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RESEARCH ARTICLE

Stable hydrogen isotopes identify leapfrog migration, degree of connectivity, and summer distribution of Golden Eagles in eastern North America

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ABSTRACT

Knowledge of the distribution and movements of populations of migratory birds is useful for the effective conservation and management of biodiversity. However, such information is often unavailable because of the difficulty of tracking sufficient numbers of individuals. We used more easily obtained feather stable hydrogen isotope ratios (δ^2H) to predict the summer grounds of the small, threatened, and migratory population of Golden Eagles (*Aquila chrysaetos*) in eastern North America. We then identified summer locations and the extent of migratory connectivity for this population. We collected δ^2H (δ^2H_f), stable carbon isotope (δ^{13}C), and stable nitrogen isotope (δ^{15}N) data from the body feathers of 47 juvenile, subadult, and adult Golden Eagles. Values of δ^{13}C and δ^{15}N suggested that all but 2 birds obtained food from terrestrial-based food webs and therefore that δ^2H data were appropriate for inferring the geographic region of molt for the majority of birds. There was relatively large interfeather variation in the δ^2H values of subadults vs. adults, suggesting that these groups molted at different times and places. The most negative δ^2H_f values from birds with known summering grounds exhibited (1) a negative correlation with their summering latitude, and (2) a positive correlation with amount-weighted δ^2H values of May–August precipitation at the summer location. These data validate the use of δ^2H_f values for inferring the summer locations of Golden Eagles of unknown origin. Likelihood-of-origin maps derived from δ^2H_f values revealed that (1) the majority of birds spent the breeding season in central Québec and Labrador, and (2) birds that wintered at southern latitudes, from approximately northern Alabama to southwestern Virginia, migrated about twice the distance of birds that wintered at northern latitudes, from Pennsylvania to New York. We observed a positive relationship between δ^2H_f values and the latitude of the wintering location, which, along with the likelihood-of-origin maps, revealed moderate patterns of leapfrog migration and migratory connectivity.

Keywords: Golden Eagle, North America, migration, stable isotopes, telemetry

Des isotopes stables de l'hydrogène dévoilent une migration de type saute-mouton, le degré de connectivité et la répartition estivale d'*Aquila chrysaetos* dans l'est de l'Amérique du Nord

RÉSUMÉ

La connaissance de la répartition et des déplacements des populations d'oiseaux migrateurs est utile pour assurer l'efficacité de la conservation et de la gestion de la biodiversité. Toutefois, de telles informations sont souvent non disponibles en raison de la difficulté de suivre un nombre suffisant d'individus. Nous avons utilisé des ratios d'isotopes stables de l'hydrogène (δ^2H) du plumage plus faciles à obtenir afin de prédire l'aire d'été réelle de la petite population menacée et migratrice d'*Aquila chrysaetos* dans l'est de l'Amérique du Nord. Nous avons ensuite identifié les localisations estivales et l'étendue de la connectivité migratoire pour cette population. Nous avons récolté des données de δ^2H (δ^2H_f), d'isotopes stables de carbone (δ^{13}C) et d'isotopes stables d'azote (δ^{15}N) à partir des plumes de corps de 47 juvéniles, immatures et adultes d'*A. chrysaetos*. Des valeurs de δ^{13}C et δ^{15}N ont suggéré que tous les oiseaux, sauf deux, se sont procurés de la nourriture dans les réseaux trophiques terrestres; elles étaient donc appropriées pour inférer la région géographique de la mue avec les données de δ^2H. Il y avait une variation inter-plumes relativement grande dans les valeurs de δ^2H des immatures et des adultes, ce qui suggère qu'ils muent à

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différents moments et endroits. Les valeurs les plus négatives de δ^2H_f des oiseaux dont on connaissait l'aire d'été présentaient (1) une corrélation négative avec la latitude d'estivage et (2) une corrélation positive avec les valeurs de δ^2H pondérées pour les précipitations de mai à août sur l'aire d'été. Ces données valident l'utilisation de valeurs de δ^2H_f pour inférer les aires d'été des individus dont on ne connaît pas l'origine. Des cartes de possibilité d'origine provenant des valeurs de δ^2H_f ont révélé que (1) la majorité des oiseaux ont passé la saison de reproduction dans le centre du Québec et le Labrador et (2) les oiseaux qui ont passé l'hiver à des latitudes plus méridionales, approximativement du nord de l'Alabama au sud-ouest de la Virginia, migrent près de deux fois la distance parcourue par les oiseaux qui hivernent à des latitudes plus nordiques, de la Pennsylvanie à New York. Nous avons observé une relation positive entre les valeurs de δ^2H_f et la latitude de l'aire d'hivernage qui, avec les cartes de possibilité d'origine, a révélé des patrons modérés de migration en saute-mouton et de connectivité migratoire.

Mots-clés: Aquila chrysaetos, Amérique du Nord, migration, isotopes stables, télémétrie

INTRODUCTION

Knowledge of the distribution of migratory animals throughout their annual cycle is critical to identifying the ecological and evolutionary processes that shape their population dynamics, as well as to developing effective conservation measures (e.g., Bauer and Hoye 2014). For example, the location and quality of habitat that migratory birds occupy during winter can profoundly affect their fitness and fecundity during the summer breeding season (e.g., Norris et al. 2004) and may have important demographic consequences (e.g., Harrison et al. 2013). Migratory connectivity, the degree to which individuals from the same breeding area migrate to the same wintering area (Webster et al. 2002), however, remains difficult to assess for many bird species because of challenges associated with tracking sufficient numbers of individuals for population-level inference. Remote telemetry systems provide precise details on year-round location (e.g., Miller et al. 2014), but the devices are costly and often challenging to deploy. Similarly, mark–recapture and light-level geolocation approaches can provide insights into migratory connectivity (e.g., Fort et al. 2012, Stanley et al. 2015), but suffer from low recapture rates for many species (e.g., Bridge et al. 2013).

Stable hydrogen isotope ratios (δ^2H) help to overcome many of these challenges and have thus become an important tool for inferring the geographic origins of migratory wildlife (e.g., Hobson 1999, Bowen et al. 2005), including patterns of avian migratory connectivity (e.g., Kelly et al. 2002, Clegg et al. 2003, Smith et al. 2003, Paxton et al. 2007, Hobson et al. 2014, Rushing et al. 2014). The basis of this approach is that the δ^2H values in animal tissues are derived from the δ^2H values of drinking water and diet. The δ^2H values of water and diet originate from the δ^2H values of precipitation (δ^2H_p), which exhibit pronounced continental-scale gradients, with lower values at higher latitudes and elevations (Bowen 2010). The relationship between the δ^2H values of precipitation and animal tissue is modified by environmental and biosynthetic isotopic discrimination. Positive relationships between the δ^2H values of feather keratin (δ^2H_f) and amount-weighted growing-season precipitation δ^2H_p values in multispecies avian datasets suggest that isotopic discrimination predictably influences δ^2H_f values across species, age classes, and years of collection (e.g., Bowen et al. 2005, Lott and Smith 2006, van Dijk et al. 2014). However, intra- and interspecific variation in such relationships can also limit δ^2H-based inferences of origin (e.g., Smith and Dufty 2005, Hobson et al. 2012, De Ruyck et al. 2013, Hallworth et al. 2013).

Eagles (Accipitridae) have immense cultural and ecological significance worldwide (Tingay and Katzner 2010, Watson 2010). In eastern North America there is a small ($n \cong 5{,}000$) population of migratory Golden Eagles (*Aquila chrysaetos*; Katzner et al. 2012a, Dennhardt et al. 2015). These migrants breed in remote areas of eastern Canada, winter in the United States east of the Mississippi River, and are geographically distinct from the much larger population of Golden Eagles in the western United States (Kochert et al. 2002, Nielson et al. 2014; Figure 1). Federal, state, and provincial regulations have long afforded Golden Eagles strong protection in the United States and Canada. Nevertheless, decision-makers are increasingly concerned about eastern Golden Eagles because of their small population size and potential susceptibility to threats (Katzner et al. 2012a). Adult Golden Eagles are known to exhibit interyear fidelity to particular summer and winter regions (Brodeur et al. 1996), but it is unknown whether adults from similar breeding locations migrate to geographically similar or distinct winter locations. For example, despite nearly a century of mark–recapture efforts, only 1 of the 1,144 encounter records for Golden Eagles in the U.S. Geological Survey's Bird Banding Laboratory dataset from 1926 to 2013 is suitable for assessing migratory connectivity of eastern Golden Eagles.

To our knowledge, no prior published isotopic studies of Golden Eagles exist. Thus, it is uncertain how well δ^2H_f values may record the geographic origins of these birds. Several considerations need to be evaluated before using isotopic data to infer eagle movements. First, it is not known whether the positive relationship that exists between δ^2H_f and δ^2H_p values for nestlings of 12 species of raptors of known origin from throughout North

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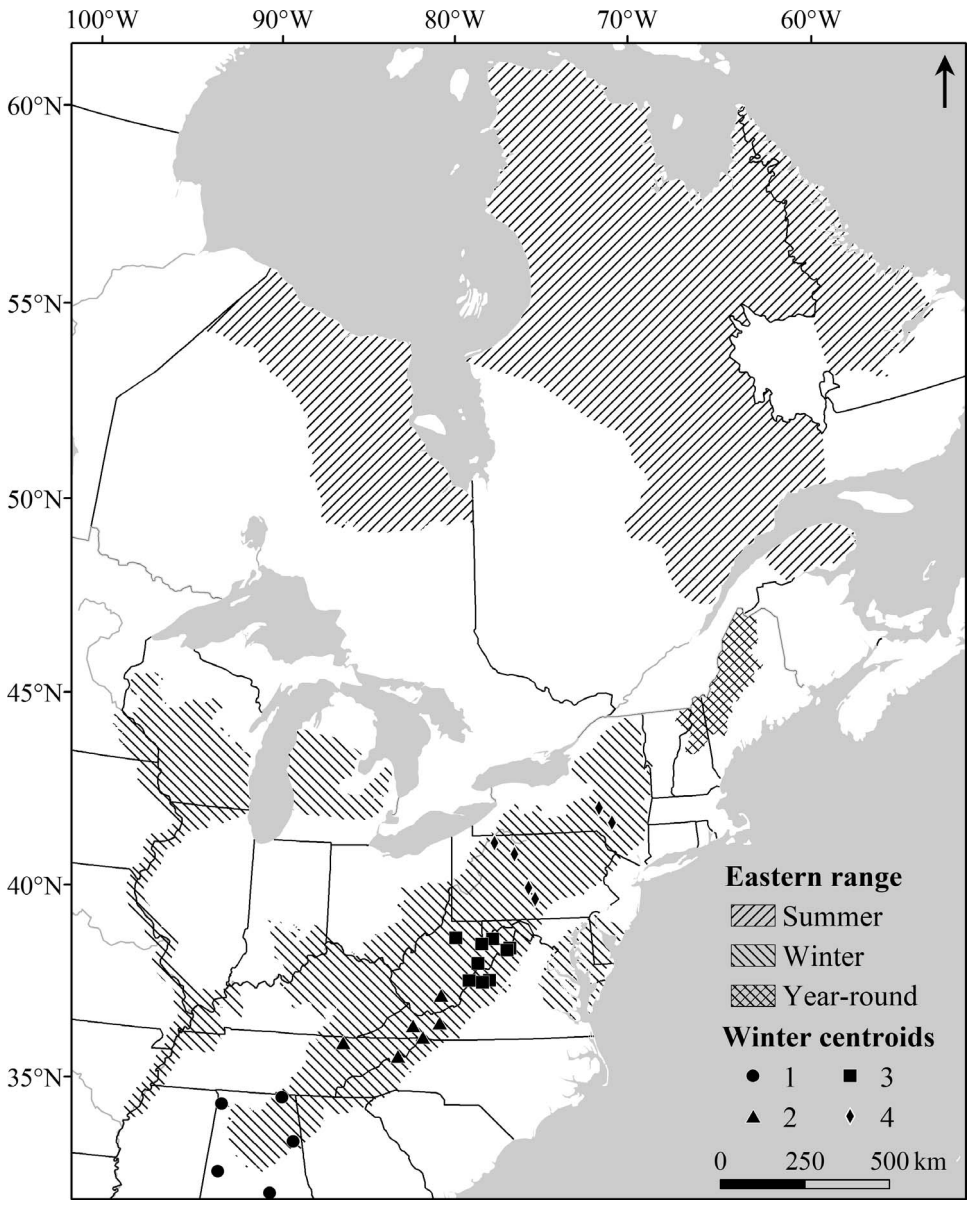


FIGURE 1. Range of Golden Eagles in eastern North America (Kochert et al. 2002, Wheeler 2007, Cadman et al. 2009, Katzner et al. 2012a, Morneau et al. 2015), along with the locations of the individuals from the 4 winter populations that were sampled for connectivity analyses. Note that some symbols represent the location of multiple birds.

America (Lott and Smith 2006) is appropriate for the conversion of δ^2H_f to δ^2H_p values for (1) nonnestling raptors and (2) eastern Golden Eagles. Second, the complex patterns of feather replacement by Golden Eagles could complicate the use of δ^2H_f for inferring geographic origin. Unlike smaller birds that molt once per year, usually following breeding, larger birds, such as Golden Eagles, molt their entire complement of feathers over the course of several years (Pyle 1997, Rohwer et al. 2009). Molting by Golden Eagles is thought to be more common during the summer breeding season, but it can occur at other times of the year (Jollie 1947, Bloom and Clark 2001). If correct, this suggests that δ^2H data from a single feather may not be indicative of the summering location of a bird. Furthermore, substantial variation in δ^2H values has been observed along the length of flight feathers from Bald Eagles (*Haliaeetus leucocephalus*), probably because the growth of flight feathers occurs over several weeks (Wassenaar 2008). Thus, flight feathers of Golden Eagles are likely to show considerable variation in isotopic values even within the same individual.

Factors such as intraspecific competition, time and energy costs associated with movement, gradients in habitat quality, and historical or genetic constraints are

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often invoked to explain patterns of strong migratory connectivity between the wintering and summering grounds of birds (Alerstam et al. 2003). However, there is insufficient understanding of the biology and ecology of Golden Eagles with which to make such specific hypotheses. Regardless of cause, an understanding of the summer locations and migration patterns of Golden Eagles has conservation implications. If migratory connectivity is strong, then eastern Golden Eagles from distinct breeding areas will be seasonally linked to distinct wintering regions. Strong connectivity would suggest that Golden Eagles have small, vulnerable subpopulations with limited ability to adapt to environmental changes (e.g., Both and Visser 2001). In contrast, if migratory connectivity is weak (i.e. populations are well mixed between their summer and winter regions), then any impacts of environmental change will spread throughout the population (e.g., Webster et al. 2002). We obtained $\delta^{13}C$, $\delta^{15}N$, and $\delta^{2}H$ values from the feathers of live-captured and museum specimen Golden Eagles to: (1) assess the potential of using these data to identify the summer locations of eastern Golden Eagles; (2) identify the summer locations used by Golden Eagles in eastern Canada; and (3) determine the degree of migratory connectivity.

METHODS

Capture of Live Birds, Deployment of Telemetry Units, and Feather Collection

Golden Eagles were trapped from November to March between 2006 and 2014, from Alabama to New York, USA, with cannon nets on wintering grounds or with a bow net while on migration (Bloom et al. 2007; Supplementary Material Table S1, Figure 1). Each bird was outfitted with a solar-recharged 45 g or 100 g ARGOS-GPS (Microwave Telemetry, Columbia, Maryland, USA) or 70 g or 95 g GPS–GSM (Cellular Tracking Technologies, Somerset, Pennsylvania, USA) telemetry unit with a Teflon ribbon (Bally Ribbon Mills, Bally, Pennsylvania, USA) harness in a backpack style (Fuller et al. 2005). Units weighed <3% of bird body mass. GSM units stored data collected outside GSM coverage and only transmitted data when birds were within GSM coverage (at latitudes lower than ~50°N). The age of each bird was determined using molt patterns (McCollough 1989, Bloom and Clark 2001), and birds were characterized as juvenile (first or second year of life; HY or 2Y), subadult (third or fourth year of life; 3Y or 4Y), or adult (older than fourth year of life; >4Y). The sex of each bird was determined genetically (Fridolfsson and Ellegren 1999). Prior to release we collected body feathers from each bird for isotopic analysis. We obtained between 3 and 7 body feathers for 14 birds, 2 body feathers for 28 birds, and a single body feather from 2 birds. We primarily analyzed body feathers because they are relatively small and thus likely to grow more quickly, and are therefore less likely to reflect temporal and spatial variation in isotopic values than flight feathers. However, on 3 occasions we collected <0.5 cm^2 clippings from near the proximal end of in-sheath (i.e. actively growing) feathers obtained on the wintering grounds, as a reference for wintering $\delta^{2}H_f$ values (Edelstam 1984).

The telemetry units collected GPS data at regular (30 s to 2 hr) intervals. We defined migration periods as occurring when birds initiated continuous north- or southbound movements along the primary axis of migration (Miller 2012); all other data were either from summer or winter grounds. We categorized the telemetry data for each bird into seasons and then calculated the centroid of the winter and summer grounds using the Spatial Analyst tool Zonal Geometry (ArcGIS 10.1; ESRI, Redlands, California, USA). We obtained centroids for birds with at least 20 days of telemetry locations from each season. We had fewer summer centroids because GSM units only transmitted data when birds were within GSM coverage. Thus, if birds died or units failed before data retrieval we could not calculate summer centroids for those birds. Also, several birds were captured during northbound migration from unknown wintering grounds (Supplementary Material Table S1). We were able to calculate winter centroids for less than half of the birds. However, because the latitudes and longitudes of the winter centroids were strongly positively correlated with trapping locations for birds captured during winter (r = 0.93 and 0.97, respectively), we used the latitude and longitude of trapping locations when assigning birds to winter populations (see below). There were sufficient telemetry data to identify the summer grounds for 6 juvenile, 7 subadult, and 7 adult birds (Supplementary Material Table S1), but only adults were inferred to have established territories based on their restricted summer movements.

Sampling of Museum Specimens

To increase our sample sizes, we obtained single body feathers from 3 specimens of eastern Golden Eagles housed in the Division of Birds collection at the Smithsonian Museum of Natural History. The age of each bird was determined as above for the live birds. We used collection date and age to infer information about summer or winter location of each bird (Supplementary Material Table S1).

Isotopic and Geospatial Analysis

Between 2 and 3 subsamples were cut along the length (from tip to base) of each feather (Wassenaar and Hobson 2006). These subsamples were cleaned and dried as in Coplen and Qi (2012). Approximately 1 mg of each cleaned subsample of feather was analyzed for $\delta^{13}C$ and

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$\delta^{15}N$ values using a Carlo Erba NC2500 elemental analyzer (CE Instruments, Milano, Italy) interfaced with a ThermoFinnigan Delta V+ isotope ratio mass spectrometer (IRMS; ThermoFisher Scientific, Bremen, Germany) at the Central Appalachians Stable Isotope Facility (CASIF) at the Appalachian Laboratory (Frostburg, Maryland, USA). The $\delta^{13}C$ and $\delta^{15}N$ data were normalized to VPDB and AIR, respectively, using a 2-point normalization curve with internal standards calibrated against USGS40 and USGS41. The among-run analytical precision (1σ) of an internal keratin standard (porcine hair and skin; product K3030, Spectrum Chemical Manufacturing Corporation, New Brunswick, New Jersey, USA) analyzed alongside these samples was 0.11‰ for both $\delta^{13}C$ and $\delta^{15}N$.

We measured δ^2H values of nonexchangeable hydrogen in feather keratin using a comparative equilibration approach (Wassenaar and Hobson 2003). Approximately 0.2 mg of each cleaned subsample, as well as international standards (USGS42 and USGS43; Coplen and Qi 2012) and the internal keratin standard, was exposed to ambient air for >72 hr for equilibration of exchangeable hydrogen in keratin (Wassenaar and Hobson 2003). Samples were then placed in a zero-blank autosampler (Costech Analytical, Valencia, California, USA) and analyzed for δ^2H values using a ThermoFinnigan high temperature conversion elemental analyzer interfaced with a ThermoFinnigan Delta V+ IRMS at CASIF. The δ^2H data were normalized to VSMOW-SLAP using a 2-point normalization curve with USGS42 and USGS43 (Coplen and Qi 2012), whose δ^2H values of nonexchangeable hydrogen are –78.5‰ and –50.3‰, respectively. The long-term analytical precision (1σ) of these standards at CASIF is 2.1‰ and 2.0‰, respectively. Our δ^2H_f values spanned a larger range (–165.5‰ to –25.7‰) than do USGS42 and USGS43, but prior studies suggest that linear extrapolation of normalization relationships for δ^2H values has minimal influence on values within ~100‰ of the range of the standards used for normalization (Kelly et al. 2009, Wiley et al. 2012). The long-term accepted δ^2H value of the internal keratin standard at CASIF is –59.5 ± 2.3‰.

Prior studies have used δ^2H values of growing-season precipitation or mean annual precipitation when developing transfer functions between δ^2H_f and δ^2H_p values for geospatial analysis (Bowen et al. 2005, Hobson 2011). However, the specific months of precipitation that most strongly influence the food webs supporting many birds (Hobson et al. 2012), including Golden Eagles, are unknown. The growing season in central–northern Quebec is approximately May–October, as based on monthly temperature data for the regions of Baie-James, Inukjuak, Kuujuak, Kuujuarapik, and Schefferville (http://www.climat-quebec.qc.ca/home.php?id=norm_entab&mpn=stats), and nearly two-thirds of annual precipitation falls during this period. Furthermore, although we do not expect a 1:1 relationship between the time of precipitation and feather formation, the period of time that molt by Golden Eagles is thought to be most common is May–August. Thus, we developed geostatistical models and maps of May–August, May–October, and mean annual δ^2H_p values for North America using the online workspace IsoMAP (Bowen et al. 2014). We used elevation, latitude, and latitude^2 as independent variables in the models, since these factors strongly influence δ^2H values of precipitation in North America (Bowen 2010). We did not include precipitation amount or longitude as independent variables in the models because they are not thought to have a large influence on spatial patterns of δ^2H_p values in North America (Bowen 2010) and because they did not contribute significantly to our models in initial tests (data not shown). We extracted δ^2H_p values from these isoscapes for the 8 adult Golden Eagles in our dataset with known summering grounds (7 individuals fitted with telemetry units, 1 museum specimen; Supplementary Material Table S1). During initial analyses we found strong positive relationships between May–August and May–October δ^2H_p values ($r^2 = 0.83$), May–August and annual δ^2H_p values ($r^2 = 0.99$), and May–October and annual δ^2H_p values ($r^2 = 0.88$), and insignificant differences in the strength of the relationships between minimum δ^2H_f values and May–August ($r^2 = 0.45$), May–October ($r^2 = 0.46$), and mean annual δ^2H_p values ($r^2 = 0.47$) for the 8 adult Golden Eagles with known summering grounds. The model and corresponding map for our May–August δ^2H_p isoscape, which we chose to use for all additional analyses, are available as jobs 41698 and 41700 at www.isomap.org, and the model summary is presented in Supplementary Material Table S2. We also extracted δ^2H_p values from the May–August isoscape for raptors of known origin ($n = 264$) for which δ^2H_f data are available (Lott and Smith 2006), as described below.

We tested the ability of δ^2H_f-based assignments to accurately record the summer grounds of eastern Golden Eagles of unknown origin using data from 8 adult birds with known summer grounds (Supplemental Material Table S1). Because the feathers collected in the present study were obtained when the telemetry units were first deployed, the δ^2H_f data provide information on where the bird was during the summer prior to capture (assuming that feathers form during the summer; see Discussion), whereas telemetry data provide location information after the time of capture. Therefore, we used adults because they establish distinct summer territories to which they return each year, whereas subadults exhibit less summer site fidelity within and between years (Miller 2012). For the 8 adults with known summer grounds, we used reduced major axis (RMA) regression to assess the relationships between their minimum δ^2H_f values and (1) the latitude of their known summering grounds, and (2) the δ^2H_p values

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of their summering grounds, as extracted from the May–August isoscape. We chose to use RMA regression because of symmetry between the dependent and independent variables (Smith 2009) and because both variables contain measurement uncertainty (McArdle 1988).

We also used RMA regression to determine the relationship between δ^2H_f and May–August δ^2H_p values for the 264 raptors of known origin in Lott and Smith (2006). The equation of the regression between δ^2H_f and δ^2H_p was: $\delta^2H_f = 1.13(\delta^2H_p) + 11.15$ ($n = 264$, $r^2 = 0.65$, $P < 0.001$). To prepare the δ^2H_f values of Golden Eagles for analysis in IsoMAP, they were rescaled to δ^2H_p by rearranging the previous equation. We used the IsoMAP assignment tool, which is based on a Bayesian probabilistic framework, to map the likelihood-of-geographic-origin for feather δ^2H_p values. These likelihood-of-origin maps are continuous probability surfaces. The standard deviation of δ^2H_p values used for these assignments was set at 22‰, which is the standard deviation of the residuals of δ^2H_p values in the previous equation relating δ^2H_f and δ^2H_p values for raptors of known origin (Lott and Smith 2006).

IsoMAP-based assignments span a longitudinal gradient across North America, but the summer nesting territories of eastern Golden Eagles are restricted to eastern Canada. Thus, we eliminated regions of biologically implausible origin by overlaying the approximate summer and year-round distribution of eastern Golden Eagles (Kochert et al. 2002, Wheeler 2007, Cadman et al. 2009, Katzner et al. 2012a, Morneau et al. 2015; Figure 1) on a likelihood-of-origin map of North America for each bird. We calculated the probability of origin (with contours set from 0.1 to 0.9 at intervals of 0.1) for each likelihood-of-origin map using the Geospatial Modelling Environment (http://www.spatialecology.com/gme/), with each contour interval ("isopleth") corresponding to a given percentage of pixels likely to contain the location of origin for an individual. For each of our 8 validation birds, we recorded the minimum isopleth contour that contained the centroid of the summering location. As a measure of the accuracy of our assignments, we then calculated the distances (direct, latitudinal, and longitudinal) between the centroid of the summering location and the centroid of the minimum isopleth contour that contained the summering location for all of the 8 validation birds. All pixels within this selected isopleth for each bird were reclassified as 1 (likely origin), and those outside as 0 (unlikely origin). We used the centroid of the likely region-of-origin for each bird as the isotope-inferred summering location of each bird. To visualize patterns of migratory connectivity, we stacked and summed each of the reclassified maps of likely summering regions for birds from each of 4 winter populations or groups (Figure 1). Statistical analyses were performed in PAST (Hammer et al. 2001).

RESULTS

Intra- and Interfeather Isotopic Variation

Average $\delta^{13}C$, $\delta^{15}N$, and δ^2H values for the 42 Golden Eagles from which 2 or more feathers were obtained varied between –23.6 and –18.8‰, 4.7 and 13.2‰, and –161.4 and –25.7‰, respectively (Figure 2 and Supplementary Material Figure S1). The average isotopic variation for $\delta^{13}C$ and $\delta^{15}N$ values between multiple feathers from the same bird (i.e. interfeather variation) was slightly larger than the average isotopic variation within feathers from the same bird (i.e. intrafeather variation; standard deviation = 0.52‰ and 0.60‰ vs. 0.39‰ and 0.44‰, respectively), whereas the average interfeather variation in δ^2H_f values (standard deviation = 16.4‰) was more than double the average intrafeather variation in δ^2H_f values (standard deviation = 7.9‰; Figure 2, Supplementary Material Figures S1 and S2). Interfeather variation in δ^2H values was smaller for the juvenile birds (captured during their first winter) than for the older birds (Figure 2). For example, the average of the standard deviation of δ^2H_f values among juveniles was 7.5‰, but it was 20.2‰ and 17.4‰ for subadults and adults, respectively. However, some of the older birds (e.g., 13D2700) displayed relatively little interfeather variation in δ^2H_f (Supplementary Material Figure S2). The δ^2H values of clips from near the proximal end of in-sheath feathers from birds captured on their wintering grounds were –34.2‰ and –40.3‰ for 2 birds from Alabama and –61.9‰ for a bird from northeastern West Virginia (Supplementary Material Figure S2).

Linking Isotope and Location Data to Assign Summer Locations

Northern latitudes generally have more negative δ^2H_p values than do southern latitudes. Given this, and the relatively large intrabird variability in δ^2H_f values for subadult and adult birds, we expected that the smallest δ^2H_f value (as well as the corresponding δ^2H_p value derived from the δ^2H_f value) from each bird would most accurately record its most northerly (i.e. summer) location. We determined how well δ^2H-based assignments recorded the summer grounds of 8 adult Golden Eagles with known breeding territories using the minimum δ^2H_f value obtained from each bird. As expected, we observed a negative relationship between the minimum δ^2H_f value from each of these adults and the latitude at which they summered (Figure 3A), as well as a positive relationship between the minimum δ^2H_f value and the May–August δ^2H_p value for the location at which they summered (Figure 3B). Furthermore, May–August δ^2H_p values derived from the minimum δ^2H_f values were within the 1σ range of variation of May–August δ^2H_p values for 7 of the 8 birds (and just outside the 1σ range of variation for the remaining bird) for the locations at which these birds

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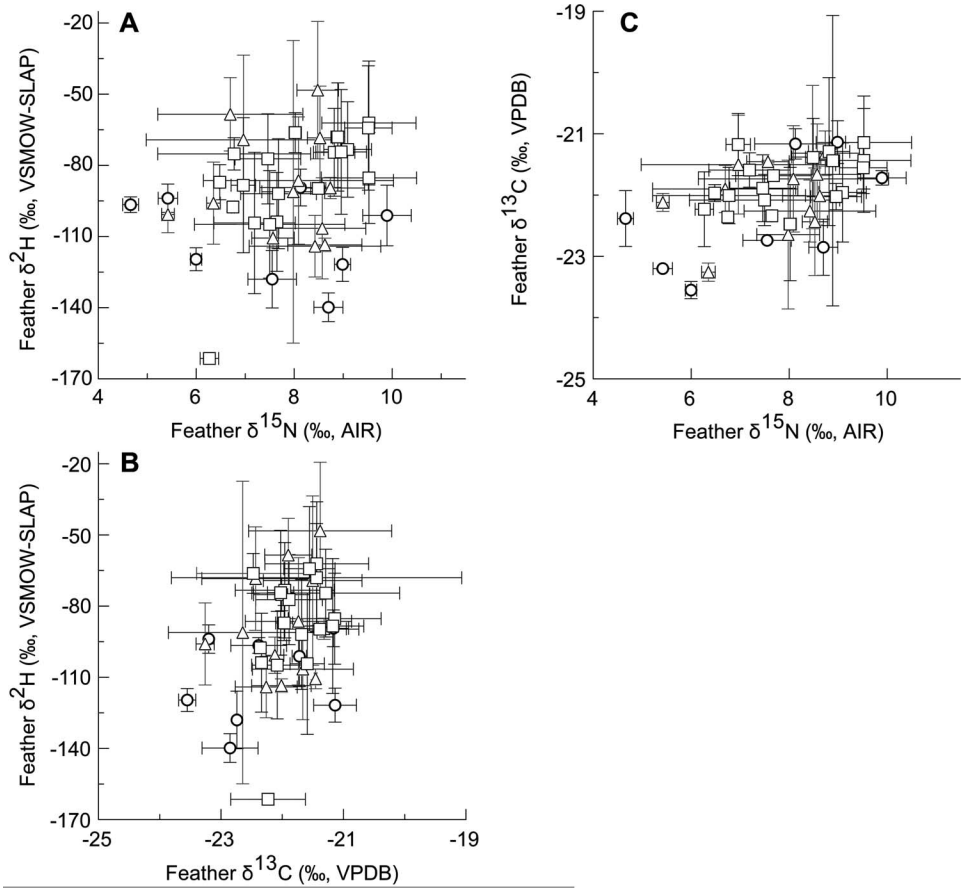


FIGURE 2. Relationship between mean (**A**) $\delta^{15}N$ and $\delta^{2}H$ values, (**B**) $\delta^{13}C$ and $\delta^{2}H$ values, and (**C**) $\delta^{15}N$ and $\delta^{13}C$ values of feathers for Golden Eagles from which at least 2 feathers were analyzed and which were likely to have been eating terrestrial prey. Circles = juvenile birds, triangles = subadult birds, and squares = adult birds. Error bars represent the interfeather variation for each bird expressed as a standard deviation.

summered (Figure 3C). In addition, the mean slope and intercept of the relationship between $\delta^{2}H_f$ and May–Aug $\delta^{2}H_p$ of the raptor data in Lott and Smith (2006) [1.13 and 11.15, respectively, as stated above] are within the 95% confidence interval of the slope and intercept (0.0 to 3.1 and −91 to 191, respectively) of the relationship between $\delta^{2}H_f$ and May–August $\delta^{2}H_p$ for the 8 validation birds.

The minimum isopleth contour that contained the known summer centroid for each of the 8 validation birds ranged between 0.2 and 0.6. The locations of 5 of these 8 birds were within the 0.3 isopleth (data not shown). Thus, we drew a 0.6 isopleth on the likelihood-of-origin map for each Golden Eagle in our dataset (Figure 4). The average straight-line distance between the known centroid of the summering location for our 8 validation birds and the centroid of the 0.6 isopleth contour was 377 ± 263 km. The average north–south distance between the known centroid of the summering location for our 8 validation birds and the centroid of the 0.6 isopleth contour was 191 ± 129 km, whereas the average east–west distance was 307 ± 258 km.

Distribution and Migratory Connectivity

To identify the primary summer locations used by Golden Eagles, we used the minimum $\delta^{2}H_f$ value from each bird to create a spatially explicit assignment of summering origin, as described above. The isotope-inferred summering locations of Golden Eagles varied between 52.1°N and 59.6°N. The greatest proportion of birds summered between 57°N and 58°N (Figure 5). As an initial test of potential leapfrog or chain migration by Golden Eagles in eastern North America, we assessed the relationship between wintering latitude and the minimum $\delta^{2}H_f$ value from each bird. We found a positive relationship between these variables (Figure 6A), implying that birds that wintered farther north had more positive $\delta^{2}H_f$ values (i.e. that they grew their feathers farther south). In addition, there was a negative relationship between wintering latitude and summering latitude (Figure 6B), also suggesting that birds that wintered farther north summered farther south. Finally, we found a negative relationship between wintering latitude and distance between the

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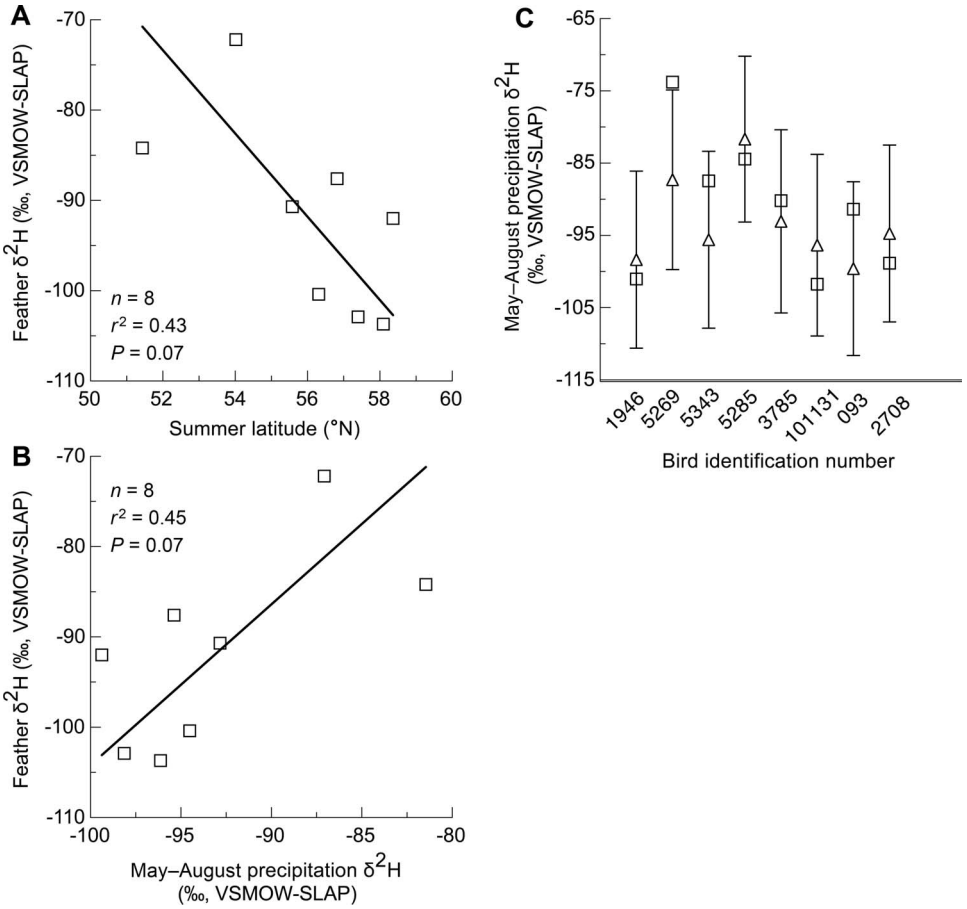


FIGURE 3. Relationship between minimum δ^2H_f (feather keratin) values and (**A**) summer latitude and (**B**) mean May–August δ^2H_p (precipitation) values (derived from an isoscape of δ^2H_p values) for 8 adult Golden Eagles with known summering grounds (latitude and longitude were determined from the centroid of the summering grounds). (**C**) Mean May–August δ^2H_p values (triangles) and δ^2H_p values calculated from minimum δ^2H_f values (squares) using the relationship between δ^2H_f and δ^2H_p values for raptors for 8 adult Golden Eagles (arrayed along the *x*-axis) with known summering grounds. Error bars on May–August δ^2H_p values represent one standard deviation.

winter and summer grounds, implying that birds that wintered farther north migrated shorter distances. In fact, birds from the most southern wintering locations appeared to migrate approximately twice the distance as those from the most northern wintering locations (Figure 6C). These relationships are summarized in stacked maps (Figure 7), which indicate (1) the summering locations of birds from the 4 wintering groups, and (2) patterns of migratory connectivity, with greater percentages of birds from more northerly winter populations summering in more southerly areas of eastern Canada, and vice versa (Figure 7).

DISCUSSION

Our results validate δ^2H-based inferences of the summer locations of Golden Eagles of unknown origin. We showed that the majority of birds spent the breeding season in central Québec and northern Labrador. Further, our results indicated moderate patterns of leapfrog migration and migratory connectivity, with implications for the understanding of the evolution of migration, as well as the conservation, of Golden Eagles. Our use of telemetry tracking to confirm isotope-inferred movements is unique and helps to provide new insight into both the broad application of this technique and the specific distribution and migratory connectivity of Golden Eagles in eastern North America.

Validating Hydrogen Isotopes for Locating Summer Origins

We used a multistep process to evaluate the extent to which δ^2H_f values may be useful for recording the geographic origin of eastern Golden Eagles. First, to constrain our analyses to terrestrial feeders, we identified feathers from birds with potential marine contributions to their diets (Lott et al. 2003). Only 2 of 47 birds had $\delta^{13}C$

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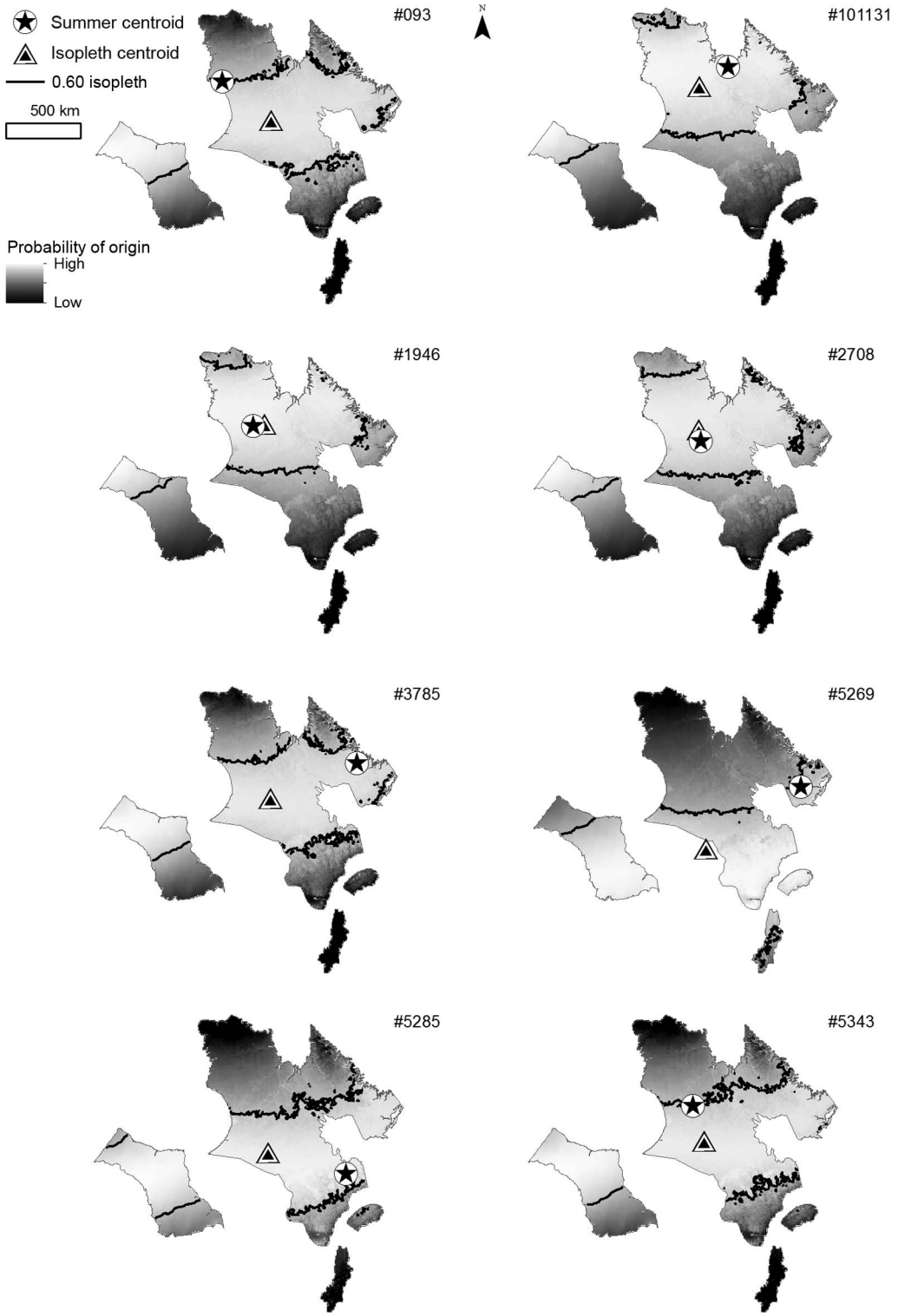


FIGURE 4. Likelihood-of-origin maps for 8 Golden Eagles with known summering locations. The stars represent the centroid of the summer location for each bird. The triangles represent the centroid of the 0.6 isopleth. The map area is the breeding range taken from Figure 1.

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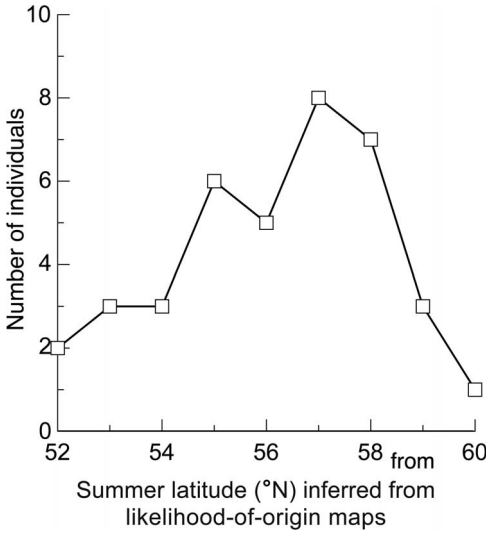


FIGURE 5. Frequencies of summer latitude values for Golden Eagles inferred from likelihood-of-origin maps.

values >–20‰ and $\delta^{15}N$ values >11‰ (Supplementary Material Figure S1), which is the approximate cutoff for distinguishing apex predators, such as Golden Eagles, with terrestrial vs. mixed marine and terrestrial diets (e.g., Yerkes et al. 2008, Newsome et al. 2010). Thus, the majority of Golden Eagles in eastern North America eat primarily terrestrial prey during the period of feather molt. However, as a conservative measure, δ^2H_f values from these 2 birds (Supplementary Material Table S1) were excluded from subsequent analyses. Previous studies have suggested that birds are an important component of the diets of Golden Eagles in eastern North America during the summer (Spofford 1971, Brodeur and Morneau 1999). Our isotope data suggest that, to the extent that waterbirds are important, they are typically birds associated with terrestrial or freshwater, rather than marine, environments.

Second, to understand how within-individual processes may have affected the interpretation of our results, we assessed variation in $\delta^{13}C$, $\delta^{15}N$, and δ^2H values within and

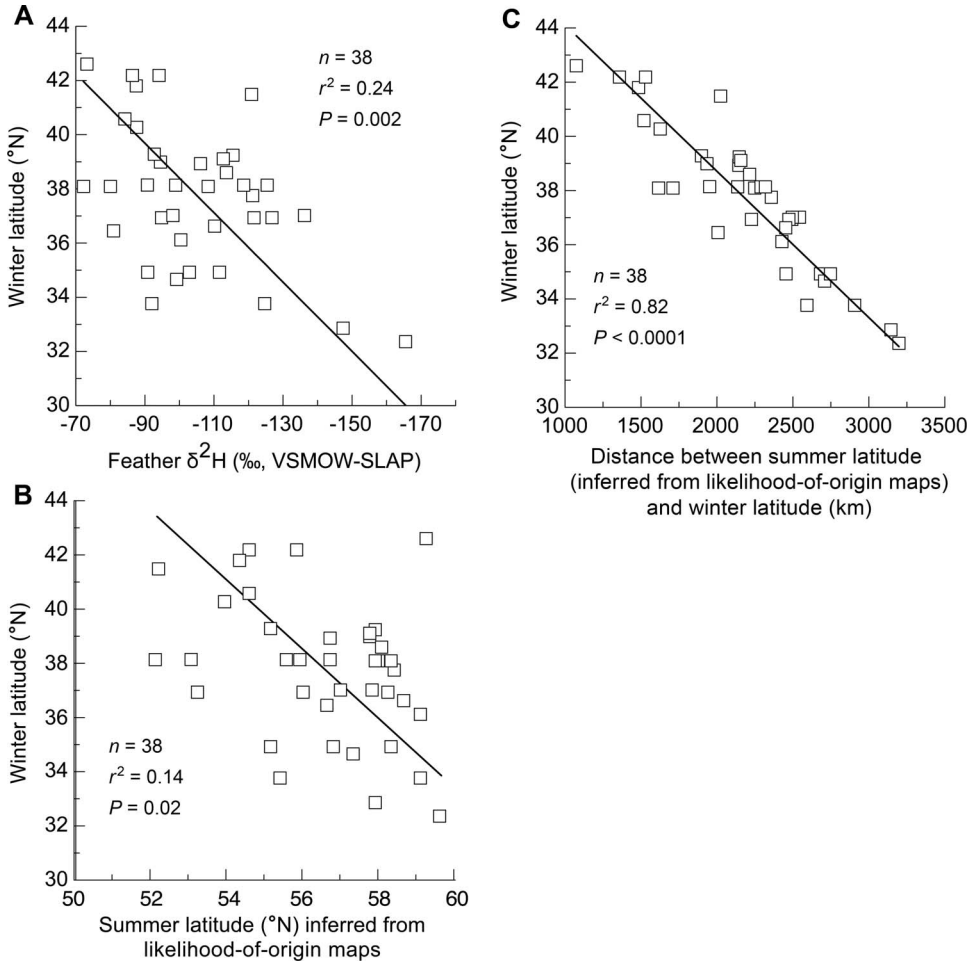


FIGURE 6. Relationships between (**A**) minimum δ^2H_f values and wintering latitude, (**B**) the isotope-inferred summer latitude and wintering latitude, and (**C**) the distance migrated and wintering latitude for Golden Eagles in eastern North America. Note that the values on the *x*-axis of panel (**A**) are reversed.

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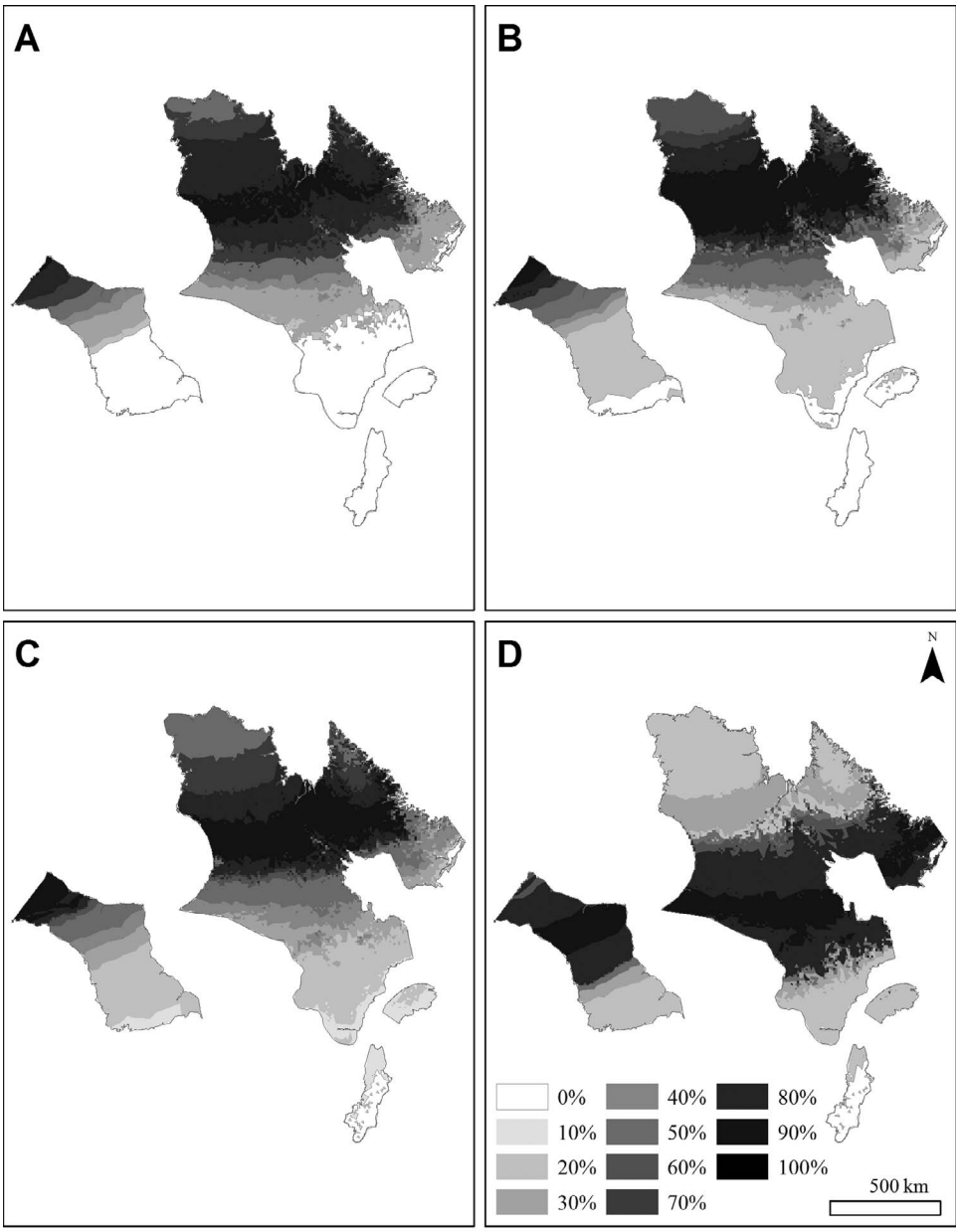


FIGURE 7. Maps of the percentage of cells with a 1 (likely origin) for the summering grounds of Golden Eagles from each of the 4 winter populations (Figure 1). Birds from winter group 1 ($n = 8$) are shown in (**A**), birds from winter group 2 ($n = 9$) in (**B**), birds from winter group 3 ($n = 14$) in (**C**), and birds from winter group 4 ($n = 7$) in (**D**). The map extent is the known breeding range shown in Figure 1.

among body feathers. We expected juvenile eagles to have the smallest inter- and intrafeather variation in isotopic values because the initial cohort of feathers on a Golden Eagle forms while the bird is in the nest (i.e. at a single location) during the summer. The relatively small inter-feather variation in isotopic values for juvenile birds captured during the winter (Figure 2, Supplementary Material Figures S1 and S2) was consistent with this expectation. Juvenile birds do not begin molting new feathers, except adventitiously, until 8–12 mo following hatching. Thus, juvenile birds captured on their wintering grounds are unlikely to have molted many new feathers (Bloom and Clark 2001). In contrast, we expected older Golden Eagles to have greater inter- and intrafeather variation in isotopic values, since we expected their feathers to form at different times and places. The larger variation in isotopic values that we observed in the body feathers of older Golden Eagles was consistent with this

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expectation. The differences in interfeather variation in δ^2H_f values among individuals suggested that the timing and location of molt differed among birds. Thus, δ^2H_f data from juvenile birds captured during the winter are likely to reveal details about the location of the natal area, whereas δ^2H_f data from subadults and adults will partly reveal the variation in locations where molting occurs. These results are consistent with those of prior studies, demonstrating that complex patterns of molt may be inferred from δ^2H_f data (e.g., Perez and Hobson 2006). Overall, our results from body feathers agree with published observations that Golden Eagles replace flight and tail feathers throughout the year, with peak molting activity during mid-to-late summer (Bloom and Clark 2001). For migrant birds, such peak molting likely occurs when birds are at their northernmost locations, which have the most negative δ^2H_p values.

Third, as a reference for winter δ^2H values, we measured δ^2H values from clips obtained near the proximal end of in-sheath feathers from 3 Golden Eagles captured on their wintering grounds (Supplementary Material Figure S2). The portion of these feathers from which the clips were taken were unequivocally grown within the past week and therefore were formed on the wintering grounds (Edelstam 1984). All 3 samples had δ^2H_f values $>-62‰$. Thus, we used this value as an approximate threshold to distinguish feathers formed in the eastern United States during winter ($\delta^2H_f > -62‰$) from feathers formed in eastern Canada during the summer ($\delta^2H_f < -62‰$).

Finally, we determined the accuracy of δ^2H-based assignments for the 8 adult Golden Eagles for which we had sufficient information (telemetry data, summer capture data) to assess their summer locations. The negative relationship between minimum δ^2H_f values and summer latitude and the positive relationship between the minimum δ^2H_f values and the May–August δ^2H_p values (Figures 3A and 3B) suggest that our approach of using the minimum δ^2H_f value from each bird for geographic assignment using May–August δ^2H_p values was appropriate. However, because of our relatively small sample size, this transfer function was unlikely to be robust for conversion of δ^2H_f values to δ^2H_p values for geospatial analysis. Thus, we followed the recommendation of Bowen et al. (2014) to evaluate whether a more generic transfer function based on our May–August δ^2H_p isoscape was appropriate for use with Golden Eagles. To do so, we asked whether the relationship between δ^2H_f values for the 264 raptors in the dataset of Lott and Smith (2006) and May–August δ^2H_p values derived for those birds could be used to estimate May–August δ^2H_p values from δ^2H_f values of our 8 validation birds. We found (1) that May–August δ^2H_p values derived from the minimum δ^2H_f values of these 8 birds were within the range of variation of May–August δ^2H_p values for the locations at which these birds summered (Figure 3C), and (2) that the mean slope and intercept of the relationship between δ^2H_f and May–August δ^2H_p values for the raptor data in Lott and Smith (2006) were within the 95% confidence interval of the slope and intercept of the relationship between δ^2H_f and May–August δ^2H_p values for the 8 validation birds. Thus, we conclude that it was appropriate to convert Golden Eagle δ^2H_f values to May–August δ^2H_p values (using the relationship that we derived from the Lott and Smith [2006] dataset) for geospatial analysis with a May–August δ^2H_p isoscape.

Our results also illustrate the value of telemetry data for validating δ^2H-inferred movements and migration pathways. This approach has received extensive use with marine animals (Pajuelo et al. 2012, Seminoff et al. 2012), but relatively little application to birds (Knoche et al. 2007, Bridge et al. 2014). Although isotope data provide less precise movement information than telemetry data, isotope data have important advantages. In particular, they are relatively inexpensive to collect and analyze, and they can be obtained from dead or injured individuals, individuals captured but not fitted with telemetry units, and individuals for which telemetry units fail. A coupling of telemetry and isotope data is likely to be invaluable for quantifying the summer distribution and patterns of migratory connectivity for other reclusive and difficult-to-track species.

Distribution and Migratory Connectivity

Our analyses illustrate the structure and degree of migratory connectivity of Golden Eagles that winter in the eastern United States. Nest survey data show that Golden Eagles have territories throughout eastern Canada (Morneau et al. 2015). However, identifying abundance from nest surveys is challenging because Golden Eagles occur at relatively low densities and the majority of the land area (>80%) in eastern Canada has not been surveyed for this species. Golden Eagles captured at any location during the winter in the eastern United States are most likely to have summered between 55°N and 58°N in eastern Canada (Figures 5 and 7). Presumably, large numbers of nesting sites and abundant prey make these latitudes quality habitat for Golden Eagles. Future study is required to determine whether Golden Eagles prefer these latitudes because of biotic factors (e.g., prey distributions), climatic factors (e.g., weather-driven determinants of lift), or other abiotic factors such as topography (e.g., nesting habitat or topographic determinants of lift).

Migratory connectivity has emerged as an important theme in avian ecology (Webster et al. 2002), with species demonstrating winter–summer linkages that range from strong (e.g., Delmore et al. 2012, Fort et al. 2012, Cormier et al. 2013) to weak (e.g., Renfrew et al. 2013, Trierweiler et al. 2014). Data from analysis of δ^2H_f have provided

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evidence of chain migration by some species (e.g., Smith et al. 2003), leapfrog migration by others (e.g., Kelly et al. 2002, Clegg et al. 2003), and, in some cases, no clear evidence of leapfrog or chain migration (e.g., Symes and Woodborne 2010, Rushing et al. 2014). Invariant migration distances relative to the wintering or summering location is evidence for chain migration. Thus, the strong negative relationship that we observed between wintering latitude and distance between the wintering and summering grounds (Figure 6C) indicates that eastern Golden Eagles do not engage in chain migration. Furthermore, the positive relationship between wintering latitude and δ^2H_f values (Figure 6A) and the negative relationship between wintering latitude and summering latitude (Figure 6B) suggest that these birds perform at least modest levels of leapfrog migration. Overall, there is a greater probability that migrants from the southern portion of the winter range originate from the northern portion of the summer range and vice versa. These results therefore confirm qualitative interpretations of migratory connectivity based on telemetry data from small numbers of Golden Eagles (Katzner et al. 2012b), and also illustrate how stable isotopes can provide a means of linking summer and winter distributions across the range of a migratory raptor.

The reasons for, and implications of, the observed patterns of migratory connectivity of eastern Golden Eagles are uncertain. For example, leapfrog migration could result from competition for the most favorable breeding or winter locations or from increased costs associated with longer migrations. If southern breeding locations are most favorable, then perhaps individuals may tolerate harsher winter conditions for the tradeoff of lesser energetic expenditures on migration (Berthold 1993), earlier arrival, and first choice of territories on breeding grounds. Regardless of their cause, these patterns of leapfrog migration are indicated in both behavior and the isotopic reflections of those behaviors, and they likely have important ecological and evolutionary implications. Documenting the summer and winter locations used by eastern Golden Eagles, as well as their patterns of migratory connectivity, thus provides a basis for better conservation, and increased understanding of the evolution of migration, of this species.

The modest degree of leapfrog migration that we observed implies that geographically variable threats could have differential impacts on subpopulations and long-term evolutionary potential. Although no Golden Eagle fatalities have yet to be reported at industrial-scale wind-energy facilities in the eastern United States, such fatalities are common in the western United States (Smallwood and Thelander 2008). Golden Eagles that summer in southern Canada are also those that winter primarily in the northeastern Appalachian Mountains, where there are increasing numbers of utility-scale wind-energy facilities. These birds could experience a disproportionately greater risk of wind-turbine mortality than those from the southwestern portion of the winter distribution where such facilities are uncommon. Overall, our results illustrate that leapfrog connectivity patterns present unique conservation challenges for Golden Eagles, including the fact that environmental changes may have spatially variable effects on population size and diversity.

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Ethics statement: This work was conducted in accordance with appropriate Institutional Animal Care and Use (IACUC) protocols, including West Virginia University IACUC protocol #11-0304, and the Animal Care Committee of the Ministère des Forêts, de la Faune et des Parcs, Québec (permits CPA-FAUNE-07-00-02 and CPA-FAUNE-2009-06).

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