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Estimating the latitudinal origins of migratory birds using hydrogen and sulfur stable isotopes in feathers: influence of marine prey base

Received: 2 May 2002 / Accepted: 21 November 2002 / Published online: 19 December 2002
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Abstract Hydrogen stable isotope analysis of feathers is an important tool for estimating the natal or breeding latitudes of nearctic-neotropical migratory birds. This method is based on the latitudinal variation of hydrogen stable isotope ratios in precipitation in North America (δD_p) and the inheritance of this variation in newly formed feathers (δD_f). We hypothesized that the typically strong relationship between δD_p and δD_f would be decoupled in birds that forage in marine food webs because marine waters have relatively high δD values compared to δD values for local precipitation. Birds that forage on marine prey bases should also have feathers with high $\delta^{34}S$ values, since $\delta^{34}S$ values for marine sulfate are generally higher than $\delta^{34}S$ values in terrestrial systems. To examine this potential marine effect on feather stable isotope ratios, we measured δD and $\delta^{34}S$ in the feathers of nine different species of raptors from both inland and coastal locations across North America. Feathers from coastal bird-eating raptors had consistently higher δD and $\delta^{34}S$ values than feathers from inland birds. Birds that had high $\delta^{34}S$ values also deviated strongly from the typical relationship between δD_p and δD_f . We recommend measuring both sulfur and hydrogen stable isotope ratios in feathers when some members of a migrant population could potentially forage in marine

habitats. We suggest using a practical cutoff of $\delta^{34}S > 10\text{‰}$ to remove marine-foraging birds from a migrant sample when using stable isotopes of hydrogen to estimate the latitudinal origins of migrants because high δD_f values for marine-foraging birds could potentially distort estimates of origins.

Keywords Coastal · Diet · Migration · Raptors · Foraging

Introduction

Hydrogen stable isotope analysis of feathers is an important tool for estimating the natal or breeding latitudes of migrating birds in North America (Meehan et al. 2001; Wassenaar and Hobson 2001). This method relies on the strong latitudinal gradient of hydrogen stable isotope ratios ($^2H/^1H$) in precipitation (δD_p) (Dansgaard 1964) and inheritance of the local precipitation isotope signal in feathers (δD_f) grown on the breeding grounds (Chamberlain et al. 1997; Hobson and Wassenaar 1997). If the relationship between δD_p and δD_f is equally dependable for all birds, one could collect a feather from any migrant and use the δD of that feather to estimate its natal or breeding latitude.

Feather δD values reflect the hydrogen isotope composition of the bird's prey (Hobson and Wassenaar 1997). After an initial fractionation between precipitation and plant carbohydrate (White 1988), δD values remain essentially unchanged through the food web from herbivores (Miller et al. 1988; Cormie et al. 1994) to primary consumers (Chamberlain et al. 1997; Hobson and Wassenaar 1997) to secondary consumers (Meehan et al. 2001). If the ultimate source water of a bird's prey is local precipitation, the hydrogen isotope signal of precipitation will be recorded in feathers. At regional or larger scales the relationship between δD_p and δD_f is usually linear, and δD_f values are typically 20–30‰ lower than values for local δD_p (Wassenaar and Hobson 2001).

In contrast to the strong latitudinal gradient of δD in meteoric waters, δD values of ocean waters are relatively

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constant, ranging from -5 to 5% , regardless of latitude (Redfield and Friedman 1965; Hoefs 1980). Birds in coastal environments may forage on marine prey, whose tissues will reflect the isotopic signal of the ocean. However, not all birds in coastal environments may be exposed to the marine isotopic signal. Coastal birds that consume insects or small vertebrates that feed on freshwater-based vegetation may have hydrogen ratios related to precipitation, whereas coastal birds foraging on prey that utilize marine resources (i.e., seabirds, fish, or marine invertebrates) would not show a strong relationship between δD_p and δD_f .

Previous studies have constructed predictive models based on the regression of known-origin δD_f values and estimated δD_p values (e.g., Hobson and Wassenaar 1997) or latitude (Kelly et al. 2002) across the breeding range of a species. These models have then been used to estimate the breeding areas of migrant populations of unknown origins from measurements of δD_f . The inclusion of marine-foraging birds in either the breeding season samples used to create predictive models or samples from unknown-origin populations of migrating or wintering birds could lead to inaccurate estimates of migrant origins. Including marine-foraging birds in predictive models could potentially distort relationships between δD_f and latitude (or δD_p) by changing the slope and/or the y-intercept. The inclusion of feathers from marine-foraging birds in a migrant sample would lead to inaccurate southerly estimates of the breeding latitudes of migrants because δD_f values of marine-foraging birds will always be higher than δD_f values predicted from δD_p .

It may not be possible to determine the extent of a marine input on hydrogen isotope ratios from the δD_f of an unknown-origin migrant bird. For example, a δD_f of 50 could indicate either a bird from a pine forest in Florida or a bird from Greenland that foraged in estuarine wetlands while the feather was being grown, resulting in a much higher δD_f value than would be expected for Greenland due to the influence of marine hydrogen. However, sulfur stable isotopes ($^{34}\text{S}/^{32}\text{S}$) in feathers may be used to identify birds exposed to marine water, allowing marine-foraging birds to be removed from migrant samples, eliminating this potential bias. Sulfur isotopes have been previously used as a tool for determining coastal or marine habitat use by birds (Hobson et al. 1997; Caccamise et al. 2000; Knoff et al. 2001). Marine sulfate generally has higher $\delta^{34}\text{S}$ values than terrestrial materials or waters (Michener and Schell 1994) and sulfur isotope analyses have been used extensively in wetlands and fisheries studies to determine the amount of marine-derived nutrients in estuarine systems (Hesslein et al. 1991; Kwak and Zedler 1997; MacAvoy et al. 2000).

Previously, Meehan et al. (2001) used hydrogen stable isotopes in feathers to estimate the natal latitudes of Cooper's Hawks captured during migration in the Florida Keys. To create a predictive model for additional species of migrating raptors in the Florida Keys, we collected feathers from nine species of diurnal raptors from a wide diversity of locations across North America. Some of

these species, particularly Peregrine Falcons (*Falco peregrinus*) and Merlins (*Falco columbarius*), forage in coastal areas within parts of their range, where they may be exposed to a marine prey base. Therefore, we evaluated the effects of a marine-based diet on δD_f values for 112 individual raptors from both inland and coastal areas across North America, and $\delta^{34}\text{S}$ from a subset of 52 of these feathers (Fig. 1). We examined the relationship between δD_p and δD_f across sample location (coastal versus inland), foraging group (bird eaters versus generalists), and species. We also examined relationships between $\delta^{34}\text{S}$ and sample location and foraging group. We then developed a protocol for identifying a marine input to feather isotope ratio using $\delta^{34}\text{S}$ values. This allowed us to create a more accurate predictive model of the relationship between δD_p and δD_f once marine "contaminated" samples were removed from the model. This protocol will lead to more accurate estimates of the breeding origins of migrating or wintering birds once marine-influenced feathers are removed from migrant samples.

Materials and methods

We collected one or two body feathers from 112 museum specimens collected across the breeding range of nine different raptor species for hydrogen and sulfur stable isotope analysis (Fig. 1). Some adult raptors replace feathers either during migration or on wintering territories (Forsman 1999). Therefore, samples were taken from either nestlings or birds in first-year plumages that were collected between 15 May and 15 August to ensure that feather samples would represent breeding areas near the collection location, not wintering birds or migrants. Original specimen collection years ranged from 1878 to 1999.

We classified feather samples from individual raptors as coming from either coastal (within 15 km of the coast) or inland (greater than 15 km from the coast) locations. We also divided species into two foraging categories based on dietary preferences. Bird eaters included Peregrine Falcons, Merlins, Sharp-shinned Hawks (*Accipiter striatus*), and Cooper's Hawks (*Accipiter cooperii*) and generalists included American Kestrels (*Falco sparverius*), Broad-

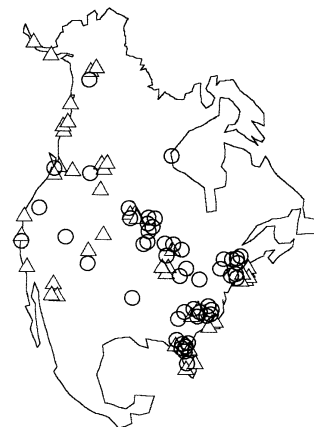


Fig. 1 Sample locations for feathers analyzed for stable isotope ratios in this study. Circles are locations for δD analysis and triangles are locations of both δD and $\delta^{34}\text{S}$ analyses

winged Hawks (*Buteo platypterus*), Red-tailed Hawks (*Buteo jamaicensis*), Red-shouldered Hawks (*Buteo lineatus*), and Northern Harriers (*Circus cyaneus*) (Johnsgard 1990).

We used published data (Hobson and Wassenaar 1997) for hydrogen isotope ratios in weighted average growing-season precipitation to create a continental contour map for δD_p . We then queried this map to acquire estimated δD_p values for each of our feather sample locations. We quantified the relationship between estimated δD_p and measured δD_f for each sample by subtracting δD_p from δD_f . This calculated variable (hereafter referred to as δD_{f-p}) was used as the dependent variable in statistical tests that evaluated location, foraging group, and species effects.

We used two-way ANOVA to examine the effects of sample location (coastal vs inland) and foraging habit (bird eaters vs generalists) on δD_{f-p} . All groups met test assumptions of normality; however, sample sizes were not equal among location/foraging groups and variances were heteroscedastic. The largest variance was associated with the smallest sample size. Thus, the probability of making a Type I error was greater than 0.05 (Zar 1999). For these comparisons we adjusted α to 0.01. To investigate the strength of the relationship between δD_p and δD_f for different sample groupings we used multiple linear regressions. Because the interaction between location and foraging habit was significant in the prior analyses, we used one-way ANOVA with location/foraging group (hereafter referred to as foraging group) as the main effect and $\delta^{34}S$ as the dependent variable to test for differences in $\delta^{34}S$ among groups. Sulfur data met test assumptions of normality and homoscedasticity. Finally, we tested for species effects on δD_{f-p} using one-way ANOVA. Data for all groups met test assumptions of normality and homogeneity of variances. All means comparisons were made with Fisher's LSD tests. Type III sum of squares were used when group sample sizes were unequal (Dunn and Clark 1987).

The relationship between δD_{f-p} and $\delta^{34}S$ was assessed using piecewise regression. A scatter plot of δD_{f-p} on $\delta^{34}S$ suggested that a two-phased linear-linear model was appropriate for the data. Piecewise regression is an exploratory technique that fits a pre-specified, multi-phased model to data, adjusting model parameters to minimize the overall sum of squares (Hintze 2001). We used linear regression and autocorrelation analyses to examine the relationship between the residuals from our final regression model (see Results) and sample day (15 May = 1), and the relationship between residuals and sample year (1878–1999) to ensure that our sampling over different days during the breeding season and over 121 years did not affect our conclusions. Statistical analyses were performed on SAS version 8.2 (SAS Institute 1999). Map building and δD_p estimation procedures were performed with the S+SpatialStats module of Splus (MathSoft 2000) after Kaluzny et al. (1998).

Hydrogen stable isotope measurements of feathers were made between December 30, 2000 and January 15, 2001 at the Stable Isotopes Laboratory at the University of New Mexico. Extraction methods for hydrogen analyses are described in Meehan et al. (2001) with the exception that, for this study, we equilibrated feathers for 2–3 weeks with hydrogen in ambient water vapor in the lab, which remained constant over the course of our analysis. Our reported δD_f values represent pooled equilibrated exchangeable and non-exchangeable hydrogen. See Wassenaar and Hobson (2002) for a description of methods for attaining non-exchangeable hydrogen values for feathers using keratin lab standards. All samples are reported in parts per thousand deviation from the standard mean ocean water (SMOW) standard, normalized on the VSMOW/SLAP scale. Correction procedures were made following Coplen (1988). The standard deviation of an analysis was $\pm 5\%$ based on repeated measurements of National Bureau of Standards 30 (NBS-30) ($\delta D = -65\%$) and an internal laboratory beet sugar standard. Sulfur isotope ratios of feathers were determined following the procedure of Giesemann et al. (1994). Approximately 2–3 mg material was loaded into tin capsules, which were reacted at 1,060°C in a He stream with excess oxygen. Reproducibility of measurements was estimated at $\pm 0.7\%$. All data are reported in per mil notation relative to the Canyon Diablo standard (CDT) where NBS-

123=17.1‰ and NBS-127=20.3‰. Both hydrogen and sulfur stable isotope measurements were made using a Delta^{plus} XL mass spectrometer in continuous flow mode.

Results

The interaction between sample location and foraging group had a significant effect on the relationship between δD_p and δD_f (δD_{f-p}) ($F_{1,108}=18.05$, $P<0.0001$). Adjusted means for δD_{f-p} for inland generalists, inland bird eaters, and coastal generalists ranged from 21.3 to 17.7 and these groups were not significantly different from each other. However, the coastal bird eaters had a mean δD_{f-p} of +36.4 and this group was significantly different from all of the other three (Fig. 2a). In addition, the predictive linear relationship between δD_f and δD_p was different for coastal bird eaters compared to the other three groups (Table 1). Y-Intercepts and slopes were similar among inland generalists, inland bird eaters, and coastal generalists. Coastal bird eaters had a more negative intercept and slope than the other groups. Once coastal bird eaters were removed, the regression of δD_p and δD_f was

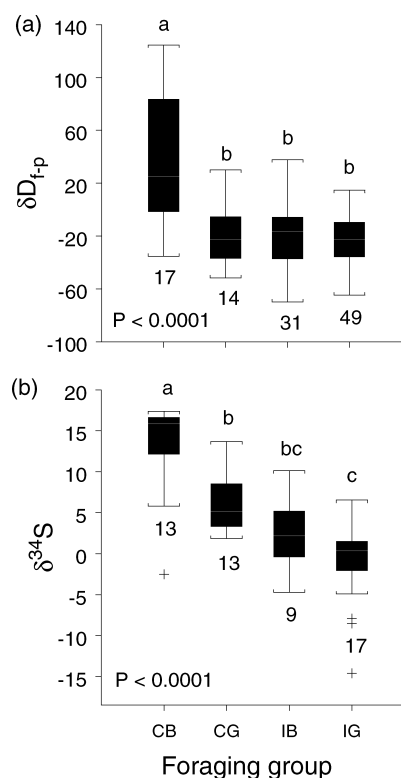


Fig. 2 Box plot showing the central 50% (boxes) and range (lines) of **a** δD_{f-p} and **b** $\delta^{34}S$ for four foraging groups of raptors: coastal bird-eaters (CB), coastal generalists (CG), inland bird-eaters (IB), and inland generalists (IG). Letters above boxes indicate group membership and numbers below boxes indicate sample size. + An outlier value

Table 1 Sample sizes, r^2 , and 95% confidence intervals for slopes and y-intercepts for regressions of δD_p and δD_f for four different foraging groups of raptors, all raptors, and all raptors after coastal bird-eaters have been removed. Note that coastal bird eaters

Group	n	r_s	y-Intercept	Y LCI	Y UCI	Slope	β LCI	β UCI
Inland generalists, IG	50	0.59	-40.0	-48.7	-31.4	0.62	0.47	0.77
Inland bird eaters, IB	31	0.37	-44.2	-61.8	-26.6	0.54	0.27	0.81
Coastal generalists, CG ^a	13	0.19	-38.8	-66.6	-11.1	0.55	-0.18	1.30
Coastal bird eaters, CB	17	0.12	-104.7	-184.3	-25.1	-0.59	-1.46	0.26
All birds except CB	95	0.46	-41.1	-48.6	-33.5	0.58	0.46	0.71
All birds	112	0.09	-52.2	-62.7	-41.7	0.28	0.11	0.44

^a With one outlier removed

Table 2 Sample size for eight raptor species included in analyses of the effects of species, feather collection date, and feather collection year on the relationship between δD_p and δD_f (δD_{f-p}), and the final regression of δD_p and δD_f

Species	Sample size
<i>Circus cyaneus</i>	15
<i>Accipiter striatus</i>	7
<i>Accipiter cooperii</i>	18
<i>Buteo lineatus</i>	4
<i>Buteo platypterus</i>	12
<i>Buteo jamaicensis</i>	18
<i>Falco sparverius</i>	15
<i>Falco peregrinus</i>	4

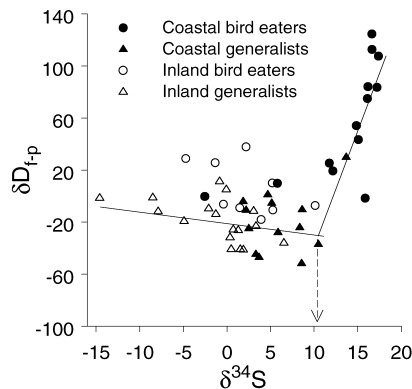


Fig. 3 The relationship between δD_{f-p} and $\delta^{34}S$ ($n=52$) showing piecewise regression lines and cutoff point of $\delta^{34}S=10‰$

significant and moderately predictive ($F_{1,93}=81.10$, $P<0.0001$, $R^2=0.46$).

$\delta^{34}S$ varied significantly among foraging groups ($F_{3,48}=23.23$, $P<0.0001$). Coastal bird-eaters had significantly higher $\delta^{34}S$ values than all other groups and coastal generalists had significantly higher values than inland generalists (Fig. 2b). Piecewise regression found two optimal slopes and intercepts for the linear-linear model, and an optimal x -value cut-off point of $\delta^{34}S=10‰$ for the end of the first model and beginning of the second. All birds with $\delta^{34}S$ values >13 were coastal bird eaters and δD_{f-p} values for these birds were much more positive than those of all other groups (Fig. 3).

(*italics*) had different slope and y-intercept compared to the other foraging groups. **Bold face** results represent the predictive stable hydrogen isotope model once coastal bird eaters were removed. *LCI* Lower confidence interval, *UCI* upper confidence interval

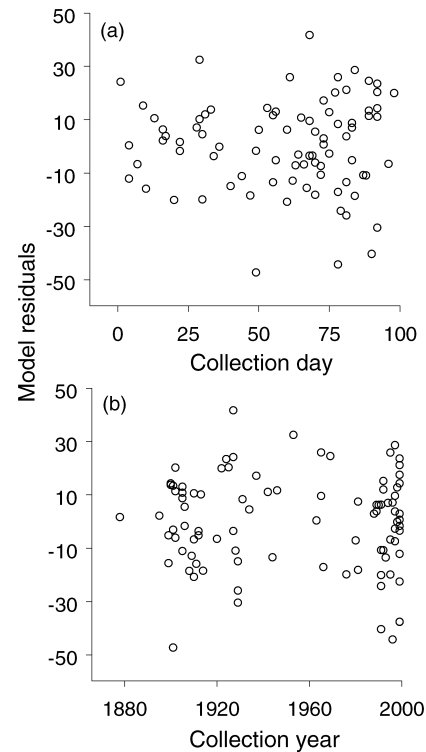


Fig. 4 Relationship between residuals from the regression of δD_p and δD_f and **a** feather sample collection day (May 15 =1), and **b** year

Coastal bird eaters had significantly different δD_{f-p} values from the other three foraging groups so we removed them from subsequent analyses. We also removed data from the two remaining Merlins because a meaningful group mean could not be generated from two individuals. The species comparison dataset had 93 birds (Table 2). There was no effect of species on δD_{f-p} ($F_{7,85}=1.54$, $P<0.16$). Residuals from the final predictive regression model were not significantly related to sample day ($F_{1,80}=0.05$, $P=0.82$) or year ($F_{1,89}=0.28$, $P=0.59$). Further, residuals were not significantly auto-correlated over time lags 1–20 (Fig. 4).

Discussion

Several studies have shown a strong relationship between δD_p and δD_f regardless of species or trophic level (Chamberlain et al. 1997; Hobson and Wassenaar 1997, 2001; Wassenaar and Hobson 2000; Hobson et al. 2001; Meehan et al. 2001; Kelly et al. 2002). In this study, δD_p and δD_f were strongly related for eight species of migratory raptors across a large geographic area, as long as these raptors did not incorporate hydrogen from marine resources. The lack of an effect of species on the relationship between δD_p and δD_f allows samples from multiple species to be pooled, greatly improving the geographic scope and applicability of predictive models. It is rarely practical or, in some cases, possible to collect numerous feathers from a single species across a large geographic range. In addition, our analysis detected no systematic effects of collection year or day on residuals for the regression of δD_p on δD_f . Although this wide range of dates may have contributed to some of the variation in our data, the predictive value of δD_f was not compromised, indicating that feathers from museum specimens may be a good resource for future isotope studies.

Hobson et al. (2000) recognized the potential for complications in hydrogen stable isotope studies involving migratory birds with a marine diet and presented data from 13 individual seabirds that showed higher δD_f values than δD_p values for Ruddy Ducks foraging in nearby freshwater systems. Our study demonstrates that the marine effect extends to secondary predators that prey on marine-foraging birds. We also demonstrate how coastal raptor foraging ecology may affect the predictive relationship between δD_p and δD_f and provide a practical means for identifying and removing marine “contaminated” birds from a sample using stable isotopes of sulfur in feathers.

Delta values for marine hydrogen and sulfur samples are both higher than delta values for terrestrial samples of these same elements. We found that coastal bird-eating raptors had both high δD_f values compared to estimates of local δD_p and higher $\delta^{34}S$ values than inland foraging birds and coastal generalists. Coastal bird-eating raptors most likely assimilate hydrogen and sulfur with a marine isotope signal when they eat seabirds, shorebirds, or any other animal that relies on a marine prey base. Because some Peregrine Falcons forage exclusively at seabird colonies (Ratcliffe 1980), Peregrines were the most likely species in our study to incorporate the marine isotope signal into their feathers. We would predict a similar decoupling of the relationship between δD_p and δD_f in the feathers of coastal Ospreys (*Pandion haliaetus*), Bald Eagles (*Haliaeetus leucocephalus*), seabirds, or herons that forage on marine fish, and shorebirds that forage on marine invertebrates.

Coastal generalists did not show a significant deviation in δD_f from predicted δD_p ; however, these birds did have significantly higher $\delta^{34}S$ values than inland generalists. High $\delta^{34}S$ values for these birds may be related to sea-salt spray and rainfall deposition of sulfate on vegetation

(Jamieson and Wadleigh 2000). Though coastal generalists were exposed to enough marine sulfate to affect their $\delta^{34}S$ values, the relationship between δD_p and δD_f for this group was not significantly different from inland birds. The strongly positive differences between δD_p and δD_f occurred when $\delta^{34}S$ was greater than 13‰, values only displayed by coastal bird-eating raptors.

Predictions of the origins of migrant birds based on measured δD values of feathers will be most accurate if birds that forage on marine-derived resources are excluded, because origins of latitude cannot be accurately predicted for these individuals. In this study, high feather $\delta^{34}S$ values effectively identified coastal bird-eating raptors, which were most likely to show deviations from predicted δD_f values. We recommend measuring both δD and $\delta^{34}S$ in studies where marine water could influence δD_f . Birds with $\delta^{34}S$ values >10‰ should be excluded from analyses of the latitudinal origins of migrants based on hydrogen isotope ratios of feathers. This is a conservative cutoff since the largest deviations from the typically strong correlation between δD_p and δD_f all occurred above $\delta^{34}S$ >13‰. No coastal generalists, inland bird eaters, or inland generalists had $\delta^{34}S$ values >13‰ in this study.

Though our $\delta^{34}S$ cutoff of 10‰ will ensure that latitudinal estimates are not confounded by marine foraging, it may occasionally lead to an unnecessary reduction in datasets. We felt that a conservative cutoff was necessary because the risk of including a marine-influenced δD_f in our estimates of migrant origins was greater than the benefit of including that portion of birds in our sample. It is possible that using $\delta^{34}S$ values to identify marine foragers could incorrectly classify individuals if they come from terrestrial (Chukhrov et al. 1980) or inland marsh (Cornwell et al. 1995) systems founded on parent materials with high $\delta^{34}S$ values (e.g., evaporite deposits). However, a continent-scaled study showed that $\delta^{34}S$ values of terrestrial plants are generally low in inland areas, where averages ranged from 0.5 to 4.4‰, and consistently high on oceanic islands, where averages ranged from 12.9 to 13.9‰ (Chukhrov et al. 1980). Our continent-scale study of sulfur isotopes in feathers showed similar patterns.

Acknowledgements This project would never have been possible without the contributions of many organizations and individuals. HawkWatch International would like to thank the Disney Wildlife Conservation Foundation for the Disney Conservation Award that funded this research. We thank the following curators, collections managers, and assistants for their invaluable contributions of feather samples for this study: David Willard and John Bates at the Field Museum of Natural History in Chicago; Kevin McGowan at the Cornell University Museum of Vertebrates; John Gerwin and Becky Browning from the North Carolina State Museum of Natural Sciences; Andrew Kratter at the Florida Museum of Natural History in Gainesville; and Tamar Danufsky at the Wildlife Collection at Humboldt State University. We are very grateful to Zachary Sharp and Viorel Atudorei for timely technical assistance throughout our laboratory analysis in New Mexico. Zachary Sharp also provided helpful comments on an earlier draft of this manuscript. We also thank Mark Chappell and an anonymous reviewer for their insightful comments during the review process. Thanks to Ruth

Smith, John DeLong, Jon Larrabee, Aaron Barna, and Steve De La Pena for lab assistance and discussion. We thank the outstanding staff of HawkWatch International for their administrative support and the Florida Fish and Wildlife Conservation Commission for their support of the Florida Keys Raptor Migration Project. Thanks to the staff of Audubon's Tavernier Science Center for office support during the writing of this paper and National Science Foundation grant EAR-9727141 for support of the stable isotope lab at the University of New Mexico.

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