676–681.

Davidson, N. C. (2014). How much wetland has the world lost? Long-term and recent trends in global wetland area. Marine and Freshwater Research 65:934–941.

Faaborg, J., R. T. Holmes, A. D. Anders, K. L. Bildstein, K. M. Dugger, S. A. Gauthreaux, Jr., P. Heglund, K. A. Hobson, A. E.

Jahn, D. H. Johnson, S. C. Latta, D. J. Levey, et al. (2010). Conserving migratory land birds in the New World: Do we know enough? Ecological Applications 20:398–418.

Flockhart, D. T. T., L. I. Wassenaar, T. G. Martin, K. A. Hobson, M. B. Wunder, and D. R. Norris (2013). Tracking multi-generational colonization of the breeding grounds by monarch butterflies in eastern North America. Proceedings of the Royal Society of London, Series B 280:20131087.

García-Pérez, B., and K. A. Hobson (2014). A multi-isotope (δ^2H, δ^{13}C, δ^{15}N) approach to establishing migratory connectivity of Barn Swallow (*Hirundo rustica*). Ecosphere 5:art21.

García-Pérez, B., K. A. Hobson, R. L. Powell, C. J. Still, and G. H. Huber (2013). Switching hemispheres: A new migration strategy for the disjunct Argentinean breeding population of Barn Swallow (*Hirundo rustica*). PLOS One 8:e55654.

Gross, K., and D. Bates (2012). Mvnmle: ML estimation for multivariate normal data with missing values. R package version 0.1-11. http://CRAN.R-project.org/package=mvnmle

Haché, S., K. A. Hobson, E. M. Bayne, S. L. Van Wilgenburg, and M. A. Villard (2014). Tracking natal dispersal in a coastal population of a migratory songbird using feather stable isotope (δ^2H, δ^{34}S) tracers. PLOS One 9:e94437.

Hallworth, M. T., C. E. Studds, T. S. Sillett, and P. P. Marra (2013). Do archival light-level geolocators and stable hydrogen isotopes provide comparable estimates of breeding-ground origin? The Auk 130:273–282.

Hebert, C. E., M. Bur, D. Sherman, and J. L. Shutt (2008). Sulfur isotopes link overwinter habitat use and breeding condition in Double-crested Cormorants. Ecological Applications 18: 561–567.

Hijmans, R. J. (2015). Raster: Geographic data analysis and modeling. R package version 2.3-24. http://CRAN.R-project.org/package=raster

Hobson, K. A. (1999). Tracing origins and migration of wildlife using stable isotopes: A review. Oecologia 120:314–326.

Hobson, K. A., K. J. Kardynal, S. L. Van Wilgenburg, G. Albrecht, A. Salvadori, M. D. Cadman, F. Liechti, and J. W. Fox (2015). A continent-wide migratory divide in North American breeding Barn Swallows (*Hirundo rustica*). PLOS One 10:e0129340.

Hobson, K. A., S. L. Van Wilgenburg, J. Faaborg, J. D. Toms, C. Rengifo, A. L. Sosa, Y. Aubry, and R. B. Aguilar (2014a). Connecting breeding and wintering grounds of Neotropical migrant songbirds using stable hydrogen isotopes: A call for an isotopic atlas of migratory connectivity. Journal of Field Ornithology 85:237–257.

Hobson, K. A., S. L. Van Wilgenburg, L. I. Wassenaar, and K. Larson (2012a). Linking hydrogen (δ^2H) isotopes in feathers and precipitation: Sources of variance and consequences for assignment to isoscapes. PLOS One 7:e35137.

Hobson, K. A., S. L. Van Wilgenburg, L. I. Wassenaar, R. L. Powell, C. J. Still, and J. M. Craine (2012b). A multi-isotope (δ^{13}C, δ^{15}N, δ^2H) feather isoscape to assign Afrotropical migrant birds to origins. Ecosphere 3:art44.

Hobson, K. A., S. L. Van Wilgenburg, T. Wesołowski, M. Maziarz, R. G. Bijlsma, A. Grendelmeier, and J. W. Mallord (2014b). A multi-isotope (δ^2H, δ^{13}C, δ^{15}N) approach to establishing migratory connectivity in Palearctic–Afrotropical migrants: An example using Wood Warblers *Phylloscopus sibilatrix*. Acta Ornithologica 49:57–69.

Hobson, K. A., and L. I. Wassenaar (Editors) (2008). Tracking Animal Migration Using Stable Isotopes. Academic Press/Elsevier, Amsterdam, The Netherlands.

Hobson, K. A., M. B. Wunder, S. L. Van Wilgenburg, R. G. Clark, and L. I. Wassenaar (2009). A method for investigating population declines of migratory birds using stable isotopes: Origins of harvested Lesser Scaup in North America. PLOS One 4:e7915.

Hostetler, J. A., T. S. Sillett, and P. P. Marra (2015). Full-annual-cycle population models for migratory birds. The Auk: Ornithological Advances 132:433–449.

IAEA/WMO (2015). Global Network of Isotopes in Precipitation. GNIP Database. http://www-naweb.iaea.org/napc/ih/IHS_resources_gnip.html

International Atomic Energy Agency (2015). RCWIP (Regionalized Cluster-Based Water Isotope Prediction) Model—gridded precipitation δ^{18}O|δ^2H| δ^{18}O and δ^2H isoscape data. International Atomic Energy Agency, Vienna, Austria.

Kalman, R. E. (1960). A new approach to linear filtering and prediction problems. Journal of Basic Engineering 82:35–45.

Lehner, B., and P. Döll (2004). Development and validation of a global database of lakes, reservoirs and wetlands. Journal of Hydrology 296:1–22.

Liechti, F., C. Scandolara, D. Rubolini, R. Ambrosini, F. Korner-Nievergelt, S. Hahn, R. Lardelli, M. Romano, M. Caprioli, A. Romano, B. Sicurella, and N. Saino (2014). Timing of migration and residence areas during the non-breeding period of Barn Swallows *Hirundo rustica* in relation to sex and population. Journal of Avian Biology 45:1–12.

Lott, C. A., T. D. Meehan, and J. A. Heath (2003). Estimating the latitudinal origins of migratory birds using hydrogen and sulfur stable isotopes in feathers: Influence of marine prey base. Oecologia 134:505–510.

Martin, T. G., I. Chadès, P. Arcese, P. P. Marra, H. P. Possingham, and D. R. Norris (2007). Optimal conservation of migratory species. PLOS One 2:e751.

Michel, N. L., A. C. Smith, R. G. Clark, C. A. Morrissey, and K. A. Hobson (2015). Differences in spatial synchrony and interspecific concordance inform guild-level population trends for aerial insectivorous birds. Ecography 38. In press.

Nebel, S., A. Mills, J. D. McCracken, and P. D. Taylor (2010). Declines of aerial insectivores in North America follow a geographic gradient. Avian Conservation and Ecology 5(2):1.

Newton, I. (2008). The Migration Ecology of Birds. Academic Press, London, UK.

Nott, M. P., D. F. Desante, R. B. Siegel, and P. Pyle (2002). Influences of the El Niño/Southern Oscillation and the North Atlantic Oscillation on avian productivity in forests of the Pacific Northwest of North America. Global Ecology and Biogeography 11:333–342.

Ofukany, A. F., K. A. Hobson, and L. I. Wassenaar (2012). Connecting breeding and wintering habitats of migratory piscivorous birds: Implications for tracking contaminants (Hg) using multiple stable isotopes. Environmental Science & Technology 46:3263–3272.

Paxton, K. L., E. B. Cohen, E. H. Paxton, Z. Németh, and F. R. Moore (2014). El Niño–Southern Oscillation is linked to decreased energetic condition in long-distance migrants. PLOS One 9:e95383.

Powell, R. L., E.-H. Yoo, and C. J. Still (2012). Vegetation and soil carbon-13 isoscapes for South America: Integrating remote sensing and ecosystem isotope measurements. Ecosphere 3: 109.

Pyle, P. (1997). Identification Guide to North American Birds, Part I: Columbidae to Ploceidae. Slate Creek Press, Point Reyes Station, California, USA.

R Development Core Team (2014). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vieanna, Austria.

Royle, J. A., and D. R. Rubenstein (2004). The role of species abundance in determining breeding origins of migratory birds with stable isotopes. Ecological Applications 14:1780–1788.

Rundel, C. W., M. B. Wunder, A. H. Alvarado, K. C. Ruegg, R. Harrigan, A. Schuh, J. F. Kelly, R. B. Siegel, D. F. Desante, T. B. Smith, and J. Novembre (2013). Novel statistical methods for integrating genetic and stable isotope data to infer individual-level migratory connectivity. Molecular Ecology 22:4163–4176.

Sanaiotti, T. M., and R. Cintra (2001). Breeding and migrating birds in an Amazonian savanna. Studies on Neotropical Fauna and Environment 36:23–32.

Scandolara, C., D. Rubolini, R. Ambrosini, M. Caprioli, S. Hahn, F. Liechti, A. Romano, M. Romano, B. Sicurella, and N. Saino (2014). Impact of miniaturized geolocators on Barn Swallow *Hirundo rustica* fitness traits. Journal of Avian Biology 45:417–423.

Sellick, M. J., T. K. Kyser, M. B. Wunder, D. Chipley, and D. R. Norris (2009). Geographic variation of strontium and hydrogen isotopes in avian tissue: Implications for tracking migration and dispersal. PLOS One 4:e4735.

Sibert, J. R., M. K. Musyl, and R. W. Brill (2003). Horizontal movements of bigeye tuna (*Thunnus obesus*) near Hawaii determined by Kalman filter analysis of archival tagging data. Fisheries Oceanography 12:141–151.

Sibert, J. R., and A. Nielsen (2002). Kftrack: An add-on package for the statistical environment R to estimate most probable track from archival tagged individuals. Pelagic Fisheries Research Program, University of Hawaii at Manoa, Honolulu, Hawaii, USA.

Sillett, T. S., and R. T. Holmes (2002). Variation in survivorship of a migratory songbird throughout its annual cycle. Journal of Animal Ecology 71:296–308.

Smith, A. C., M. A. Hudson, C. M. Downes, and C. M. Francis (2015). Change points in the population trends of aerial-insectivorous birds in North America: Synchronized in time across species and regions. PLOS One 10:e0130768.

Still, C. J., J. A. Berry, G. J. Collatz, and R. S. DeFries (2003). Global distribution of C3 and C4 vegetation: Carbon cycle implications. Global Biogeochemical Cycles 17(1):1006.

Taylor, C. M., and D. R. Norris (2009). Population dynamics in migratory networks. Theoretical Ecology 3:65–73.

Terzer, S., L. I. Wassenaar, L. J. Araguás-Araguás, and P. K. Aggarwal (2013). Global isoscapes for δ^{18}O and δ^{2}H in precipitation: Improved prediction using regionalized climatic regression models. Hydrology and Earth System Sciences 17:4713–4728.

Thode, H. G. (1991). Sulphur isotopes in nature and the environment: An overview. In Stable Isotopes in the Assessment of Natural and Anthropogenic Sulphur in the Environment (H. R. Krouse and V. A. Grinenko, Editors). Wiley, New York, NY, USA. pp. 1–26.

Van Wilgenburg, S. L., and K. A. Hobson (2011). Combining stable-isotope (δD) and band recovery data to improve probabilistic assignment of migratory birds to origin. Ecological Applications 21:1340–1351.

Wassenaar, L. I., and K. A. Hobson (2003). Comparative equilibration and online technique for determination of non-exchangeable hydrogen of keratins for use in animal migration studies. Isotopes in Environmental and Health Studies 39:211–217.

Webster, M. S., and P. P. Marra (2005). The importance of understanding migratory connectivity and cross-seasonal interactions. In Birds of Two Worlds: The Ecology and Evolution of Migration (R. Greenberg and P. P. Marra, Editors). Johns Hopkins University Press, Baltimore, MD, USA. pp. 199–209.

West, J. B., G. J. Bowen, T. E. Cerling, and J. R. Ehleringer (2006). Stable isotopes as one of nature's ecological recorders. Trends in Ecology & Evolution 21:408–414.

West, J. B., G. J. Bowen, T. E. Dawson, and K. P. Tu (Editors) (2010). Isoscapes: Understanding Movement, Pattern, and Process on Earth through Isotope Mapping. Springer, Dordrecht, The Netherlands.

Wunder, M. B. (2010). Using isoscapes to model probability surfaces for determining geographic origins. In Isoscapes: Understanding Movement, Pattern, and Process on Earth through Isotope Mapping (J. B. West, G. J. Bowen, T. E. Dawson, and K. P. Tu, Editors). Springer, Dordrecht, The Netherlands. pp. 251–270.

Zazzo, A., F. J. Monahan, A. P. Moloney, S. Green, and O. Schmidt (2011). Sulphur isotopes in animal hair track distance to sea. Rapid Communications in Mass Spectrometry 25:2371–2378.