

VARIATION IN THE STABLE-HYDROGEN ISOTOPE COMPOSITION OF NORTHERN GOSHAWK FEATHERS: RELEVANCE TO THE STUDY OF MIGRATORY ORIGINS

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Abstract. The analysis of stable-hydrogen isotope ratios in feathers (δD_f) allows researchers to investigate avian movements and distributions to an extent never before possible. Nonetheless, natural variation in δD_f is poorly understood and, in particular, its implications for predictive models based on stable-hydrogen isotopes remain unclear. We employed hierarchical linear modeling to explore multiple levels of variation in the stable-hydrogen isotope composition of Northern Goshawk (*Accipiter gentilis*) feathers. We examined (1) inter-individual variation among goshawks from the same nest, and (2) intra-individual variation between multiple feathers from the same individual. Additionally, we assessed the importance of several factors (e.g., geographic location, climate, age, and sex characteristics) in explaining variation in δD_f . Variation among individuals was nearly eight times the magnitude of variation within an individual, although age differences explained most of this inter-individual variation. In contrast, most variation in δD values between multiple feathers from an individual remained unexplained. Additionally, we suggest temporal patterns of δD in precipitation (δD_p) as a potential explanation for the geographic variability in age-related differences that has precluded the description of movement patterns of adult raptors using δD_f . Furthermore, intra-individual variability necessitates consistency in feather selection and careful interpretation of δD_f -based models incorporating multiple feather types. Finally, although useful for describing the movements of groups of individuals, we suggest that variability inherent to environmental and intra-individual patterns of δD_p and δD_f , respectively, precludes the use of stable-hydrogen isotopes to describe movements of individual birds.

Key words: *Accipiter gentilis*, feathers, hierarchical linear model, hydrogen, migration, stable isotope, variation.

Variación en la Composición de Isótopos Estables de Hidrógeno de las Plumas de *Accipiter gentilis*: Relevancia para los Estudios sobre el Origen de la Migración

Resumen. El análisis de los cocientes de isótopos estables de hidrógeno presentes en las plumas (δD_f) permite a los investigadores estudiar los movimientos y distribuciones de las aves en un grado nunca antes posible. Sin embargo, la variación natural en δD_f es poco entendida, y particularmente sus implicaciones sobre modelos que hacen predicciones con base en isótopos estables de hidrógeno aún permanecen poco claras. Empleamos un modelo lineal jerárquico para explorar múltiples niveles de variación en la composición de isótopos estables de hidrógeno en las plumas de *Accipiter gentilis*. Examinamos (1) la variación entre individuos de un mismo nido y (2) la variación entre varias plumas de un mismo individuo. Además, determinamos la importancia de varios factores (e.g., aislamiento geográfico, clima, edad y características sexuales) para explicar las variaciones en δD_f . La variación entre individuos fue casi ocho veces mayor que la variación en un mismo individuo, aunque diferencias en la edad explicaron la mayoría de esta variación entre individuos. De manera contrastante, la mayor parte de la variación en los valores de δD entre varias plumas de un mismo individuo permaneció inexplicada. Además, sugerimos patrones temporales de δD en la precipitación (δD_p) como una posible explicación para la variabilidad geográfica en las diferencias relacionadas con la edad que han imposibilitado la descripción de los patrones de movimiento de aves rapaces adultas utilizando δD_f . Asimismo, la variabilidad intra-individual requiere que exista coherencia en la selección de plumas y una interpretación cuidadosa de los modelos basados en δD_f que incorporen múltiples tipos de plumas. Finalmente, a pesar de ser útiles para describir los movimientos de grupos de individuos, sugerimos que la variabilidad inherente al ambiente y los patrones intra-indivi-

duos de δD_p y δD_f , respectivamente, impiden el uso de isótopos estables de hidrógeno para describir los movimientos de aves individuales.

INTRODUCTION

The analysis of stable-hydrogen isotope ratios in feathers (δD_f) has allowed researchers to describe patterns of avian movements and distributions in a variety of avian taxa (Hobson 2003). Although based on well-established principles (Meehan et al. 2003), and despite the increasing popularity of the stable-hydrogen isotope technique, few studies have addressed natural variation in the hydrogen isotope composition of feathers.

Meehan et al. (2003) were the first to examine in detail the variation in δD_f among individuals from the same location. They found feathers of adult Cooper's Hawks (*Accipiter cooperii*) had considerably higher δD values than those of their offspring, and that the magnitude of the difference varied with both geographic location and the feather sampled, with no difference in δD_f between the adult sexes. More limited, secondary examinations of inter- and intra-individual variation in the hydrogen isotope composition of passerine feathers have produced mixed results. For example, Clegg et al. (2003) found no difference in δD_f values between the adult sexes of Wilson's Warblers (*Wilsonia pusilla*) at multiple sites in western North America. Adult and nestling Loggerhead Shrike (*Lanius ludovicianus*) feathers contained similar δD values at a single study site in Texas, although nestling sample size was very small (Hobson and Wassenaar 2001). Similarly, the association between feather δD values and geographic location was generally consistent for both adult and young Black-throated Blue Warblers (*Dendroica caerulescens*; Chamberlain et al. 1997, Rubenstein et al. 2002, D. R. Rubenstein, pers. comm.). Likewise, this association was consistent for both adult sexes of Wilson's Warblers, although within-individual δD_f values were consistently higher in body feathers than in flight feathers (Kelly et al. 2001). In contrast, Chamberlain et al. (1997) reported no difference in the isotopic composition between tail and body feathers of individual Black-throated Blue Warblers, but provided no estimate or test of the difference. Clearly, the uncertainty surrounding variation in the hydrogen isotope composition of feathers warrants a

more thorough evaluation of its natural variation.

To this end, we employed hierarchical linear modeling (HLM) to address three primary objectives using feathers from Northern Goshawks (*Accipiter gentilis*; hereafter goshawks): (1) to explore variation in the hydrogen isotope composition of feathers among individuals from the same nest; (2) to explore variation in the composition of multiple feathers sampled from the same individual; and (3) to assess the importance of several factors (e.g., geographic location, climate, age, and sex characteristics) in explaining variation in the δD values of feathers. Finally, we consider the relevance of multilevel variation in δD_f to the use of stable-hydrogen isotope ratios for describing patterns of goshawk migration and the movements of birds in general.

HYPOTHESES: VARIATION AMONG INDIVIDUALS

As the association of measurements within individuals typically is stronger than the association of measurements among individuals, we expected variation in δD_f among individuals to exceed variation between feathers within individuals. Additionally, based on previous work with accipiters (Meehan et al. 2003), we also expected age-related differences in δD_f ; specifically, we expected adults to have higher δD_f values than their offspring. Meehan et al. (2003) presented three nonexclusive hypotheses to explain the isotopic discrepancies between adults and nestlings.

Migrant prey. Premise: adults derive feather tissue grown early in the breeding season (e.g., inner primaries) from the muscle tissue of migrant avian prey; because δD values are higher at more southerly latitudes, the muscle tissues of prey migrating from more southerly locations are likely to possess δD values greater than those of the local, northern environment. If the incorporation of δD -enriched migrant tissues into adult feathers explains age-related differences, then δD values of adult feathers grown when migratory prey are no longer available should settle into equilibrium with the local environment (i.e., contain δD_f values similar to those of

their nestlings, which begin growing juvenile feathers after migratory prey become scarce).

Nonbreeding season tissue reserves. Premise: adults grow feathers using tissue reserves accumulated at lower latitudes or elevations. If δD -enriched tissue reserves explain age-related differences, then no differences in δD_f values between adults and nestlings should exist in non-migratory populations.

Evaporative cooling. Premise: during the physiologically demanding breeding season, evaporative cooling from the upper respiratory tract results in the fractionation of body water; the heavier deuterium isotopes are retained differentially, resulting in body water enriched with higher δD values (Wolf and Martinez del Rio 2000, 2003, McKechnie et al. 2004), and are then incorporated into feathers. Meehan et al. (2003) assert that evaporative cooling is likely commonplace both in females, during incubation and brooding, and in males, during food provisioning of the female and offspring. If evaporative cooling explains age-related differences in δD_f , the discrepancy between adult and nestling feathers should be a function of air temperature (and relative humidity) during the breeding season (McKechnie et al. 2004); specifically, we would expect the magnitude of the difference to be smaller in cooler (or humid) climates and larger in warmer (or arid) climates.

Additionally, we propose that temporal patterns of δD in precipitation (δD_p) mask the true magnitude of age-related differences in accipiters. More importantly, however, we suggest that temporal patterns of δD_p explain the geographic variability in age-related δD_p differences that has heretofore inhibited the use of δD_f to describe patterns of adult raptor movements.

HYPOTHESES: VARIATION WITHIN INDIVIDUALS

In goshawks and other raptor species, nestling flight feathers and their greater coverts emerge simultaneously (Boal 1994); likewise, adults replace flight feathers and their greater coverts concurrently (Wheeler 2003; ADS, pers. obs.). Consequently, we predicted there would be no measurable isotopic difference between feathers in adults or nestlings. Furthermore, we expected the extent of between-feather variation to be independent of an individual's age and sex.

METHODS

FEATHER COLLECTION

From June to August of 2002 and 2003 we obtained feather samples from 111 goshawks (28 adult females, 15 adult males, and 68 nestlings) from 52 nesting territories in western North America (Fig. 1, Table 1); we sampled each nest only once. As in other accipiters, adult goshawks molt primaries annually beginning near the initiation of incubation, typically in mid-April to mid-May (Squires and Reynolds 1997, Wheeler 2003). Primaries are molted serially from the innermost primary (P1) to the outermost primary (P10). Females typically begin molting before males, but either sex may arrest molt during periods of elevated energy demands (Henny et al. 1985, Palmer 1988). The molt status of adult goshawks captured during the mid- to late-nestling stage agreed generally with the findings of Henny et al. (1985); that is, adult goshawks replaced P1 and P2 consistently on the breeding grounds. Thus, from adults we collected 1–3 cm from the distal tip of a fresh inner primary (usually P2) and its associated greater covert (hereafter collectively referred to as the “feather sample”) to represent feathers replaced on the breeding grounds. From nestlings we collected the equivalent sample from their juvenile plumage (Duxbury et al. 2003). We obtained feather samples from at least one adult and one nestling in 33% of nests ($n = 17$), but in most cases we sampled adults (27%; $n = 14$) or nestlings (40%; $n = 21$) only; one to five individuals were sampled from each nest. Additionally, from the Kaibab Plateau, Arizona, we obtained greater coverts from 15 goshawks (2 adult females, 3 adult males, and 10 nestlings) from nine nesting territories (Fig. 1). Although we do not include them in our statistical analysis (see below), we present the general patterns in hydrogen isotope composition for comparison. None of our sampled nests were near enough to a marine ecosystem to warrant consideration of possible marine influences on δD_f values (Lott et al. 2003).

STABLE-ISOTOPE ANALYSES

Feather samples were analyzed at the Stable Isotope Hydrology and Ecology Lab at the National Water Research Institute (Environment Canada, Saskatoon, Saskatchewan) during March 2003 and January 2004. Although feathers were ana-

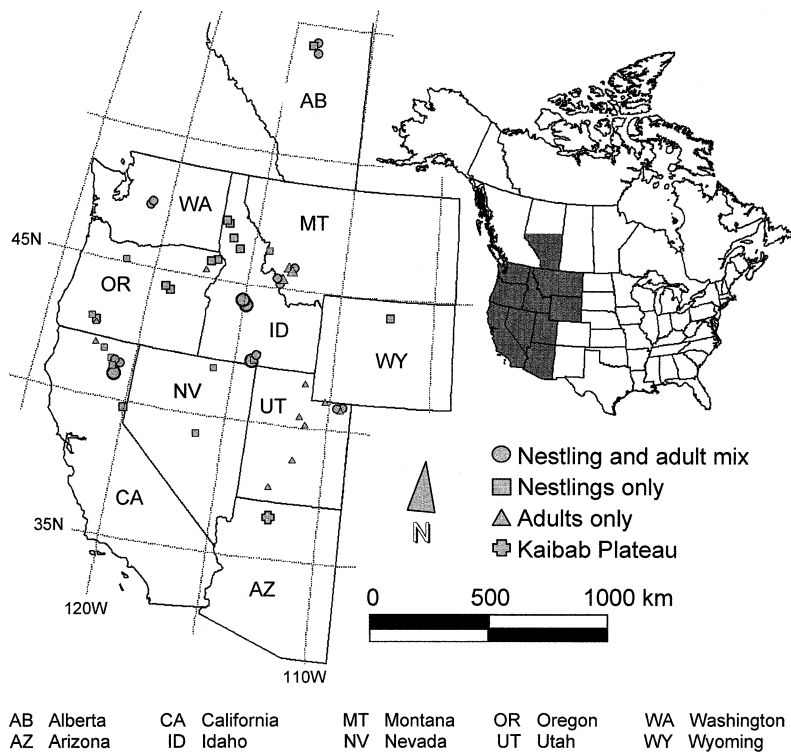


FIGURE 1. Location and composition of Northern Goshawk feather samples (inner primary and its greater covert; $n = 111$ individuals) from 52 nesting territories in western North America. Kaibab Plateau, Arizona, samples ($n = 15$ individuals) comprise only greater coverts. Point size indicates the number of individuals sampled at each location (small = 1; medium = 2–3; large = 4–5), excluding the Kaibab Plateau.

lyzed in two separate sessions, an inner primary and its associated greater covert were always analyzed in the same analysis session. Prior to stable-isotope analysis, we cleaned goshawk feathers of surface oils and debris using a 2:1 chloroform to methanol solution and air dried them for 48 hr in a fume hood. From the same location on each feather (along the distal rachis), we clipped and packaged samples weighing $0.35 (\pm 0.01)$ mg into silver capsules (Elemental Microanalysis 4×3.2 mm). Samples were comparatively equilibrated with keratin standards

prior to analysis (Wassenaar and Hobson 2003); thus, we report δD values only for the nonexchangeable component of feathers. The isotopic ratios of samples were measured using the pyrolysis and continuous-flow isotope-ratio mass spectrometry techniques described elsewhere (Wassenaar and Hobson 2003). Feather δD results are reported in parts per thousand (‰) deviation from the VSMOW-SLAP standard scale. Repeated analyses of hydrogen isotope reference material yielded a measurement repeatability of better than $\pm 1.0\%$.

TABLE 1. Distribution of Northern Goshawk feather samples collected from 52 nesting territories in western North America during 2002 and 2003.

Age and sex class	Year		Geographic extent	
	2002	2003	Latitude ($^{\circ}$ N)	Longitude ($^{\circ}$ W)
Adult females	21	7	37.6–54.3	109.4–122.5
Adult males	14	1	40.1–47.4	109.6–122.2
Nestlings	30	38	39.1–54.3	109.5–122.5

STATISTICAL ANALYSES

Our study involves a multilevel design in which we measured δD in multiple feathers within individuals, which themselves were grouped within nests (Fig. 2). Hierarchical linear models, an application of generalized linear mixed models to hierarchically structured data, provide the framework within which we can model this multilevel relationship explicitly (Littell et al. 1996, McCulloch and Searle 2001, Bryk and Raudenbush 2002, Goldstein 2003). We conducted all HLM-related analyses within the MIXED procedure of SAS/STAT Version 8.2 (SAS Institute 1999). SAS code is available from the primary author.

Unexplained variation. First, we explored the multilevel distribution of stable-hydrogen isotope variation in goshawk feathers by constructing an unconditional means model, which decomposes the total unexplained variation into independent components at each level of the hierarchy (Bryk and Raudenbush 2002).

Variance structure. Subsequently, we assessed three competing variance-covariance (hereafter variance) structures that model the variability in δD_f ; the variance structures differed in the specification of intra-individual variation (Fig. 2). The simplest of these models, the variance components model, implied a common intra-individual variation for all individuals (i.e., differences in δD between feathers were similar for all individuals; Fig. 2a). We also assessed two models with increasingly complex variance structures by estimating separate intra-individual variances for (1) adults and nestlings (age dependent, Fig. 2b), and (2) adult females, adult males, and nestlings (age and sex dependent, Fig. 2c). As in other accipiters (Meehan et al. 2003), feathers from nestlings of both sexes contained similar isotopic information; thus, we did not distinguish between nestling sexes.

Using a saturated model (i.e., main effects and all two-way interactions), we assessed variance structures using restricted maximum likelihood (REML) estimation, which provides unbiased estimates of variance parameters. We selected among competing variance structures using second-order Akaike’s Information Criterion (AIC_c) model selection information (Burnham and Anderson 2002). Furthermore, because we sampled feathers from goshawks in two different breeding seasons, we included sampling year as a ran-

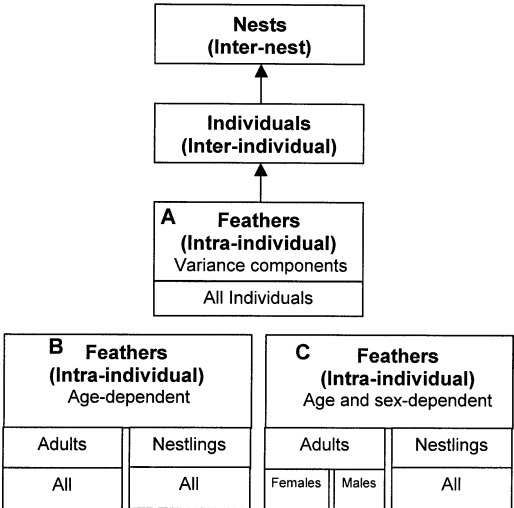


FIGURE 2. Schematic illustrating the hierarchical structure of stable-hydrogen isotope (δD) variation in Northern Goshawk feathers and three competing models of δD variance structures: the variance components model (A) and two models specifying increasing complexity in intra-individual variation (B, C). See text for a description of each model. Parentheses indicate the variance parameter estimated at each level of the hierarchy.

dom effect in our assessment of variance structures; in all circumstances, year effects were negligible and thus excluded from the final variance structure.

Fixed effects. Once we identified the best-fitting variance structure, we assessed the importance of geographic location (latitude and longitude), climate (average air temperature), and an individual’s age (adult vs. nestling) and sex (adults only) in explaining variation in δD_f . Other covariates with an apparent controlling effect on δD_p , such as elevation and distance from the coast, are different manifestations of the effect of air temperature on δD_p (Gat 1996, Araguas-Araguas et al. 2000); thus, by using average air temperature as a covariate, we effectively incorporate the effects of altitude and distance from the coast on δD_p . We obtained interpolated monthly average air temperature data (Meehan et al. 2004), and calculated a weighted average (based on the number of days in the month) from April to August, a time period representing the core of the goshawk nesting period (Reynolds and Squires 1997). Beginning with the saturated model, we conducted a backwards elimination of non-important interactions. As this

study was exploratory in nature, we retained interactions at the $\alpha = 0.05$ level and all main effects in the final model. We report results from either the last iteration prior to removal (i.e., eliminated interactions) or the final reduced model (i.e., main effects, retained interactions). We calculated simultaneous confidence intervals to evaluate contrasts of adjusted means for the age/sex main effect (ADJUST = SIMULATE option in the LSMEANS statement of PROC MIXED) with a familywise $\alpha = 0.05$ (Westfall et al. 1999). We used MLwiN version 1.10 (Rasbash et al. 2000) to assess the model assumptions of normally distributed errors and homogeneous variance; both assumptions were met. Unless otherwise indicated, we report means \pm SE.

TEMPORAL PATTERNS OF δD_p

To explore the effect of temporal patterns of δD_p on age-related discrepancies in δD_f , we examined the trend in δD_p from March to September for our 52 nest territories in western North America (Fig. 1). We derived the δD_p trend from interpolated monthly estimates of δD_p generated by Meehan et al. (2004). For comparative purposes, we examined the corresponding trend in δD_p (1975–1982) for an insular Cooper’s Hawk study site in British Columbia (Meehan et al. 2003) using data from the International Atomic Energy Agency database (IAEA 2001). Subsequently, we compared δD_p between feather growth periods of adults and nestlings.

RESULTS

Most variation in the stable-hydrogen isotope composition of goshawk feathers was attributable to differences among nests (Table 2). δD_f values decreased significantly from south to north and from west to east (Table 3). Additionally, δD_f values decreased with increasing air temperature during the core of the goshawk breeding season (Table 3). Together, geographic location (i.e., latitude and longitude) and average air temperature explained a majority of the variation among nests (Table 2). Of greater concern, however, is the appreciable variation we found both among and within individuals.

VARIATION AMONG INDIVIDUALS

Inter-individual variation was more than eight times the magnitude of variation between feathers (Table 2). Nearly all of the variation occur-

TABLE 2. Distribution of variation in the stable-hydrogen isotope ratios (δD) of Northern Goshawk feathers. The variance partition coefficient, derived from an unconditional means model, summarizes the portion of total variance in a dependent variable occurring at a given level of a hierarchy or, in the case of partitioned intra-individual (i.e., between feathers) variation, within a level of a hierarchy (Goldstein 2003).

Covariance parameter estimated	Variance-partition coefficient	Percent variation explained ^a
Among nests	0.60	63
Among individuals	0.36	86
Between feathers	0.04	<1
Between feathers (partitioned by age and sex)		
Adult females	0.43	
Adult males	0.54	
Nestlings	0.03	

^a Percent change in the variance component after the final model was specified.

ring among individuals was attributable to large age-related differences in δD_f values (Tables 2 and 3). δD_f values were considerably higher in adult females ($t_{58.2} = 14.4$, $P < 0.001$; 95% CI: 30.1–41.9‰) and adult males ($t_{37.6} = 15.6$, $P < 0.001$; 95% CI: 35.2–47.9‰) relative to their nestlings; we found no sex-related difference in adult δD_f values ($t_{76.6} = 2.5$, $P = 0.23$; 95% CI: –13.7–2.6‰). We observed similar patterns in our Arizona sample after adjusting for geographic location and breeding season temperature: feathers of nestlings ($-60.8 \pm 4.9\%$) had lower δD values than feathers from adults ($-12.0 \pm 7.2\%$). Furthermore, when we considered only those nests with both adult and nestling samples, adult δD_f values were comparably high (95% CI of average inner primary difference: 23.9–39.2‰). Differences in δD_f between adults and nestlings increased with temperature, but only in adult females (Table 3).

VARIATION WITHIN INDIVIDUALS

The extent of between-feather variation differed greatly among goshawks of different age and sex classes (Table 2, Fig. 3). Estimating separate intra-individual variances for adult females, adult males, and nestlings resulted in the best-fitting variance model (Age and Sex-Dependent model, Fig. 2c; Table 4). Stable-hydrogen isotope composition was least variable between feathers in nestlings and approximately 14 and 18 times more variable within adult females and

TABLE 3. Results of a hierarchical linear model describing the relationship between the stable-hydrogen isotope (δD) composition of Northern Goshawk feathers and feather type, age and sex class, climate, and geographic location (i.e., latitude, longitude). The analysis was based on samples from 111 individuals (28 adult females, 15 adult males, and 68 nestlings). Global tests are reported for all classification variables and eliminated interaction terms. Parameter estimates of zero indicate the reference category in classification variables. Least-squares means are reported for feather and age and sex classes, as they are more readily interpretable. Denominator degrees of freedom were corrected using the Kenward and Roger (1997) method, as recommended by Schaafje et al. (2001).

Parameter	Numerator df	Denominator df	Estimate	SE	F	P
Intercept	1	56.9	386.2	187.2	2.1	0.04
Feather	1	68.2			8.1	<0.01
Greater covert			-72.6	2.3		
Inner primary			-71.0	2.3		
Feather \times latitude	1	68.2			6.1	0.02
Greater covert	1	68.2	-0.2	0.1	6.1	0.02
Inner primary	0		0.0	0.0		
Age and sex	2	80.0			4.9	0.01
Adult females			-61.6	3.0		
Adult males			-56.1	3.2		
Nestlings			-97.7	2.1		
Age and sex \times temperature	2	77.8			4.5	0.01
Adult females	1	74.0	3.2	1.5	6.4	0.03
Adult males	1	56.4	-4.8	2.9	4.8	0.10
Nestlings	0		0.0	0.0		
Temperature	1	57.2	-42.4	17.2	6.2	0.02
Temperature \times latitude	1	56.1	1.0	0.4	6.3	0.01
Latitude	1	56.6	-14.7	4.5	10.4	<0.01
Longitude	1	51.6	-1.3	0.6	4.7	0.03
Eliminated interactions (in order of elimination)						
Age and sex \times latitude	2	60.0			0.2	0.83
Feather \times longitude	1	67.1			0.6	0.44
Feather \times age and sex	2	29.0			1.0	0.40
Temperature \times feather	1	67.2			1.0	0.32
Age and sex \times longitude	2	67.5			1.5	0.24
Temperature \times longitude	1	43.7			3.0	0.09
Latitude \times longitude	1	42.1			2.3	0.14

adult males, respectively (Table 2). Inner primaries had, on average, higher δD values than greater coverts ($t_{68.6} = 5.0$, $P < 0.001$; 95% CI: 0.96–2.3‰), although the difference was noticeable only in nestlings (Fig. 2). Furthermore, the magnitude of the isotopic difference between feather types decreased slightly with latitude in all age classes (Table 3). Nonetheless, differences in the δD_f values attributable to feather type did little to explain the variation within an individual (Table 2).

TEMPORAL PATTERNS OF δD_p

Throughout most of North America, interpolated monthly estimates of δD_p show a marked but consistent fluctuation throughout the goshawk breeding season (Fig. 4). Specifically for our 52 nest locations, the stable-hydrogen isotope com-

position of precipitation is depleted early in the breeding season (April–May), when adult goshawks begin molting new primaries, relative to δD_p later in the breeding season (e.g., June–July), when nestlings grow their juvenile plumage (Difference of 2-month averages: $-26.3 \pm 0.6\text{‰}$). Nonetheless, isotopic equilibration between an individual's feathers and their diet occurs gradually (ca. 20–45 days; Bearhop et al. 2002); therefore, although seasonal differences in δD_p (Fig. 4) should manifest themselves in δD_f , the stable-hydrogen isotope composition of feathers likely reflects that of precipitation prior to feather growth (e.g., adult feathers grown in April–May reflect precipitation in March–April, juvenile feathers grown in June–July reflect precipitation in May–June). As a result, larger average δD discrepancies between feather growth

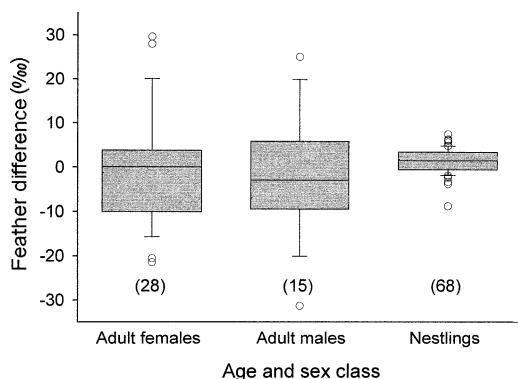


FIGURE 3. Box plots showing difference in the stable-hydrogen isotope (δD) ratio between an inner primary and the associated greater covert, sampled from the same individual. Mean, central 50% (boxes), and 5th and 95th percentiles of the difference are illustrated for adult females, adult males, and nestlings; unfilled circles represent outliers. Differences are (inner primary-greater covert). Sample sizes are indicated in parentheses.

periods are probable (difference of 2-month averages: $-38.1 \pm 1.1\text{‰}$). Even if the stable-hydrogen isotope composition of nestling feathers reflects that of the entire growing season prior to feather growth (i.e., March–June), pronounced δD discrepancies still exist (Difference: $-19.1 \pm 0.1\text{‰}$).

Seasonal patterns of δD_p near the insular Cooper's Hawk study site in British Columbia (Meehan et al. 2003) exhibited greater consistency than inland goshawk nest locations (Fig. 4).

DISCUSSION

Hierarchical linear modeling enabled us to explore multiple levels of variation in the stable-hydrogen isotope composition of goshawk feathers, such as that among individuals within a nest, and between feathers within an individual. Most of the variation among nests was explained by factors with well-established relationships with δD_p . Specifically, δD_p relates inversely with latitude, elevation, and distance from the coast; the latter two are probable explanations for the inverse relationship we observed between δD_f and longitude, as both increase from west to east in western North America. Interestingly, we observed a negative relationship between temperature and δD , contrary to the typical positive relationship between the two factors (Dansgaard 1964, Rozanski et al. 1993); however, this relationship was weak and probably spurious, re-

TABLE 4. Second-order Akaike's Information Criterion (AIC_c) for three competing models of stable-hydrogen isotope variation in Northern Goshawk feathers. See text for model descriptions.

Model	k^b	AIC _c model selection ^a		
		AIC _c	ΔAIC_c	w_i
Age and sex-dependent	5	1480.8	0.0	1.000
Age-dependent	4	1514.9	34.1	0.000
Variance components	3	1615.4	134.6	0.000

^a AIC_c: Second-order Akaike Information Criterion; ΔAIC_c : Difference for model relative to the smallest AIC_c in the model set; w_i : Akaike weight, interpreted as the probability that model i is the Kullback-Leibler model best approximating reality (Burnham and Anderson 2002).

^b Number of variance parameters estimated.

sulting ostensibly from a correlation between latitude and temperature at our sampling sites ($r = 0.24$, $P < 0.01$). For example, an *ad hoc* analysis within the confines of our final HLM assessing the importance of the order of variable entry into a model revealed that the main effect of temperature disappeared altogether when latitude was removed as a covariate from the model; conversely, latitude remained a strong predictor of δD_f regardless of whether temperature was included as an explanatory variable.

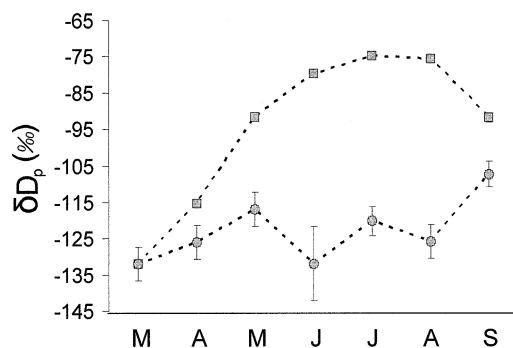


FIGURE 4. Average trend in the stable-hydrogen isotope ratios of precipitation (δD_p) from March–September at 52 Northern Goshawk nest sites in western North America (squares) and a Cooper's Hawk population on Vancouver Island, British Columbia, Canada (circles; Meehan et al. 2003). Interpolated δD_p estimates for goshawk nests derived from Meehan et al. (2004); δD_p estimates for Vancouver Island (1975–1982) derived from IAEA (2001). Trend increments are shown \pm SE; those of goshawks nests are too small to be noticed.

As we expected, variation in δD_f among individuals far exceeded variation between feathers within individuals. Nonetheless, to extract the greatest utility from the stable isotope technique, we must understand the factors that contribute to inter- and intra-individual variability.

VARIATION AMONG INDIVIDUALS

Our findings that adults had higher, southerly-biased δD_f values relative to their offspring, parallel those in the related Cooper's Hawk (Meehan et al. 2003), but conflict with work on passerines (Chamberlain et al. 1997, Hobson and Wassenaar 2001, Rubenstein et al. 2002). We consider Meehan et al.'s (2003) three nonexclusive hypotheses as they may apply to goshawks.

Migrant prey. Meehan et al. (2003) analyzed the middle primaries of three adults, presumably grown later in the breeding season when migrant prey are absent, and found that δD_f values remained elevated, comparable to those of the inner primaries from the same birds. More convincingly, perhaps, we found the same pattern of elevated δD_f values in adult goshawks relative to their offspring from populations in northern Arizona, Utah, northern Nevada, and southern Idaho, all of which consume primarily nonmigratory mammalian prey (Squires and Reynolds 1997).

Nonbreeding season tissue reserves. Meehan et al. (2003) reported higher δD values in adults relative to nestlings for a largely nonmigratory population of Cooper's Hawks. Similarly, we observed the same pattern in a population of goshawks in Arizona where birds are mainly sedentary (R. Reynolds, pers. comm.). Furthermore, feathers are apparently synthesized from immediate dietary intake or short-term reserves (Murphy 1996). This idea is supported by work with other isotopes (e.g., ^{13}C , ^{15}N), although the possibility exists that long-term stores are used to some extent in feather synthesis (Bearhop et al. 2002).

Evaporative cooling. The discrepancy between adult and nestling feathers was a function of air temperature during the breeding season, although only in adult females. Comparable δD_f values between sympatric nonbreeding adults and nestlings would provide further support for this hypothesis, but we were unable to obtain samples from any nonbreeding goshawks. If accipiters indeed utilize evaporative cooling throughout the breeding season, the evaporative

cooling hypothesis correctly predicts the elevated δD values in a small sample of adult feathers grown throughout the breeding season (Meehan et al. 2003). However, the use of evaporative cooling during the breeding season does nothing to explain elevated δD_f values in adult feathers grown during the nonbreeding season. We suggest an examination of the influence of relative humidity on δD_f , both independently and in combination with temperature.

Assessment. For accipiters, the causes of age-related discrepancies in δD_f values remains largely unexplained, but seemingly originate physiologically rather than ecologically. Furthermore, the causes responsible for enriched inner primaries in adult accipiters exerts an effect on δD_f up to 20–40‰ beyond the age-related differences reported in previous (30–80‰; Meehan et al. 2003) and current work (30–45‰), an effect hitherto masked by temporal patterns of δD_p .

Interestingly, the evaporative cooling hypothesis potentially could explain the discrepant patterns in raptors and passerines. That is, most raptor species molt during the physiologically challenging breeding season (Wheeler 2003). Undertaking an energetically demanding molt (Walsberg 1983, Lindström et al. 1993) concurrently with reproduction might increase the frequency of evaporative cooling, as well as exacerbate its enriching effect on feather stable-hydrogen isotope composition. Conversely, most passerines delay molt until after breeding, and generally complete their molt prior to migration. In most North American migratory passerines, the growth of both nestling and adult feathers occurs during a period of relative stability in environmental δD values (i.e., June–August). Thus, differences in molt phenology may explain the presence or absence of age-related variation in δD_f values between raptors and passerines, respectively. A study of passerines that molt concurrently with reproduction would be ideal, although inducing feather molt (Grubb 1989) in breeding passerines may prove instructive. Furthermore, we may gain similar insight from sympatric species associations with different molt strategies. For example, Dunlin (*Calidris alpina*) in northern Alaska molt during the breeding season (Holmes 1966), while the related White-rumped (*C. fuscicollis*) and Baird's Sandpipers (*C. bairdii*) molt subsequent to breeding (Farmer et al. 2003).

Temporal patterns of δD_p seemingly explain much of the geographic variability in age-related discrepancies of δD_f . For example, the most extreme age-related difference to date occurred in an insular population of Cooper's Hawks from British Columbia (95% CI: 65–80‰; Meehan et al. 2003). However, seasonal patterns of δD_p near the study sites exhibit greater consistency than inland locations. Specifically, relative to the nestling feather growth period, the stable-hydrogen isotope composition of precipitation during the adult feather growth period lacks the depletion characteristic of other areas. Thus, the incorporation of adjustments for δD_p results in a discrepancy comparable to those in Cooper's Hawks and goshawks from other regions.

VARIATION WITHIN INDIVIDUALS

As in the present study, other researchers have found differences in δD values between feathers of an individual (Kelly et al. 2001, Meehan et al. 2003). To our knowledge, however, we are the first to document δD differences between feathers grown simultaneously. Nonetheless, we have no ready explanations for either the small, but consistent δD discrepancies between feathers in nestlings, or the variable, often substantial δD discrepancies exhibited by adults. Nor can we rationalize the differential retention of heavy isotopes in primaries versus greater coverts. Furthermore, the large variation between feathers of adults relative to nestlings remains unexplained.

CONCLUSIONS AND RECOMMENDATIONS

As suggested by Meehan et al. (2003), differences in δD_f values between adults and nestlings are inconsequential when studying migratory origins if the differences are consistent. We provide evidence that age-related δD_f discrepancies are sufficiently consistent to enable the prediction of adult origins using stable-hydrogen isotopes, once geographic and temporal patterns of δD_p are considered, with the following stipulations: (1) that δD_f be modeled explicitly as a function of δD_p , and (2) that separate models be constructed for adults and nestlings using δD_p information most representative of the period of feather growth. Thus, migratory origins of adult accipiters may be inferred, although likely with less precision than those of juveniles due to intra-individual variability. Intra-individual variability in adult goshawks is also problematic in that feather selection can greatly influence pre-

dictions derived from δD_f values and it represents a source of variation that necessitates cautious interpretation of δD_f -based models incorporating multiple feather types. Finally, we suggest that the variation inherent in environmental and within-individual patterns of δD_p and δD_f , respectively, precludes the use of stable-hydrogen isotopes for describing movements of individual birds, and we question the utility of average relationships in representing the movement of any particular individual.

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