USING HYDROGEN ISOTOPE GEOCHEMISTRY TO ESTIMATE THE NATAL LATITUDES OF IMMATURE COOPER'S HAWKS MIGRATING THROUGH THE FLORIDA KEYS[1]

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Abstract.   We constructed a regression model for the relationship between stable-hydrogen isotope ratios in immature Cooper's Hawk (*Accipiter cooperii*) feathers (δD_f) and precipitation in areas where feathers were grown (δD_p) across much of the latitudinal and longitudinal extent of the species' breeding range. We used our model to estimate δD_p values from δD_f values of immature Cooper's Hawks captured during migration in the Florida Keys. We compared these estimated δD_p values to a published map of δD_p values of North American precipitation to learn the latitudinal origins of migrants. We reviewed previous migration banding studies to estimate the longitudinal range of migrants. Our analysis suggested that most of the immature Cooper's Hawks migrating through the Keys originated in natal areas in the Mid-Atlantic and Southeast regions of the continent. We found no difference in the passage date of northern and southern birds or in the latitudinal origins of males and females. This new information will aid in the interpretation of population trends generated from the ongoing migration count in the Keys.

INTRODUCTION

Each fall, large numbers of migrating raptors concentrate at locations along the edges of large water bodies, the margins of deserts, and the tops of mountain ridges (Mueller and Berger 1967, Hoffman 1985). The concentration of migrants along these geographic features affords researchers the opportunity to observe raptors from vast areas of the continent. Consequently, several of these locations have become raptor migration count sites (Heintzelman 1979, Kerlinger 1989). An important product of migration counts has been the estimation of long-term population trends of raptor species passing through these sites (Bednarz et al. 1990, Titus and Fuller 1990).

Trend information provided by migration counts is particularly valuable for assessing the population status of raptor species. Population trends are difficult to estimate with breeding-season studies due to the large home ranges and subsequent low breeding densities of raptors (Fuller and Mosher 1981, Titus et al. 1989). To properly estimate trends using breeding-season studies, large study areas must be surveyed over several years (Wiens 1981). Such efforts are logistically complicated and labor intensive and, therefore, costly. Consequently, populations of many raptor species have received little monitoring attention during the breeding season (Fuller 1996). In contrast, a migration count requires the efforts of two observers to sample thousands, sometimes millions, of migrants of multiple species (Kerlinger 1989). Though migration counts have their own suite of methodological problems (Dunn and Hussell 1995), they are relied upon as an integral part of assessing raptor population status (Fuller 1996, Kirk and Hyslop 1998).

Knowledge of the geographic origins and destinations of migrants monitored along an individual flyway allows wildlife managers to relate population trends observed at migration count sites to specific regions (Viverette et al. 1996). Relating trends to specific regions enables managers to assess the impact of management practices and conservation strategies on raptor populations at a regional scale (Senner and Fuller 1989, Kirk and Hyslop 1998). To date, banding has been the primary method by which researchers have attempted to learn the origins of migrants at count sites. This method has produced valuable information on the migratory routes and winter ranges of North American raptors. Unfortunately, it has provided very little information on the breeding ranges of migrants, since raptors banded during migration are encountered at extremely low rates during the breeding season (Clark 1985, Evans and Rosenfield 1985). An additional problem with the band encounter method is that descriptions of migrant ranges may be biased toward patterns of human habitation and land use, because acquiring data is dependent upon people encountering banded birds (Nichols and Kaiser 1999).

In 1997, two studies described a new technique for estimating the breeding latitudes of wintering Neotropical migrant songbirds using the ratios of stable-hydrogen isotopes in the birds' feathers (Chamberlain et al. 1997, Hobson and Wassenaar 1997). These applications of stable-hydrogen isotope analysis were based on two general principles. First, when a songbird grows a feather on its breeding grounds, the ratio of stable-hydrogen isotopes fixed in feather keratin (δD_f) is closely related to the stable-hydrogen isotope ratio in local precipitation (δD_p; Chamberlain et al. 1997, Hobson and Wassenaar 1997). Second, δD_p values in North America decrease, generally, with increasing latitude (Dansgaard 1964, Rozanski et al. 1993). These studies demonstrated that δD_f values of wintering songbirds could be compared with continental maps of δD_p to estimate the approximate breeding

latitude at which the feathers were grown. Kelly and Finch (1998) noted that this stable isotope technique promised to be a valuable tool for researchers studying birds during migration.

We used stable-hydrogen isotope analysis to estimate the natal latitudes of immature Cooper's Hawks (*Accipiter cooperii*) observed at a raptor migration site. We focused on immature migrants because, unlike most songbirds, many adult raptors do not replace all of their feathers on or near their breeding grounds (Alerstam 1990). Instead, feather molt may take from several months to many years, depending on the size and migratory habits of the species (Forsman 1999). Since adults may grow feathers during migration or on the wintering grounds, analyzing their feathers might not lead to correct estimates of their breeding latitudes. In contrast, all feathers of immature raptors are grown during the nestling and post-fledging stage at, or very near, their natal site (Palmer 1988). Thus, analyzing the feathers of immature birds should lead to correct estimations of their natal latitudes.

We chose Cooper's Hawks as our study species for two reasons. First, songbirds are a substantial component in the diet of Cooper's Hawks (Rosenfield and Bielefeldt 1993). Thus, by comparing our results with previous work on insectivorous passerines, we hoped to gain some insight into the effect of trophic position on the relationship between δD_f and δD_p. Second, Cooper's Hawk population status has been difficult to estimate using common measures such as the Breeding Bird Survey and Christmas Bird Count (Mosher 1989, Rosenfield et al. 1991). Regardless, some authors have suggested declines for eastern Cooper's Hawk populations. As a result, Cooper's Hawks have been assigned extirpated, endangered, threatened, or species of special concern status in 16 eastern states, though these designations may be based on incomplete information (Rosenfield et al. 1996). Cooper's Hawks are particularly conspicuous and abundant at several migration count sites. Therefore, population trends for this species may be best monitored by migration counts. However, breeding-season band recoveries for this species are rare (U.S. Bird Banding Lab, unpublished data). Thus, the breeding areas of Cooper's Hawks monitored during migration are not well known.

To describe the natal origins of migrating immature Cooper's Hawks using stable-hydrogen isotope analysis, we constructed a regression model that expressed the relationship between δD_f and δD_p values across much of the species' breeding range. We then used this model to estimate the natal latitudes of immature Cooper's Hawks migrating through the Florida Keys. With natal latitudes estimated, we tested for relationships between the latitude of origin and the passage date and sex of migrants. Our results indicate that stable-hydrogen isotope analysis is a powerful tool for learning the regional origins of migrating raptors observed at migration count sites. Using this technique, we improved our ability to (1) link population trends observed at a migration count site with specific geographic regions and (2) look for differences in the migratory behavior of individuals of different sexes and from different latitudes.

METHODS

FEATHER COLLECTION

To obtain δD_f values for our regression model, we collected and analyzed Cooper's Hawk feathers from five locations: Vancouver Island, British Columbia, Canada (BC); north-central North Dakota, USA (ND); northern Wisconsin, USA (WI); Bernalillo County, New Mexico, USA (NM); and Suwannee County, Florida, USA (FL). At the BC, ND, and WI sites, we collected body feathers from nestlings or dependent fledglings during June and July of 1999. For the NM site, we sampled nestling body feathers from museum specimens collected at nests during the breeding seasons of 1990 through 1999. At the FL site, we collected clippings of flight feathers from dead nestlings and breeding males during the breeding seasons of 1995 through 1999. Adult male feathers were used for the FL site because there were few nestling feather samples available. Because adult male Cooper's Hawks in Florida remain on their breeding territories during most of the year (B. Millsap, pers. comm.), we assumed that the δD_f values of these birds were similar to those of the nestlings in the area. To apply our model, we collected breast feathers from migrating immature Cooper's Hawks captured during the fall of 1998 at a newly established raptor migration counting and banding site in the Florida Keys, 20 km northeast of Marathon, Florida, USA (Lott 1998, Lott 1999).

STABLE ISOTOPE ANALYSIS

Stable-hydrogen isotope ratios were determined for feather samples during the fall of 1999 in the Stable Isotopes Lab at the University of New Mexico. We began by cleaning feathers with a mild solution of detergent and water to remove oils and parasites that may have been on the samples (Chamberlain et al. 1997). Next, we placed cleaned feathers individually into glass flasks using forceps and submerged them in water with a δD value of $-95‰$ for 14 days at room temperature (23°C). Chamberlain et al. (1997) found that this soaking procedure produced a constant δD value for the non-carbon-bound exchangeable hydrogen (approximately 13% of total hydrogen) incorporated in the feather keratin of all samples. We decanted the water after soaking the feathers, dried them within the open glass flasks in an oven for 2 hr at 150°C, and allowed them to cool for 10 min. Immediately after cooling, samples weighing 0.1 to 0.2 mg were packed into silver capsules, pyrolized using a Finnigan MAT TC-EA elemental analyzer, and analyzed for their isotopic composition using a Delta^{Plus} XL mass spectrometer in continuous flow mode. Samples were reduced at 1,400°C in the presence of glassy carbon, producing H_2 gas. The hydrogen gas was separated from others with a gas chromatograph. Finally, the hydrogen gas entered the mass spectrometer and a δD_f value was determined for the sample. We calibrated δD_f values to international standards for hydrogen isotopic analysis and report them in per mil notation (‰). By repeatedly analyzing samples of standards such as benzoic acid and biotite, we determined the SD of our lab procedures to be approximately 7‰. Because the value for isotopic fractionation at room temperature between the soaking water and the exchangeable hydrogen in feather samples was not known, we were not able to determine the δD value for the non-exchangeable hydrogen in samples. Thus, the δD_f values we report are for the pooled, equilibrated exchangeable and non-exchangeable hydrogen in each sample. Readers are encouraged to see to Wassenaar and Hobson (2000a) for updated methods for determining the δD value of non-exchangeable hydrogen in complex organic materials such as feathers.

MODEL BUILDING AND APPLICATION

Prior to statistical analysis, we interpolated δD_p values for the geographic center of each Cooper's Hawk breeding population in our sample using Hobson and Wassenaar's (1997) map of weighted-average δD values for North American, growing-season precipitation. After analyzing feathers, we constructed a linear regression model that described the relationship between δD_f values and interpolated δD_p values. To assess the precision of our model, we computed 95% confidence intervals for estimating δD_p values from the δD_f values of migrants. (Hereafter, these estimates are referred to as δD_x values.) Separate confidence intervals were generated for estimating δD_x values from a mean of δD_f values and an individual δD_f value (Ramsey and Schafer 1997).

Next, we used the model to learn the latitudinal origins of immature Cooper's Hawks captured during fall migration in the Florida Keys. This was done by computing δD_x values for the migrants and comparing them to Hobson and Wassenaar's δD_p map to identify the approximate latitudes associated with the δD_x values.

Our estimation of the longitudinal extent of Keys migrants was based on a review of migration studies of Cooper's Hawks (Duncan 1981, Holt 1991), Sharp-shinned Hawks (*Accipiter striatus*; Duncan 1982, Clark 1985, Evans and Rosenfield 1985), American Kestrels (*Falco sparverius*; Layne 1982, Duncan 1985), and Red-tailed Hawks (*Buteo jamaicensis*; Houston 1967, Brinker and Erdman 1985, Holt 1991). Taken together, these studies suggest that raptors migrating from points east of the Great Lakes head south-southwest to southwest, following the coast and mountains of eastern North America. Raptors migrating through the central Great Lakes migrate south-southeast to south-southwest; individuals that reach the Gulf of Mexico may head west toward Texas or east toward Florida. Migrants traveling through the western Great Lakes and points westward also migrate south-southeast to south-southwest. If these individuals encounter the Gulf, they tend to travel along its western edge. Given these migratory patterns, we believe that the western extent that we set for migrants through the Keys is appropriate.

We looked for a relationship between the latitudinal origin and the passage date and sex of migrants by testing a general linear model with δD_x as a continuous dependent variable, sex as a categorical independent variable, Julian banding date as a continuous independent variable, and a sex by date interaction term (Sall and Lehman 1996). We used δD_x as an approximation of latitudinal origin, with low values representing birds from higher latitudes and high values representing birds from lower latitudes. We used banding date as a surrogate for passage date through the Keys.

In order to insure that the assumptions of our statistical methods were met, we tested the appropriate distributions for deviations from normality using Shapiro-Wilk tests (Sall and Lehman 1996). When necessary, we used Bartlett's test to check for homogeneity of variance across distributions. We used $\alpha = 0.05$ when determining the significance of all tests. All statistical procedures were conducted using SAS JMP IN, version 3.2.6 statistical software (SAS Institute 1999).

RESULTS

REGRESSION MODEL

Our model ($\delta D_f = -34 + 1.0\ \delta D_p$, $r^2 = 0.83$, $n = 60$, $F_{1,58} = 281.34$, $P < 0.001$; Fig. 1) described a clear positive relationship between δD_f and δD_p throughout the breeding range of the Cooper's Hawk. The 95% confidence intervals for the model intercept and slope were –27‰ to –42‰ and 0.90 to 1.15, respectively. Results at individual feather collection sites demonstrated that (1) δD_f values were lower than δD_p values at all sample locations and (2) differences between δD_f and δD_p values at individual sites were fairly consistent across the species' range (Table 1).

The 95% confidence interval for estimating a δD_x value from a mean δD_f value was approximately $\delta D_x \pm$ 3‰ (Fig. 1, A). The 95% confidence interval for estimating a δD_x value from an individual δD_f value was approximately $\delta D_x \pm 16$‰ (Fig. 1, B).

Shapiro-Wilk tests indicated that distributions of δD_f values per study site and regression residuals were not significantly different from normal. Bartlett's test indicated that variances in δD_f across sites were not significantly different. Thus, assumptions of linear regression were met.

ESTIMATES OF ORIGINS

The mean δD_x value for our sample of migrants was –29‰ (Fig. 2). When we compared this mean to Hobson and Wassenaar's map of δD_p, we located it at approximately 37°N latitude. Since the 95% confidence interval for estimating a δD_x value from a mean δD_f value was $\pm$ 3‰, our estimate of 37°N latitude might vary by $\pm$ 1.5° latitude, or $\pm$ 166 km. Since a Shapiro-Wilk test indicated that the distribution of δD_x values was not significantly different from normal (Fig. 2), it seemed reasonable to use the "68-95-99.7 rule" for normal distributions (Moore 1995) to describe the dispersion of migrants. The SD of our sample of migrants was 11‰ (Fig. 2). We compared this SD to the δD_p map and found that 68% of the migrants originated between approximately 29°N and 39°N latitude (Fig. 3).

Results from the test of the general linear model indicated that there were no relationships ($n = 46$, $F_{3,42} = 0.58$, $P = 0.6$) between the origins of migrants and their passage date ($n = 45$, $t_{41} = -1.08$, $P = 0.3$), sex ($n = 46$, $t_{42} = 0.80$, $P = 0.4$), or combinations of date and sex ($n = 45$, $t_{41} = -0.54$, $P = 0.6$, Fig. 4). Shapiro-Wilk tests indicated that distributions of δD_x values for each sex and for model residuals were not significantly different from normal. Bartlett's test indicated that variances in δD_x were not significantly different between sexes. Thus, assumptions of general linear models were met.

DISCUSSION

RELATIONSHIP BETWEEN δD_f AND δD_p

The strong positive relationship between δD_f and δD_p shown in our model was similar to the results of several other researchers exploring the relationship between the δD values of animal tissues and precipitation (Miller et al. 1988, Cormie et al. 1994, Chamberlain et al. 1997, Hobson and Wassenaar 1997). Our results showed that (1) at all sample locations, δD_f values for Cooper's Hawks were lower than δD_p values and (2) the difference between the δD_f and δD_p values was fairly consistent across the species' range (Table 1). These patterns are similar to those

observed for insectivorous songbirds. The isotopic difference of $-34‰$ (our model intercept) between precipitation and feathers is partly a result of fractionation that occurs when precipitation is incorporated into plant carbohydrate (White 1988, Hobson and Wassenaar 1997). Based on controlled diet experiments with Red-winged Blackbirds (*Agelaius phoeniceus*), Hobson and Wassenaar (1997) concluded that, after this initial fractionation, the δD values of birds' feathers were the same as those of their food. Superficially, our model looks very similar to those produced by Hobson and Wassenaar (1997; $\delta D_f = -31 + 0.9 \, \delta D_p$) and Wassenaar and Hobson (2000b; $\delta D_f = -27.4 + 1.1 \, \delta D_p$), reinforcing their hypothesis that the relationship between δD_p and δD_f is similar across trophic levels. Unfortunately, the methods used to estimate δD_f values differed slightly in each of these three studies. Thus, concluding that there is no effect of trophic status on the relationship between δD_p and δD_f would be inappropriate. We echo the request of Wassenaar and Hobson (2000a), that future studies involving stable-hydrogen isotope analysis incorporate standardized lab techniques for estimating the δD value of non-exchangeable hydrogen in feathers. Such standardization is necessary for valid inter-laboratory comparisons. As these new techniques are adopted, we can expect to (1) gain a clearer picture of the true degree of fractionation across trophic levels in an ecosystem and (2) begin to settle on specific models appropriate for use at given trophic levels.

Some of the variation in the relationship between δD_f and δD_p in our model was likely a result of collecting feathers from "populations" that spanned up to 300 km distance or 500 m elevation while δD_p values are known to vary locally due to differences in storm trajectory (Friedman et al. 1992) and elevation (Ingraham et al. 1991). This incorporated spatial variation may have affected the width of our confidence intervals. The width of the intervals was a measure of the precision of our model and, thus, the geographic resolution of our application of the stable-hydrogen isotope analysis method. Although the incorporation of this variation decreased the precision of our model and the subsequent resolution of its application, we believe that it was important variation to capture. Incorporating this variation expanded confidence intervals, making conclusions more conservative. The alternative would be to create an overly precise model that ignores local-scale variation in δD_p and, as a result, may lead to incorrect conclusions on the origins of migrants.

A second set of variation incorporated into our model was probably related to sampling feathers across multiple years while the average δD_p value at a given locale has been shown to vary slightly among years (Ingraham et al. 1991, Friedman et al. 1992). Ideally, it would be best to reduce the effect of annual variation in δD_p by collecting samples from breeding and migrating birds during the same year (Wassenaar and Hobson 2000b). Researchers must decide, based on their questions of interest, if the increased precision attainable by collecting all feather samples during a single year is worth the additional expense and effort.

A third factor affecting the observed relationship between δD_p and δD_f was related to building a model with interpolated δD_p estimates instead of actual δD_p values for each breeding population. Measurements of δD_p are taken at relatively few locations across the continent. Thus, attempting to relate the δD_x values of migrants to actual δD_p values would not be very productive. In order to connect migrant δD_x values with geographic locations, it is necessary to have some estimation of how δD_p values are distributed across the continent. Our reliance on kriged maps (e.g., Hobson and Wassenaar 1997) for placing migrants made it necessary to incorporate interpolated δD_p

values into our model. With continued work, however, we expect δD_p maps to increase in accuracy as (1) δD_p values are accumulated for more locations across the continent and (2) the effects of elevation and weather patterns at various scales on δD_p become better understood.

ESTIMATES OF ORIGINS

Although thousands of Cooper's Hawks have been banded at migration sites, breeding-season band encounters are rare and our understanding of the migratory movements of many regional populations remains incomplete (Rosenfield and Bielefeldt 1993). Several raptor species, including the Peregrine Falcon (*Falco peregrinus*), Common Buzzard (*Buteo buteo*), and the Eurasian Kestrel (*Falco tinnunculus*), show well-documented patterns of leapfrog migration, where populations from high latitudes migrate beyond conspecifics of lower latitudes (Alerstam 1990). Palmer (1988) speculated that northern Cooper's Hawks are more migratory than southern ones. Given these prevailing ideas, and the lack of band encounter data related to Keys migrants, our *a priori* expectation was that immature Cooper's Hawks migrating through the Keys were mostly from the northern half of their range, which extends from southern Canada to central Florida (Fig. 3, Rosenfield and Bielefeldt 1993). It appears now that a small proportion of Keys migrants are from the northern half of their range and that most come from the Mid-Atlantic and Southeastern regions of the continent (Fig. 3). This new information will prove useful when interpreting abundance trends produced by the ongoing migration count in the Keys. The Keys migration count might now be considered important for monitoring immature Cooper's Hawks in a region where their status is imperfectly monitored by breeding season studies or other migration counts.

Our 95% confidence interval for estimating a δD_x value from the mean δD_f value of a group of migrants was $\delta D_x \pm 3‰$ (Fig. 1A). At 37°N latitude, this interval translated to $\pm 1.5°$ latitude. Given that (1) the breeding range of Cooper's Hawks in eastern North America spans more than 20° latitude and (2) most immature Cooper's Hawks migrating through the Keys were from within 10° latitude, the $\pm 1.5°$ latitudinal accuracy was more than adequate for estimating the regional origins of Keys migrants (Fig. 3). It is important to note that δD_p values do not vary consistently with latitude; e.g., δD_p contours are much wider in southeastern North America than they are in the northern part of the continent (Fig. 3). Thus, 95% confidence intervals for δD_x values will translate into more or fewer degrees of latitude depending on the region of interest.

Chamberlain et al. (1997) suggested that, depending upon the latitudinal range of a species, the δD value of a single migratory bird's feather could be used to link an individual with one of three or four breeding regions along a latitudinal gradient in North America. Our 95% confidence interval for estimating a δD_x value from the δD_f value of an individual ($\delta D_x \pm 16‰$) was a quantification of this point. Across North America, δD_x values for Cooper's Hawks varied from $-5‰$ in FL to $-82‰$ in BC, a range of 77‰. With this confidence interval and range in mind, an immature Cooper's Hawk captured during migration from a low latitude (e.g. $\delta D_x = -10‰$; 95% CI = 6‰ to $-26‰$) could have a significantly different δD_x value than a mid-latitude individual (e.g. $\delta D_x = -45‰$; 95% CI = $-29‰$ to $-61‰$). In addition, a mid-latitude individual could have a significantly different δD_x value from a high-latitude individual (e.g. $\delta D_x = -79‰$; 95% CI = $-63‰$ to $-95‰$). In this way, an individual Cooper's Hawk captured during

migration could be ascribed to, at best, one of three latitudinal groups. For species with a greater latitudinal range than Cooper's Hawks, the number of possible groups could increase. For species with limited latitudinal ranges, stable-hydrogen isotope analysis may not be precise enough to provide useful information on their latitudinal movements.

We estimate the total latitudinal range of immature Cooper's Hawks migrating through the Keys to be approximately 15° latitude, or 1,665 km (Fig. 3). Given this range, we wanted to see if there was a relationship between the latitudinal origin of migrants and their passage date. Learning if northern and southern populations pass a migration site at different times would be useful for interpreting within-season abundance patterns in migration counts. Our general linear model results showed that there was not a clear, linear relationship. Figure 4 shows that birds from different latitudes were captured in the Keys in a fairly random pattern over time. However, note the slight suggestion in Figure 4 that birds from the highest latitudes passed through the Keys during the second half of the season, while birds from middle and low latitudes passed through the Keys throughout the season.

Knowing if males and females migrating past count sites originated at different latitudes would also be helpful when connecting migration count trends to specific regions. Our general linear model showed that there was no such difference (Fig. 4). Thus, if sex-specific trends were observed in the Keys, they would not reflect patterns of productivity at different locations.

We acknowledge that the patterns we described for immature Cooper's Hawks migrating through the Keys may be appropriate for the 1998 season only. We sampled migrants during a single year in the Keys, while there may have been differential patterns of reproductive success across regions in that year. This could result in erroneous descriptions of latitudinal origins, as can be seen in the following example. If Cooper's Hawk productivity were particularly low in the northern half of their breeding range and particularly high in the southern half during the breeding season before we sampled feathers from migrants, we might conclude that most of the immature Cooper's Hawks migrating through the Keys came from the Southeast. On the other hand, had productivity been unusually high in northern latitudes and low in southern latitudes, we might have concluded the opposite. If the goal of researchers is to understand the mean latitudes of origin of raptors through a migration site, we recommend that investigators pool feathers collected over more than one year. This should eliminate the confounding effect of differential reproductive success across space within a single year on estimates of origins.

In this study, we considered stable isotopes of hydrogen only. Although looking at stable isotopes of hydrogen yielded valuable information on latitudinal origins, it provided no information on the longitudinal origins of Keys migrants. Chamberlain et al. (1997) suggested that the analysis of stable isotopes of other elements, such as carbon and sulphur, could be used to gain additional information on the approximate origins of migratory animals. They added that hydrogen, carbon, and sulphur are abundant in feathers, allowing researchers to use these elements to learn the origins of migrants without the use of destructive sampling methods. Wassenaar and Hobson (1998) showed slight longitudinal trends in stable-carbon isotopic signatures for butterflies and suggested that a bivariate analysis of stable-carbon and hydrogen isotopes may increase our ability to pinpoint the origins of populations. Wassenaar and Hobson (2000b) recently showed that bird feathers take on different stable-carbon isotope ratios depending on their participation in C_3- or C_4-based food webs. Using these patterns, they increased the precision

with which they could connect populations of birds with specific locations. Ultimately, the utility of carbon, sulphur, or any other element for learning the origins of migrating birds will depend on our finding predictable isotopic patterns at regional and continental scales. Readers interested in learning more about using stable isotopes to track the movements of migratory animals are encouraged to read Hobson's (1999) review.

In conclusion, we found that stable-hydrogen isotope analysis was an effective method for learning the natal origins of raptors observed during migration. The regional-scaled resolution of the technique proved to be more than adequate for our application. The method yielded a substantial amount of information in a much shorter time and with much less cost and effort than would have been required had the band-encounter method been used. Further, the estimation of origins of migrants derived from stable-hydrogen isotope analysis did not incorporate the biases of the band-encounter method resulting from the dependence of band-encounter data on people finding and properly reporting banded birds. Although at this stage the stable isotope method has limitations regarding its precision and resolution, the method offers a substantial step forward for migration researchers.

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TABLE 1. Summary of sample size, δD_f ($\bar{x} \pm$ SD), and interpolated δD_p (Hobson and Wassenaar 1997) for each study site.

Site	n	δD_f	δD_p
British Columbia	19	-111‰ ± 4‰	-79‰
North Dakota	2	-105‰ ± 3‰	-72‰
Wisconsin	22	-95‰ ± 8‰	-54‰
New Mexico	11	-84‰ ± 8‰	-49‰
Florida	6	-47‰ ± 7‰	-21‰
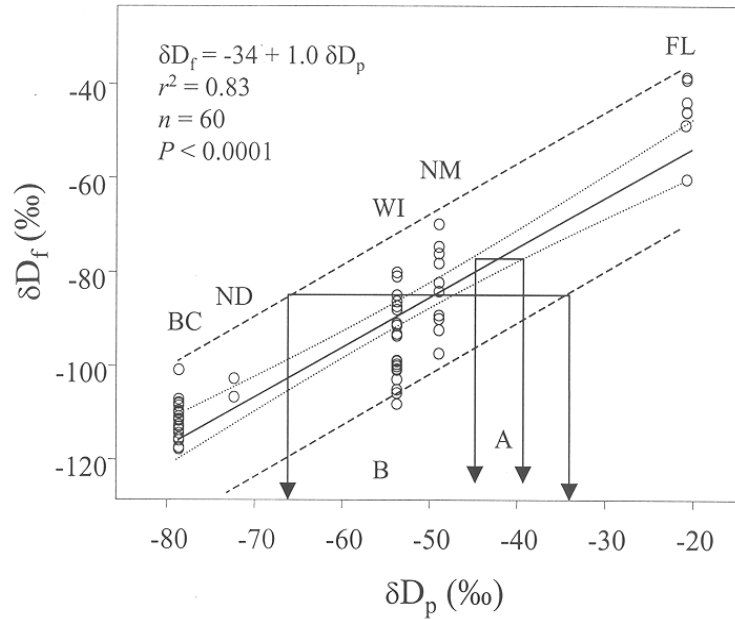
FIGURE 1. Regression model for the relationship between δD_f values of immature Cooper's Hawks and interpolated δD_p values (Hobson and Wassenaar 1997) from natal areas where feathers were grown. Two 95% inverse prediction intervals are also shown: one (A; $\delta D_x \pm 3‰$) for predicting δD_x values from the mean δD_f value of a group of migrants and another (B; $\delta D_x \pm 16‰$) for predicting a δD_x value from the δD_f value of an individual migrant.
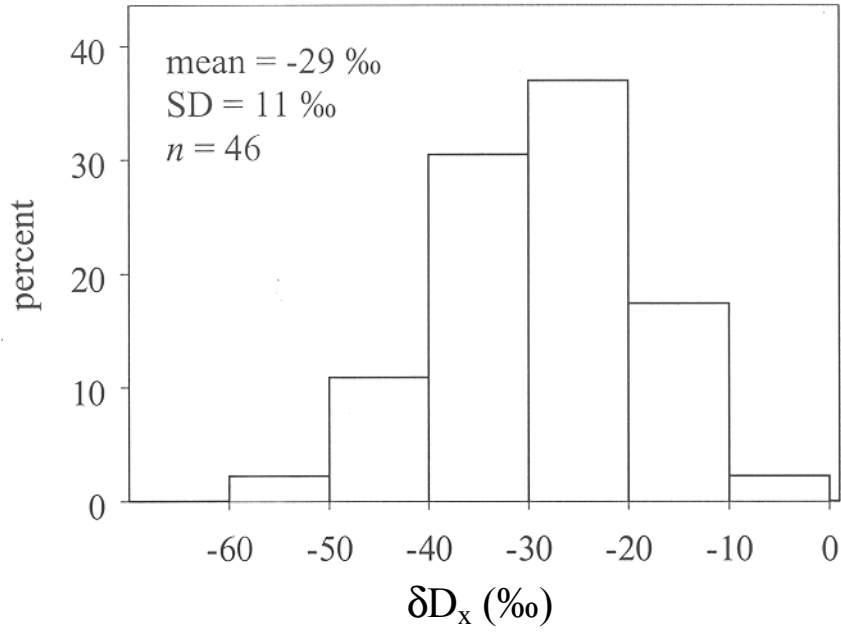
FIGURE 2. Histogram depicting the distribution of δD_x values estimated from the δD_f values of 46 immature Cooper's Hawks captured during fall migration 1998 in the Florida Keys.
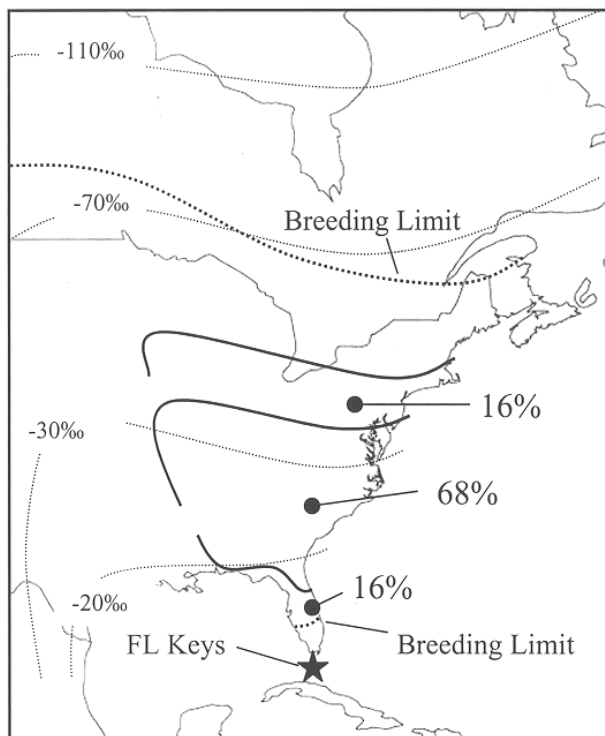
FIGURE 3. Approximate regional origins of 46 immature Cooper's Hawks captured during fall migration 1998 in the Florida Keys, as inferred from stable-hydrogen isotope analysis of migrants' feathers (latitude) and previous migration banding studies (longitude). Also shown are (1) the northern and southern limits of the breeding range of Cooper's Hawks in eastern North America (Rosenfield and Bielefeldt 1993; heavy dotted lines) and (2) δD_p values from Hobson and Wassenaar (1997; light dotted lines).
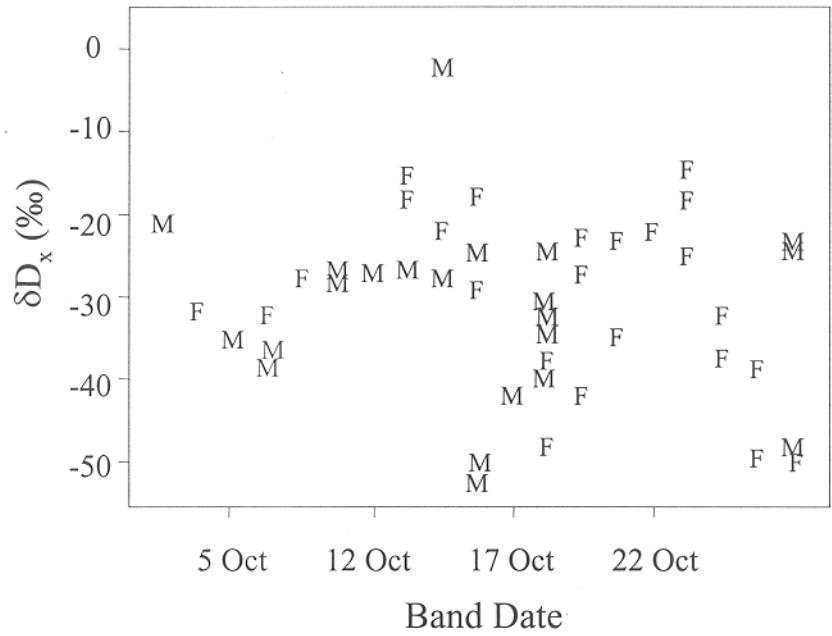
FIGURE 4. Scatter plot of δD_x values versus band date for 46 immature Cooper's Hawks captured during fall migration 1998 in the Florida Keys. Symbols indicate whether migrants were male (M) or female (F).