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A GEOGRAPHIC-INFORMATION-SYSTEM APPROACH TO ESTIMATING THE ORIGIN OF MIGRATORY RAPTORS IN NORTH AMERICA USING STABLE HYDROGEN ISOTOPE RATIOS IN FEATHERS

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Abstract.—Analysis of stable hydrogen isotope ratios in feathers (δD_f) is a promising method for investigating population connectivity in migratory birds. Stable hydrogen isotope ratios in precipitation (δD_p) vary across North America with respect to latitude, elevation, and seasonal air-mass trajectories. A strong relationship between δD_f and δD_p at locations of feather growth has been documented for several bird species. Some studies have used measurements of δD_f to plot the origins of migrants on maps of long-term weighted-average, growing-season North American δD_p (hereafter "δD_p maps") using the observed relationship between δD_f and δD_p from a reference sample of known-origin birds. The accuracy of this method depends on the strength of the δD_f and δD_p relationship and accuracy of the δD_p maps. Recently, a high-resolution (1-km^2) model of North American δD_p was published (Meehan et al. 2004) that accounts for the effect of elevation on δD_p where previous models did not. We compared δD_f measurements from a geographically diverse sample of 264 raptor feathers with δD_p estimates for feather-sample locations. We documented a strong relationship between raptor δD_f and δD_p across North America. However, we also documented substantial regional variation in this relationship. We created a "base map" of North American raptor δD_f that incorporated the regional variation described by our sample. We plotted δD_f values from migrant Sharp-shinned Hawks (*Accipiter striatus*) captured in eastern Nevada directly on this map to demonstrate how it can be used to view the origins of migrants. *Received 2 December 2004, accepted 10 October 2005.*

Key words: *Accipiter striatus*, annual cycle, avian migration, geographic information systems, population connectivity, Sharp-shinned Hawk, stopover.

Un Procedimiento Basado en Sistemas de Información Geográfica para Estimar el Origen de las Aves Rapaces Migratorias en Norte América Usando los Cocientes de Isótopos Estables de Hidrógeno Presentes en las Plumas

Resumen.—El análisis de los cocientes de isótopos estables de hidrógeno presentes en las plumas (δD_f) es un método promisorio para investigar la conectividad entre poblaciones en las aves migratorias. Los cocientes de isótopos estables de hidrógeno presentes en la precipitación (δD_p) varían a través de Norte América con respecto a la latitud, la elevación y las trayectorias estacionales de las masas de aire. En varias especies de aves, se ha documentado una fuerte relación entre δD_f y δD_p en las localidades donde crecen las plumas. Algunos estudios han empleado medidas de δD_f para ubicar el origen de los migrantes en mapas basados

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en promedios ponderados de valores de δD_p medidos a través de varios años en Norte América ("mapas δD_p"), utilizando la relación observada entre δD_f y δD_p en una muestra de referencia de aves de origen conocido. La exactitud de este método depende de qué tan estrecha es la relación entre δD_f y δD_p, y de la exactitud de los mapas δD_p. Recientemente se publicó un modelo de δD_p de alta resolución para Norte América (Meehan et al. 2004) que, a diferencia de los modelos previos, tiene en cuenta el efecto de la elevación sobre δD_p. En este estudio comparamos medidas de δD_f de una muestra geográficamente diversa de 264 plumas de aves rapaces con estimados de δD_p para los sitios donde las plumas fueron obtenidas. Documentamos una fuerte relación entre δD_f y δD_p en las rapaces a través de Norte América. Sin embargo, también documentamos que esta relación varía considerablemente entre regiones. Creamos un mapa base de δD_f para las rapaces que incopora la variación regional descrita por nuestra muestra. Ilustramos el uso de este mapa para determinar el origen de los migrantes ubicando sobre éste los valores de δD_f medidos en individuos migratorios de la especie *Accipiter striatus*.

Several studies have measured stable hydrogen isotope ratios in feathers (δD_f) of birds at migratory stopover or wintering sites to estimate the areas where these feathers were grown (Chamberlain et al. 1997; Hobson and Wassenaar 1997, 2001; Hobson et al. 2001; Meehan et al. 2001; Wassenaar and Hobson 2001; Kelly et al. 2002; Rubenstein et al. 2002; Smith et al. 2003, 2004; DeLong et al. 2005). This method has been described as a major breakthrough in the ability to establish connectivity among breeding, migrant, and wintering populations (Kelly and Finch 1998, Hobson 1999, Webster et al. 2002, Rubenstein and Hobson 2004). However, precise methods for estimating the origins of migrants and for representing these data spatially are still in the early stages of development.

Estimating migrant origins on the basis of δD_f relies on two basic patterns in biogeochemistry. First, stable hydrogen isotope ratios in weighted-average growing-season precipitation (δD_p) show strong geographic variation across the ranges of many species of migratory birds (Chamberlain et al. 1997, Hobson and Wassenaar 1997). Second, the local environmental signal of δD_p is transferred to the feathers of birds through their diet during feather growth (Chamberlain et al. 1997, Hobson and Wassenaar 1997, Hobson et al. 1999a). Thus, measurements of δD_f from migrants will be indicative of the δD_p of the area where the feathers were grown (Chamberlain et al. 1997, Hobson and Wassenaar 1997). In the case of hatching-year birds, this will be the natal area, because their feathers are typically grown on or near the nest site.

Growing-season δD_p values decrease with increasing latitude and altitude because of the strong negative relationship between temperature and δD_p (Dansgard 1964). At a continental scale, the coarse spatial pattern of decreasing δD_p values with increasing latitude is affected by topography, such that high-latitude, low-elevation areas can have δD_p values similar to those of lower-latitude, high-elevation areas (Dansgard 1964). Regional patterns in growing-season δD_p are further modified in complex ways by more diffuse effects, such as seasonal air-mass trajectories and local evaporation rates (Rozanski et al. 1993, Bowen and Wilkinson 2002). Large-scale maps of spatial patterns in δD_p have been created that account for variation in δD_p in relation to latitude, altitude, and other sources of variation (Meehan et al. 2004, Bowen et al. 2005). Previously, stable-isotope studies of animal movement have relied on simple models of δD_p that did not account for these effects. Elevation-explicit models of large-scale patterns in δD_p should help refine the accuracy of stable hydrogen isotope studies of animal movement (Hobson et al. 2004, Meehan et al. 2004).

Several studies have described a strong relationship between δD_f and δD_p within various groups of birds across different regions of North America and Europe (Chamberlain et al. 1997; Hobson and Wassenaar 1997; Wassenaar and Hobson 2000; Hobson et al. 2001, 2004; Meehan et al. 2001; Rubenstein et al. 2002; Lott et al. 2003). Many of these studies are not directly comparable because of differences in laboratory methods used to measure δD_f and in the models used to estimate δD_p for feather-collection sites. Some of these studies took a two-step approach in using measurements of δD_f to estimate the origins of migrants. First, the relationship between δD_f and estimated δD_p was quantified using a reference sample of known-origin birds from throughout the source range of the study species. Second, the δD_f and δD_p relationship was used to estimate the origins of unknown-origin birds—for example, birds sampled during migration or at a wintering site (Chamberlain et al. 1997, Hobson and Wassenaar 1997, Meehan et al. 2001, Wassenaar and Hobson 2001). Predictive regression models were constructed from the reference sample using measurements of δD_f as the dependent variable and estimates of δD_p as the independent variable. The regression equations from these models were then used to inversely predict δD_p from measurements of δD_f from migrants of unknown origins. Finally, distributions of predicted δD_p values for migrants were plotted on maps of δD_p to illustrate their potential origins (Hobson et al. 1999b, Meehan et al. 2001, Wassenaar and Hobson 2001, Smith et al. 2004, DeLong et al. 2005). Several published studies have constructed models from reference samples with limited geographic coverage. If the relationship between δD_f and δD_p varies regionally, limited or inappropriate spatial distribution of reference samples may violate the important regression assumption that reference samples are representative of the source regions of a migrant population, compromising the accuracy of predictions.

Here, we (1) quantify the relationship between δD_f and δD_p for North American raptors, using a large sample of known-origin birds with extensive geographic coverage; and (2) use this relationship to create a geographic information system (GIS) "base map" of δD_f that can be used to estimate the origins of migrant raptors from measurements of δD_f at stopover or wintering sites anywhere in North America. We assembled a reference sample of 264 feathers from 12 species of raptors from known locations across most of North America to document the strength of the relationship between raptor δD_f and δD_p and to describe regional variation in this relationship across the continent. We then used this reference sample and an elevation-explicit model of North American δD_p (Meehan et al. 2004) to create a GIS base map of continental patterns in δD_f that accounted for regional variation in the δD_f and δD_p relationship. We demonstrate how this base map can be used to plot the origins of migrants using δD_f values from Sharp-shinned Hawks (*Accipiter striatus*) captured during fall migration in the Goshute Mountains, Nevada. Our base map of North American raptor δD_f is available (see Acknowledgments).

METHODS

Feather-sample collection.—We collected one to two contour feathers from 264 individual raptors of 12 species from 255 locations across most of North America (Fig. 1). We obtained feathers from 16 different ornithology collections in the United States and Canada, and six feathers from two researchers (see Acknowledgments). We selected samples to achieve broad spatial coverage within the breeding ranges of most North American species of diurnal raptors and to achieve representative coverage of all habitats within these ranges. All samples were taken from nestlings or birds in juvenal plumages that were assumed to be collected at or near their natal territory on the basis of collection date. Within-year sample-date criteria varied across species and locations. We used Johnsgard (1990) to choose dates that minimized the chance that specimens were collected during spring migration, during fall migration, or after postfledging dispersal. In most cases, this resulted in collection dates in June or July, with some exceptions ranging into May, August, or, in a few cases, September. Original specimen collection years ranged from 1874 to 2003. No samples were taken from birds in downy plumages, because very young individuals may have δD_f values related to their parents' wintering site rather than the local food web (Duxbury et al. 2003). We only collected feathers with relatively exact location, such as cities, small and well-defined geographic features, or counties in areas with regionally low δD_p variance. Data for each of the reference population feather samples used here are available (see Acknowledgments).

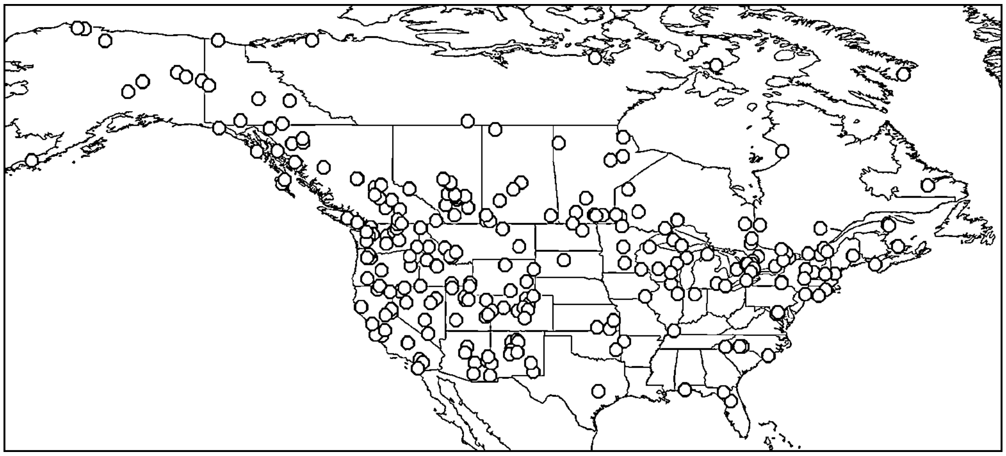

Fig. 1. A map of North America showing sample locations of feathers analyzed in this study. Detailed location data for each sample are available (see Acknowledgments).

Estimates of stable hydrogen isotope ratios in precipitation for each feather-sample location.—For samples with "exact" location information (e.g., the name of a city), we created a circular buffer with a 10-km radius around the location for estimates of δD_p for that site. We used buffers because it was often difficult to tell from specimen data whether the specimen was collected at or near the reported location. We took this approach, rather than using point estimates for each location, because specimens were collected by many different collectors across many years, without a standard protocol for reporting location. For locations that reported only county as geographic location, we used the "county" layer in ARCVIEW, version 3.2 (ESRI, Redlands, California), to acquire county polygons for each sample. For specimens with geographic-feature locations such as small lakes or creeks, we created polygons with 10-km buffers around each feature. We used the Meehan et al. (2004) map of North American weighted-average, growing-season δD_p (hereafter "the MPM"; see Acknowledgments). Finally, we acquired mean estimates for δD_p from the MPM for each sample-location polygon using the "summarize zones" feature of the ARCVIEW SPATIAL ANALYST, version 2.0, extension (McCoy and Johnston 2001).

Stable-isotope laboratory methods.—The base-map and Goshute-migrant feather samples were analyzed for stable hydrogen isotope ratios (δD_f) between 19 February and 14 April 2004 at the Stable Isotope Hydrology and Ecology Lab at the National Water Research Institute of Environment Canada in Saskatoon, Saskatchewan, following the detailed analytical protocols described in Wassenaar and Hobson (2003). All δD_f results are reported in delta (δ) notation, in per-mil units (‰) and normalized on the standard VSMOW-SLAP scale. Repeat analysis of standards during feather analyses yielded a laboratory repeatability of ±1.0‰ for homogenized keratin samples. However, repeatability of feathers reanalyzed several months to a year after their original analysis showed statistically significant shifts in δD_f values between analyses (paired t-test: P values < 0.03 for five of six sample groups; n = 28–40 per sample group). Systematic shifts in δD_f values between analyses spanned from 9.2‰ to –6.4‰ per sample group (a range of 15.6‰), and the direction and magnitude of these shifts differed significantly among groups ($F = 20.44$, df = 5 and 179, $P < 0.0001$). Because δD_f values from repeat analyses were strongly correlated with original analyses (r^2: 0.90–0.98), we standardized original δD_f values among studies using regressions from repeat analyses for all six sample groups. For example, the equation used to standardize δD_f values for the migrant Sharp-shinned Hawk feathers reported here was: standardized δD_f value = –13.90 + 0.90 × original δD_f value.

This step standardized results among several concurrent studies, because all corrections were made on the basis of the same repeat analysis session. Use of our base map in future studies will require that a subset of the feathers used to create the map are reanalyzed at the same time as the migrant samples. Limited supplies of original base-map feathers are available for this purpose by request from HawkWatch International (HWI; see Acknowledgments).

Quantifying the relationship between stable hydrogen isotope ratios in feathers and in precipitation.—We used least-squares regression to quantify the relationship between measured δD_f and estimated δD_p for our reference population samples. We explored several models of the δD_f and δD_p relationship that included covariates for species, feather-sample collection year, or within-season feather-collection date. None of these covariates contributed significantly to the models (all $P > 0.05$), and they were not considered further. We mapped the regional trend in regression residuals to illustrate spatial variation in the relationship between δD_f and δD_p. We used inverse distance weighting (Johnston et al. 2001) to interpolate δD_f and δD_p regression residual values for each 1-km^2 grid cell for North America. We set several interpolation input parameters to account for the fact that each of our reference feather-sample locations typically had only a single δD_f value, and δD_f is known to vary within raptor populations (Meehan et al. 2001). First, we used a large number of nearest neighbors ($n = 20$) for interpolations, so that regional patterns of residuals would reflect multiple samples within a region. Second, we set the weighting coefficient for each sample to a value of 1.0 to reduce the effect of any single observation on regional trends and to limit the affect of distant points on local values (Johnston et al. 2001). We conducted all statistical analyses using JMPIN, version 3.2.6 (Sall and Lehman 1996). We performed all spatial analyses and interpolations using the SPATIAL ANALYST extension in ARCVIEW (McCoy and Johnston 2001).

Geographic-information-system base maps of stable hydrogen isotope ratios in feathers of North American raptors.—We created a map of continental patterns in raptor δD_f using a two-step process. First, we used the regression equation from our reference population sample to create an initial map of estimated raptor δD_f values using the "map calculator" feature in SPATIAL ANALYST with the MPM as a base layer. This step multiplied each 1-km^2 grid cell of the MPM by the slope of the regression equation and subtracted the intercept (e.g., $\delta D_f = 0.908 \times$ MPM $\delta D_p - 5.619$). This produced an elevation-explicit map of estimated δD_f values for each 1-km^2 grid cell in North America by incorporating the MPM's treatment of the effect of elevation on δD_p. Next, we used a map calculator to add our interpolated regression residuals to this layer to adjust the general relationship between δD_f and δD_p by the regional variation in this relationship that we documented in our sample of raptor feathers (*sensu* Bowen and Wilkinson 2002). This produced a final map of estimated North American raptor δD_f (with 1-km^2 resolution) using the equation: $\delta D_f = 0.908 \times$ MPM $\delta D_p - 5.619$ + interpolated $\delta D_f/\delta D_p$ regression residual.

To assess the accuracy of predictions made by this map, we acquired map-based predictions of δD_f for all 264 of our original feather sampling sites and compared measured δD_f values with map-predicted δD_f values. Predicted and measured δD_f values were strongly correlated (r^2 = 0.94). The mean difference between predicted and measured δD_f values was (mean ± SD) 0.1 ± 8.2‰. Ninety-five percent of all predicted δD_f values were within 17.6‰ of measured values.

Example application: Estimating the origins of migrant Sharp-shinned Hawks.—We used breeding habitat associations and previous band-recovery information to geographically limit our estimations before estimating the origins of migrants using δD_f (Smith et al. 2004, DeLong et al. 2005). We used a GIS coverage for North American biomes (Brown et al. 1998) to eliminate a large number of areas within the breeding range of Sharp-shinned Hawks that did not have suitable breeding habitat (e.g., deserts and grasslands). Therefore, our final estimations of the origins of migrant Sharp-shinned Hawks include only forested areas where Sharp-shinned Hawks are known to breed. We applied further constraints based on Hoffman et al. (2002), who demonstrated that Sharp-shinned Hawks banded in the Intermountain West only infrequently originate from breeding areas east of the eastern front of the Rocky Mountains or west of the Sierra and Cascade ranges within the continental United States.

For each of the 173 measured δD_f values from our migrant sample, we plotted the measured value ±8‰. This incorporated our assessment of map accuracy in the description of origins of migrants. For each δD_f value on our base map, we calculated the percentage of individuals in our migrant sample whose range of estimated

δD_f values included this value, creating a relative-frequency histogram. For example, 36 of 173 migrants in our sample (21%) had ranges of estimated δD_f values that included a δD_f value of –97‰. We considered all δD_f values that included <5% of our migrant sample to represent rare sources of migrants and did not plot these values. We used natural breaks in the data to split the resulting distribution into three different categories of relative abundance (abundant: >28% or more of all samples per δD_f value; fairly common: 17–26%; and uncommon: 5–13%) that indicate the relative contribution of any predicted δD_f value on our feather map to the migrant sample. We assigned colors to each of these categories and displayed each δD_f value on our map of North American raptor δD_f with its corresponding relative-abundance color to produce a spatial histogram of the relative contribution of different source populations to our migrant sample. Thus, the relative abundance of migrants was represented spatially, without reference to the overall distribution of migrant δD_f values, and in proportion to abundance for each δD_f value on the map. This approach will work equally well for migrant δD_f samples that are normally distributed (Meehan et al. 2001) or skewed. The latter may be expected when more migrants at a given location are locally dispersing birds (DeLong et al. 2005) or when a small number of birds at a site are short-distance migrants and a larger number are long-distance migrants from farther north (e.g., Peregrine Falcons [*Falco peregrinus*] captured in the Florida Keys; HWI unpubl. data).

Results

Relationship between stable hydrogen isotope ratios in feathers and in precipitation in North American raptor feathers.—The broad geographic extent of our reference sample produced a wide range of estimated δD_p values for feather-sample locations (–13‰ to –149‰) that were well distributed along the *x*-axis of our regression model (Fig. 2). Values of δD_p in our sample are representative of the full range of δD_p values encountered across most North American raptor breeding populations. Reference samples represented a similarly wide range of altitudes, from sea level to 3,180 m. However, some geographic regions had small feather sample sizes or were missing samples (e.g., northern Quebec, Nunavut, and the southern and southeastern United States; Fig. 1). Still, the present study represents the most geographically extensive reference sample of feathers used to investigate the relationship between δD_f and δD_p for any North American bird group.

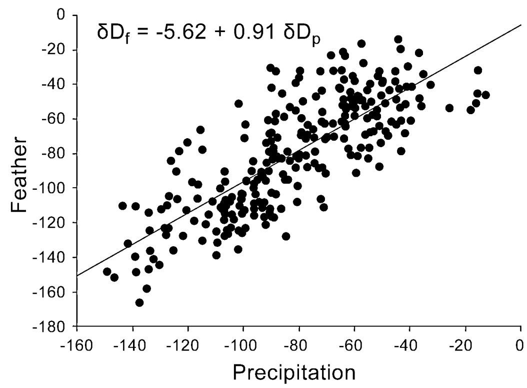

Fig. 2. Regression model showing the relationship between δD in raptor feathers (δD_f) and δD in precipitation (δD_p) across North America. The model is based on a sample of 264 raptor feathers from 12 species from 255 different locations. Estimates of δD_p are from Meehan et al. (2004).

The overall relationship between δD_f and δD_p for North American raptors was strong (F = 426.95, df = 1 and 245, $r^2 = 0.62$, $P < 0.0001$). The slope of the regression equation was 0.908, and the 95% confidence interval (CI) for the slope was slightly lower than 1 (0.82–0.99). Our regression model had a *y*-intercept of –5.6 that did not differ significantly from 0 (95% CI for the intercept: –13.1 to 1.9). Mapped residuals from the δD_f–δD_p regression showed strong patterns of regional variation, which indicates that the relationship between δD_f and estimates of δD_p may not be the same across all of North America (Fig. 3). In general, regression residuals were relatively high (indicating more positive δD_f values than expected from local δD_p) along the Pacific Coast and within the arid Southwest, and residuals were relatively low within the northern continental interior.

North American maps of estimated stable-hydrogen isotope ratios in feathers.—Several important geographic patterns in δD_f values are apparent in Figure 4. As in previous coarse maps of stable hydrogen isotopes in precipitation, δD_f values tend to decrease with both latitude and

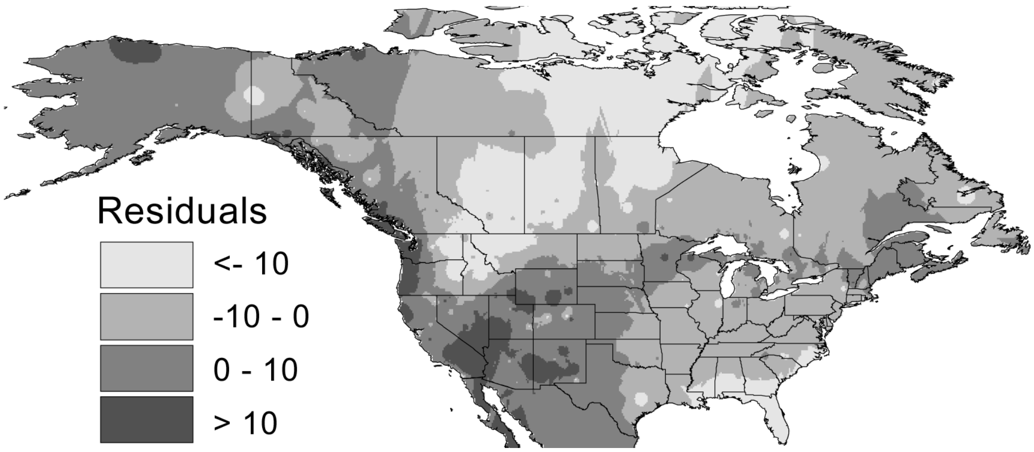

FIG. 3. Interpolated map of regional variation in the δD_f–δD_p relationship across North America. Positive residual values indicate feather samples with higher δD values than expected from local precipitation. Negative residual values indicate feather samples with lower δD values than expected from local precipitation.

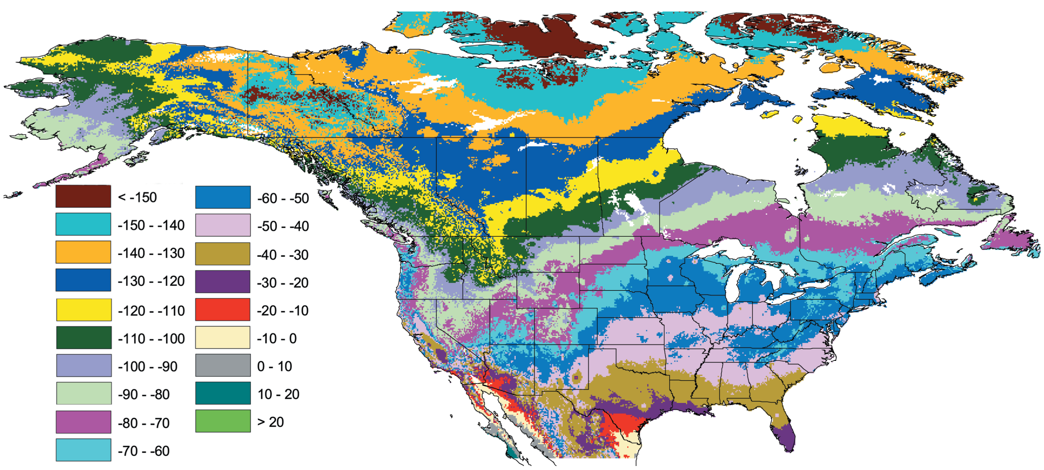

FIG. 4. Map of δD_f for North American raptors. Given standardized lab analysis, δD_f values from raptors of unknown origin captured during migration or at wintering sites can be plotted directly on the map to view their origins. In general, δD_f values decrease with increasing latitude. However, regional complexity in spatial patterns of δD_f increases in areas of topographic relief and along the Pacific coast, making interpretation of results based solely on δD_f problematic for some species, particularly in western North America. This map should be considered carefully in relation to the geographic range of a study species before sampling δD_f at migration or wintering sites to evaluate whether measurements of δD_f can clearly differentiate among potential source areas.

elevation. And as in other elevation-explicit maps of δD_p, δD_f values are more homogeneous in areas with little topographic relief (e.g., the central and eastern United States) and become increasingly complex in areas with greater topographic relief (e.g., most of the western United States and, to a lesser extent, the Appalachians and Ozarks in the east). In coastal areas (particularly within western North America), δD_f values tend to be higher than in inland areas at similar latitudes, and there is a relatively steep gradient of decreasing δD_f values moving from west to east along the Pacific Coast. Similar patterns of decreasing δD_f values between –80‰ and –130‰ occur latitudinally within the mountainous west and longitudinally in Alaska, converging at δD_f values below –130‰ in the Yukon Territory. The yellow band of δD_f values in Figure 4 (range: –110‰ to –120‰) illustrates the complexity of redundant δD_f values in the west, showing that migrants with δD_f values ranging from –110‰ to –120‰ could originate from high-elevation areas within the Rocky Mountains in Idaho and Montana, from lower-elevation mountainous areas in southern and central British Columbia, or from across the interior of Alaska.

Maps of the estimated origins of migrant Sharp-shinned Hawks.—Figure 5 displays a map and frequency histogram of the estimated origins of fall migrant Sharp-shinned Hawks sampled in the Goshute Mountains, Nevada. The δD_f value for the study site on our base map was –73‰. Estimated origins were most frequent within the range of δD_f values between –108‰ and –126‰, representing two possible major source areas for Goshute migrants: (1) the Northern Rockies from Idaho and Montana north through British Columbia, (2) the forests of interior Alaska, or both. Knowledge gained from band-recovery studies suggests that the former is the more likely source area (Hoffman et al. 2002). Estimated origins were also relatively common in areas with δD_f values between –82‰ and –107‰, representing either (1) high-elevation forests in Central Idaho, eastern Oregon, and eastern Washington; (2) forested areas of central and western Alaska; or (3) coastal forests of western British Columbia. Few migrant Sharp-shinned Hawks seemed to originate from forests near the migration banding site in Nevada or from areas to the far north within the western breeding range of Sharp-shinned Hawks in the Yukon Territory.

Discussion

Relationship between stable hydrogen isotope ratios in feathers and in precipitation in North American raptors.—As in previous stable hydrogen isotope studies, we found a strong relationship between raptor δD_f and δD_p across

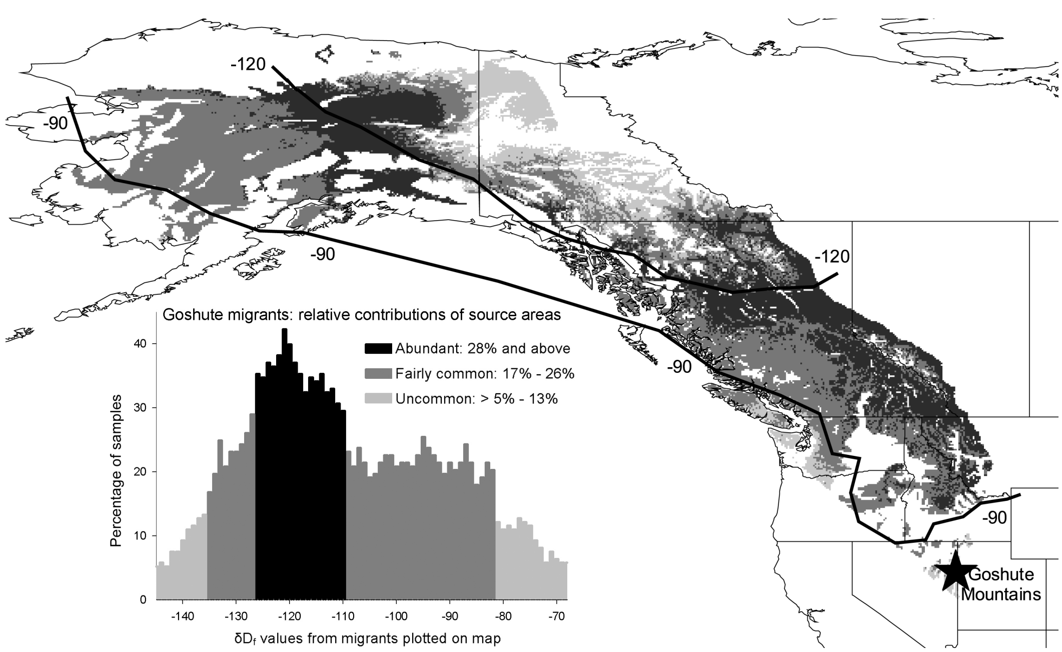

Fig. 5. Estimated origins of Sharp-shinned Hawks captured during fall migration in the Goshute Mountains, Nevada (star). Darker colors indicate δD_f values that contribute larger numbers of birds to the migrant sample. Black lines follow generalized contours of δD_f values from our base map of North American raptor δD_f.

North America using a large sample of raptor feathers from 12 species. The regression equation describing this relationship differed from regression equations in previous studies with passerines (Hobson and Wassenaar 1997, Wassenaar and Hobson 2000, Hobson et al. 2001, Bowen et al. 2005) and raptors (Meehan et al. 2001, DeLong et al. 2005). We believe that comparative biological interpretations of regression equations in stable-isotope studies should proceed cautiously at this point, because regression equations may differ among studies for many reasons. We propose three nonexclusive hypotheses to explain differences in regression equations among studies, all of which need further testing.

First, differences may be attributable to a lack of standardization among studies, both in lab methods for measuring δD_f and in the choice of models used for estimating δD_p for feather-collection sites. Our repeat analyses question the comparability of results among studies conducted during different periods within the same lab, and questions remain about the comparability of results from different labs. Although the virtual equilibration of feather samples with keratin standards is theoretically promising (Wassenaar and Hobson 2003), more empirical data from repeat measurements of feather samples among seasons within the same lab and among labs are necessary to address the comparability of results among studies. In addition, previous studies have used a number of different δD_p models (Hobson and Wassenaar 1997, revised in Wassenaar and Hobson 2000; Meehan et al. 2004; Bowen et al. 2005) to estimate δD_p for feather-collection sites, and systematic differences among these models may affect regression equations.

Second, differences in regression equations among studies may be attributable to ecophysiological differences among avian taxa. This should be addressed experimentally or by field studies that compare δD_f among a number of species representing different ecological groupings and trophic positions within the same study area. Complementary local sampling of δD in precipitation, plant material, and important prey items for each species would help to explain taxonomic differences in the relationship between δD_f and δD_p if they exist. All samples should be analyzed in the same lab at the same time to control for possible lab-related variation when making these comparisons.

Finally, differences in regression equations among studies may be attributable to regional differences, as shown here, in the δD_f and δD_p relationship. Our reference sample included more samples from the Pacific Coast and the southwestern United States than previous studies. Unlike samples from interior or eastern locations, feathers from these regions tend to be more enriched in deuterium in relation to local precipitation. Thus, the wider spatial distribution of samples in the present study (compared with earlier studies that focused on eastern or central North America) could be responsible for the more positive intercepts observed for our reference sample. Until the consistency of the δD_f and δD_p relationship among taxa is clarified, the maps of estimated δD_f produced here should be used only for studies involving migrant raptors. Similarly, until the comparability of δD_f measurements among studies and labs is confirmed with empirical data, unknown-origin samples will have to be standardized for use with our base map by reanalyzing a subset of the feathers that were used to create the map. These feathers can be obtained by request from HWI.

Regional variation in the relationship between isotope ratios in feathers and in precipitation.—This is the first study to demonstrate regional variation in the relationship between δD_f and δD_p. Feather samples from the arid Southwest and the Pacific Coast had consistently higher δD_f–δD_p regression residuals compared with other areas of North America. Residuals were also relatively low in the northern continental interior. These regional patterns may be the result of regional anomalies in the δD_p model used to estimate δD_p for feather-sample locations or differences in plant or avian ecophysiology in these regions. Wolf and Martínez del Rio (2000) found that the body-water pool of White-winged Doves (*Zenaida asiatica*) in the southwest was ~20‰ enriched compared with local source moisture, and McKechnie et al. (2004) found that this enrichment may be attributable to the preferential evaporation of light isotopes during evaporative cooling in hot and arid environments. This physiological factor may contribute to relatively enriched values for δD_f in arid regions. Sternberg et al. (1984) showed that δD values in desert plants with the CAM photosynthetic pathway tended to be more enriched in relation to local precipitation than C_3 or C_4 plants. Thus, more enriched δD_f values in the Southwest may reflect the higher proportion of CAM plants in this region.

High residual values along the Pacific Coast and low residual values within the continental interior may be the result of the δD_p model not fully accounting for the isotopic depletion of Pacific air masses as they move across the continent from west to east (Yonge et al. 1989, Rozanski et al. 1993). The MPM is based on generalized relationships between temperature, altitude, and δD_p across all of North America. This model accounts for regional deviations from these large-scale relationships in the same way that we have in the present study, by adjusting estimated δD_p values by interpolated model residuals from nearby δD_p sampling stations (Meehan et al. 2004). However, there are less than five of these stations along the Pacific Coast, which potentially limits the ability of this step to account for this potentially strong effect. Alternatively, there may be regional aspects of plant or avian ecophysiology along the Pacific Coast that led to relatively enriched environmental signals for δD that are reflected in the feathers of birds. Another possibility may be that growing-season estimates of δD_p for this region do not accurately reflect local δD_p during the exact period when juvenile raptor feathers are being grown (Smith and Dufty 2005). Although at this point unexplained, the relationship between δD_f and estimated δD_p along the Pacific Coast is very different from this same relationship inland. Increased sampling for both δD_f and δD_p along transects from the Pacific Coast inland at different latitudes would help to improve models of δD_f and δD_p in western North America.

Plotting migrant distributions on geographic-information-system base maps of stable hydrogen isotope ratios in feathers.—For the present study, we gave an example of one possible approach to plotting the origins of migrants on our base map of δD_f using Sharp-shinned Hawks sampled on migration in the Goshute Mountains of Nevada. We see this as a heuristic exercise to demonstrate the value of a δD_f base map and the power of GIS approaches. Together, they allow for spatially explicit estimations of the origins of migrants based on multiple criteria, including measurements of δD_f, habitat associations, and geographically defined "flyway" boundaries. We view the development of more robust approaches for plotting migrant distributions on such base maps as an important area for future research. Until methods are developed to truly address the error inherent in this approach, and additional validations of the base map are made by independent data sets, estimations of the origins of migrants using this approach should be viewed as preliminary, particularly in studies with small migrant-population sample sizes.

This GIS-based approach could be extended to include additional data for other intrinsic markers that display geographic variation, such as morphology, genetics, or other stable isotopes such as carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$). It is critical to realize, however, that this will be the case only if these data can be accurately mapped at the appropriate spatial scale to improve our ability to estimate the origins of migrants (e.g., the entire range of possible source origins of a migrant population). Given the spatial heterogeneity of δD, $\delta^{13}C$, and $\delta^{15}N$ across the breeding range of most migratory species, continuous and spatially explicit predictive surfaces for stable-isotope distributions (such as the model of North American raptor δD_f produced here) may produce more accurate descriptions of the origins of migrants than discrete site-classification models that assign samples to only a small number of potential source populations, not the entire range of populations that could be contributing to a migrant sample (Wassenaar and Hobson 2000, Farmer et al. 2003, Hebert and Wassenaar 2005). Classification models assume clinal variation in areas between sampled reference populations. This assumption is likely untenable for stable carbon and nitrogen isotopes, which vary tremendously at local or regional scales because of both natural and anthropogenic effects (Kelly 2000, Hebert and Wassenaar 2001, Dawson et al. 2002, Graves et al. 2002, Cerling et al. 2004), and is not valid for stable hydrogen isotopes in areas with large topographic relief, where δD_p may vary between sampling sites because of the effect of elevation (Bowen and Wilkinson 2002, Meehan et al. 2004).

Our study and previous studies of large-scale patterns in δD_p demonstrate that geographic variation in δD can be mapped at the relevant physical scale of the entire range of potential source areas for migrant populations, primarily because of the detailed understanding of the effects of environmental and physical parameters (such as temperature and elevation) on the geographic distribution of δD (Dansgard 1964, Rozanski et al. 1993). A similarly mechanistic understanding has not been developed to describe geographic variation in other stable isotopes. To assess whether additional intrinsic markers will be helpful in delineating the origins of migrants, much more geographically widespread sampling is necessary to accurately map variation in these parameters at the relevant spatial scale for their use in estimating the origins of migrants (Webster et al. 2002, Rubenstein and Hobson 2004). Of particular interest would be the discovery of any other marker that could help to discriminate among regions where δD_f values are redundant (e.g., interior Alaska and the southern Rocky Mountains).

A plea for standardization of methods and for increased comparative studies.—North American growing-season δD_p models have evolved rapidly during the brief history of the use of stable- hydrogen isotopes to track animal movements (Hobson and Wassenaar 1997, Meehan et al. 2004, Bowen et al. 2005). Large-scale models of δD_p will most likely continue to evolve as the spatial coverage of δD_p sampling stations from which models are built increases (Welker 2000). To avoid confusion in future comparative studies, care should be taken to clearly state which δD_p model was used for deriving δD_p estimates, and comparative studies should use the same models for δD_p estimates for feather-collection sites. As δD_p models are revised, δD_f data from reference population samples could also serve as independent data sets to compare δD_p models (Meehan et al. 2004). In addition, we emphasize, as have others, that for direct comparisons among studies, careful attention must be paid to standardization of δD_f measurements (Wassenaar and Hobson 2003). We are skeptical that current lab methodologies produce comparable results among studies both within and among labs.

Only by comparing and eventually pooling standardized results across numerous studies involving different taxa and regions will we be able to arrive at the sample sizes and geographic coverage that will be necessary to understand continental patterns in δD_f. To this effect, we view our base map of δD_f as a work-in-progress to be improved upon by others as sample sizes grow for standardized measurements of δD_f for more species and more regions, and as additional maps are created of geographic patterns in δD_p. For the sake of future comparative studies, all sample data from the present study, including δD_f values and sample locations, are released for general use on the HWI website (see Acknowledgments), and we encourage other investigators to do the same. Using the methods outlined here, and web-available δD_f and δD_p data, more accurate maps of δD_f can be created as future studies collect additional samples in areas where this study had poor geographic or taxonomic representation.

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