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Enriched feather hydrogen isotope values for Wood Thrushes sampled in Georgia, USA, during the breeding season: implications for quantifying dispersal

Larkin A. Powell
University of Nebraska-Lincoln, lpowell3@unl.edu

Keith Hobson
Prairie and Northern Wildlife Research Center

Enriched feather hydrogen isotope values for Wood Thrushes sampled in Georgia, USA, during the breeding season: implications for quantifying dispersal

L.A. Powell and K.A. Hobson

Abstract: We used an analysis of deuterium values (δD) of 151 Wood Thrush (*Hylocichla mustelina* (J.F. Gmelin, 1789)) feathers collected during the breeding season at the Piedmont National Wildlife Refuge in Georgia, USA, to determine fidelity to the study site. We compared δD values in feathers of birds with known molt locations and birds with unknown molt locations. Mean feather value of δD was –24.8‰ (SD = 10.5‰, range = –48.0‰ to –5.5‰), and we were unable to determine a site-specific signature to assess fidelity of breeders within our sample. We used an information criterion approach to evaluate multiple hypotheses to explain the high variation in δD, and the geographic location of sample sites within the study area was selected as the best model. Feather δD values were higher than expected from mean growing-season rainfall δD values predicted for our study site. We discuss possible explanations for the enriched δD values and postulate that heat stress during molt may have contributed to our results. We suggest that future stable isotope data collection consider the potential for small-scale variation in feather δD values; information on diet gathered simultaneously with feather samples may be valuable for future studies.

Résumé : L'analyse des teneurs de deutérium (δD) dans les plumes de 151 grives des bois (*Hylocichla mustelina* (J.F. Gmelin, 1789)) récoltées durant la saison de reproduction dans la réserve faunique nationale de Piedmont en Géorgie, É.-U., nous a servi à déterminer la fidélité au site d'étude. Nous avons comparé les valeurs de δD dans des plumes d'oiseaux ayant un site de mue connu et d'oiseaux de site de mue inconnu. La valeur moyenne de δD est de –24,8 ‰ (ET = 10,5 ‰, étendue = –48,0 ‰ à –5,5 ‰); nous sommes incapables d'identifier une signature spécifique au site qui permettrait d'évaluer la fidélité des reproducteurs dans notre échantillon. Nous utilisons une méthode basée sur le critère d'information pour évaluer les différentes hypothèses explicatives de la forte variation de δD; nous avons retenu la position géographique de l'échantillon dans la zone d'étude comme le meilleur modèle. Les valeurs de δD des plumes sont plus élevées qu'attendu d'après les valeurs de δD des précipitations moyennes prédites pour notre site d'étude durant la saison de croissance. Nous examinons les explications possibles des teneurs enrichies de δD et nous concluons que le stress thermique durant la mue a pu contribuer aux résultats observés. Nous proposons que les récoltes futures de données sur les isotopes stables tiennent compte des variations à petite échelle des teneurs de δD dans les plumes; des données sur l'alimentation récoltées au moment du prélèvement des échantillons de plumes pourraient s'avérer utiles dans ces études futures.

[Traduit par la Rédaction]

Introduction

Biologists have recently used measurements of stable isotopes, such as those of carbon (δ^{13}C), nitrogen (δ^{15}N), sulfur (δ^{34}S), hydrogen (δD), and strontium (δ^{87}Sr), in animal tissues to determine the location of individuals during a previous time period (reviewed by Hobson 1999; Webster et al. 2002; Hobson 2005). Such methods are useful for providing previous locations of animals because tissues in individuals reflect the signature of isotopes of foods previously eaten, and biogeochemical processes cause these signatures to vary spatially (Hobson 1999). In North America, the con-tinental latitudinal gradient for deuterium in feathers (δD_f), caused by trends in this isotope in growing-season precipitation (δD_p), has proven especially useful (Hobson 2005).

Feathers are metabolically inactive following formation and so provide a discrete record of location during the period of feather replacement (Hobson 1999). To date, most stable-isotope studies focused on determining migratory pathways or connectivity between breeding, wintering, and stopover sites; biologists capture birds during migration and use stable isotopes to approximate an individual's location prior to migration. However, Hobson et al. (2004) recently used stable hydrogen and carbon isotope analyses to provide

L.A. Powell.[1] School of Natural Resources, University of Nebraska – Lincoln, Lincoln, NE 68583-0974, USA.
K.A. Hobson. Canadian Wildlife Service, 11 Innovation Boulevard, Saskatoon, SK S7N 3H5, Canada.

[1]Corresponding author (e-mail: lpowell3@unl.edu).

evidence for breeding and natal dispersal of Ovenbirds (*Seiurus aurocapillus* (L., 1766)) and American Redstarts (*Setophaga ruticilla* (L., 1758)) sampled in central and southern Saskatchewan, Canada. Such dispersal analysis using stable isotopes is based on the assumption that the study species molts prior to migration, at the end of the prior growing season.

Biologists commonly seek to determine if animal populations are increasing or decreasing in size. Identification of regions with declining populations or low breeding fidelity can potentially lead to changes in habitat management with the goal of reversing population declines. Under recent continental-scale concerns of bird population declines, biologists have used field studies of productivity and survival to assess populations across large, regional areas (e.g., Donovan et al. 1995; Simons et al. 2000). However, these field studies require intense monitoring of birds and their nests, which is very labour-intensive and expensive. Stable-isotope analyses potentially provide a new method of assessing population stability.

The Wood Thrush (*Hylocichla mustelina* (J.F. Gmelin, 1789)) is a species of concern in Georgia, as populations there have declined 1.9% per year during 1966–1996 (Sauer et al. 1997). Wood Thrushes molt tail feathers during August and September presumably on or close to the breeding grounds (Pyle et al. 1987; Roth et al. 1996). Thus, we hypothesized that a captured individual's tail feathers have potential to provide a record of the bird's location in the previous breeding season. Our goal was to determine if stable-isotope analyses could be used to determine fidelity and general population stability of Wood Thrushes in a breeding region, following the approach of Hobson et al. (2004). Our objectives were to (*i*) compare δD_f values and associated variance of values between samples of birds with known molt locations and birds with unknown molt locations and (*ii*) compare δD_f values and variance of values between sex and age classes, as well as among samples collected throughout our single population.

Materials and methods

Field collections

We obtained tail feathers from adult and juvenile Wood Thrushes at the Piedmont National Wildlife Refuge (henceforth, Refuge; Fig. 1) in Georgia during 1994–1996 as part of a large study on the population dynamics of the species (Powell et al. 2000*a*; Lang et al. 2002). The 14 146 ha Refuge (33.08°N, 83.67°W; elevation 100–180 m) is principally mature pine/hardwood forest dominated by loblolly pine (*Pinus taeda* L.), oaks (genus *Quercus* L.), and hickories (genus *Carya* Nutt.). We also collected some feathers from Wood Thrushes in one forest compartment at the Oconee National Forest, which borders the Refuge to the North.

Wood Thrushes were captured in systematic or target mist nets between April and August (Powell et al. 2000*a*), and were aged as hatch-year (HY) or after-hatch-year (AHY) based on plumage characteristics (Pyle et al. 1987). We removed the right, outermost rectrix from each bird and placed the feathers in individual, labeled envelopes. We originally collected the feathers to be used in a study of ptilochronology (Grubb 1989); accordingly, we obtained a sample from each

bird during its first capture within a breeding season, and upon recapture, the replacement feather was sampled.

Isotopic methods

Feathers were cleaned in a 2:1 chloroform:methanol solvent rinse and prepared for δD analysis at the National Water Research Institute in Saskatoon, Saskatchewan, Canada. We used keratin standards to correct for uncontrolled isotopic exchange between samples and ambient water vapor. The values reported here are equivalent to nonexchangeable hydrogen (Wassenaar and Hobson 2003).

Stable hydrogen isotope measurements on feathers and keratin standards were performed on H_2 derived from high-temperature flash pyrolysis of feathers and continuous flow – isotope ratio mass spectrometry (CF–IRMS). Pure H_2 was used as the sample analysis gas and the isotopic reference gas. A Eurovector 3000TM (Milan, Italy) high temperature elemental analyzer (EA) with an autosampler was used to automatically pyrolyze feather samples to a single pulse of H_2 gas. The resolved H_2 sample pulse was then introduced to the isotope-ratio mass spectrometer (Micromass IsoprimeTM with an electrostatic analyzer; Micromass, Manchester, UK) via an open-split capillary. All δD results are expressed in units of per thousand (‰) and normalized on the Vienna Standard Mean Ocean Water – Standard Light Antarctic Precipitation (VSMOW–SLAP) standard scale. Repeated analysis of hydrogen isotope intercomparison material IAEA-CH-7 (–100‰) was routinely included as a check to eliminate variation owing to isotope exchange with ambient water vapor. Our δD values may not be comparable with those reported by others, as not all laboratories follow this recommended standardization technique. Based on within-run replicate measurements of laboratory keratin standards, we estimate our measurement error to be ±2‰ for δD.
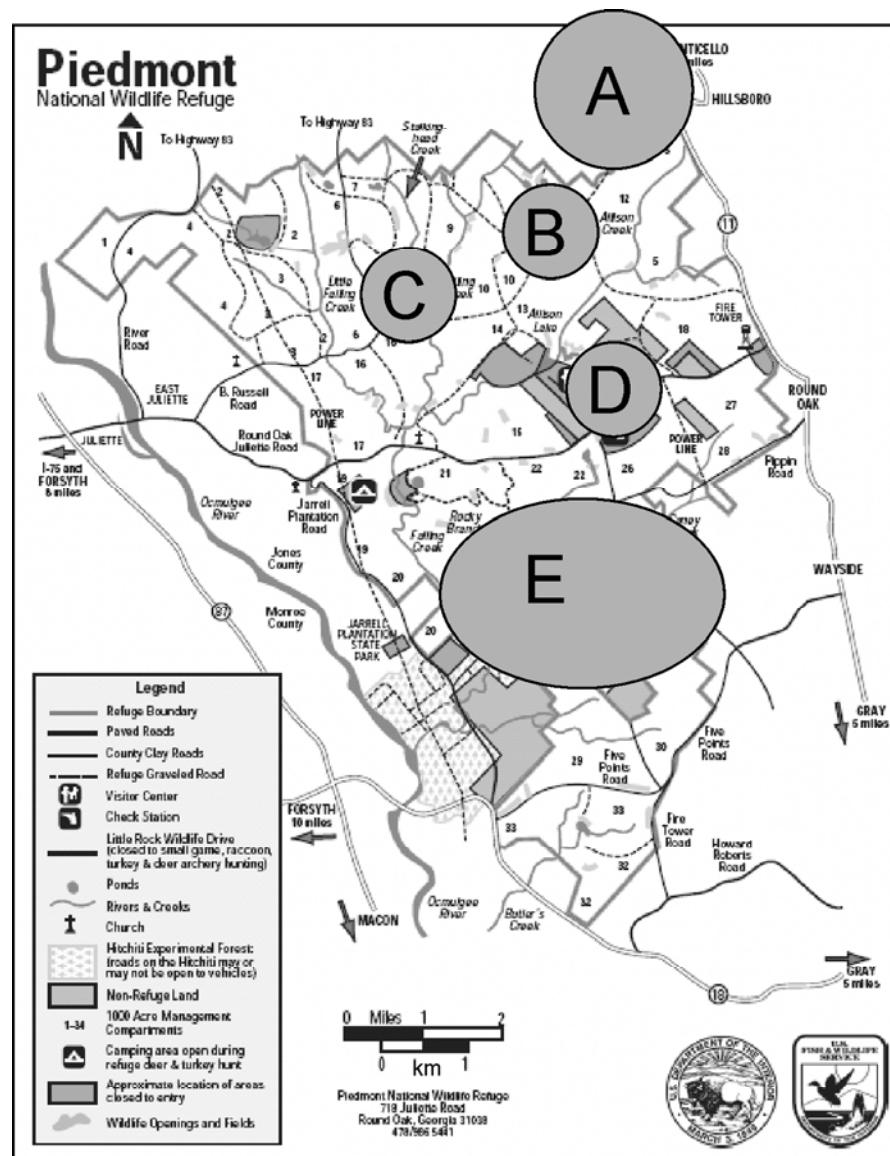
Statistical analyses

We removed feathers from newly captured adults during April and August from our analyses to eliminate biases from migrating birds. We developed the following a priori hypotheses regarding the variation of δD_f values that we expected in our sample:

1. Sex-related variation: males and females could have different rates of fidelity to the study area (Clarke et al. 1997), causing the mean isotope ratios for males and females to differ.

2. Refuge-specific signature: the study area should have a specific isotopic signature, causing the mean δD_f values to vary between the sample of birds assumed to have molted at the study site and the sample of birds with unknown molt locations (Hobson et al. 2004).

3. Local geographic variation: wood thrushes could have differential rates of fidelity to different areas of the study site (Lang et al. 2002), causing mean δD_f values to vary among geographic sampling locations on the study site.

4. Annual variation: annual precipitation patterns may produce differences in mean δD_f values among the growth years for feathers in our sample.

We used an information–theoretic approach (Burnham and Anderson 2002) to compare models representing these

Fig. 1. Map of the Piedmont National Wildlife Refuge in Georgia, showing locations of samples indicated by matching letters in Fig. 4 (base map by US Fish and Wildlife Service).

hypotheses. We used a traditional general linear model (PROC MIXED; SAS Institute Inc. 2000) to evaluate variation in isotope values among sex, year, and geographic sample groups. We report F statistics and P values for these results, but we used model-specific Akaike's information criterion corrected for small sample size (AIC_c) values, produced by PROC MIXED, to compare the relative strength of each model. In addition to models for the four hypotheses above, we also included a null model (no difference in means among categories) and an additive model for sex and fidelity (combination of hypotheses 1 and 3 above).

The hypotheses, above, might explain differences in mean δD_f values, but we also assessed differences in variance of δD_f values among groups. Our a priori expectation was that birds assumed to have molted at the study site (HY, known second-year (SY), and known after-second-year (ASY)) would show minimal variation in δD_f values, as these individuals would have grown their feathers at the study site. Also, we expected the variation in δD_f values from birds

thought to have molted at the study site to be less than the variation among the sample of birds (aged as AHY) for which the previous year's location was unknown. To test for differences in variance in δD_f values, we used one-tailed F tests for homogeneity of variance (Levene's test for homogeneity of variance, PROC GLM; SAS Institute, Inc. 2000).

We also assessed variation in δD_f values using only feathers from birds known (HY or replacement feathers) or assumed (known SY, known ASY) to have molted at the study site. Our a priori expectation was that birds assumed to have molted at the study site (HY, SY, and ASY) would show minimal variation in δD_f values, as they would have grown their feathers at the study site.

Results

We collected 151 tail feathers from 132 Wood Thrushes during 1994–1996. Our sample was stratified by sex (female: 58; male: 84; unknown: 9) and age (HY: 7; SY: 1;

Table 1. Stable hydrogen isotope values (‰; mean ± SD) measured in feathers of adult (AHY, after-hatch-year) and juvenile (HY, hatch-year) Wood Thrushes (*Hylocichla mustelina*) sampled during the breeding season at the Piedmont National Wildlife Refuge in Georgia.

Age	Sex	n	δD_f
HY	Unknown	8	−29.1±19.2
AHY	Pooled	131	−24.4±10.3
AHY	Male	76	−24.5±10.5
AHY	Female	54	−24.1±10.2
SY	Male	1	−45.6
ASY	Pooled	10	−28.7±10.7
ASY	Male	8	−31.5±8.8
ASY	Female	2	−17.6±13.5

Note: Second-year (SY) and after-second-year (ASY) ages were determined from banding records. Sample size corresponds to the number of individuals tested for isotopes.

AHY: 133; ASY: 10). We collected 120 feathers from individuals that had not been previously banded; thus, we had no knowledge of their prior molting locations. However, 31 of the 151 tail feathers came from birds that could be assumed to have molted their feathers in the vicinity of the Refuge. For example, we collected seven feathers from HY birds, which would have grown their feathers at or near the Refuge during the year of collection. Twelve adults were recaptured within the same breeding season (10 in 1994, 2 in 1995) and had feathers taken during both capture occasions. Although we did not know the previous molting location of the birds, the replacement feathers were taken later in the same breeding season; we assumed that the replacement feathers were grown while the birds were in the vicinity of the Refuge.

We found a wide range of δD_f values (−24.8‰ ± 10.3‰ (mean ± SD), range −49.1‰ to −3.4‰, $n = 151$; Table 1). Feather δD values were normally distributed in our sample (Shapiro–Wilks' test, $W = 0.987$, $P = 0.179$). The variation also existed among feather samples from birds assumed to have grown their feathers at the Refuge (−25.9‰ ± 10.5‰, range −48.0‰ to −5.5‰, $n = 31$); similar variation existed among the restricted set of replacement feathers (−23.9‰ ± 11.1‰, range −48.0‰ to −5.5‰, $n = 12$; Fig. 2).

Repeated sampling of individuals across years also demonstrated considerable variation in δD_f values (Fig. 3). Within-individual variation during the same year, in contrast, was low; of three birds that were sampled twice within 4 days (and feathers were assumed to represent a double sample of the same individual), the stable hydrogen isotope ratios differed by only 2.8‰ ± 2.5‰.

The model that best described the variance in δD_f values among the entire sample of feathers was the local geographic variance model (AIC$_c$ = 1028.3, Akaike weight (w_i) = 0.9988). Stable hydrogen isotope values differed among capture locations within the study site ($F_{[4,143]}$ = 4.51, $P = 0.002$; Table 2, Fig. 4) and variance was heterogeneous among the five capture locations ($F_{[4,143]}$ = 3.24, $P = 0.014$).

All other models were not expected to be useful models ($\Delta AIC \geq 14.0$) and the null model was the worst model (AIC$_c$ = 1054.3, ΔAIC = 26.0; Table 3). The second-best

Fig. 2. Variation in stable hydrogen isotope values (‰; δD_f) from Wood Thrush (*Hylocichla mustelina*) feathers sampled during the breeding season at the Piedmont National Wildlife Refuge and Oconee National Forest in Georgia. Sample groups are (A) feathers grown to replace previously sampled feathers of adults (feather known to have been grown at study site, $n = 12$), (B) feathers from juveniles (feather known to have been grown at study site, $n = 7$), (C) feathers from AHY birds that had been previously captured at the study site in a previous year (feather assumed to have been grown at study site, $n = 31$), and (D) feathers from AHY birds that were not previously captured (previous molt location unknown, $n = 120$). Box plots indicate mean, 25th and 75th percentiles, and outliers.
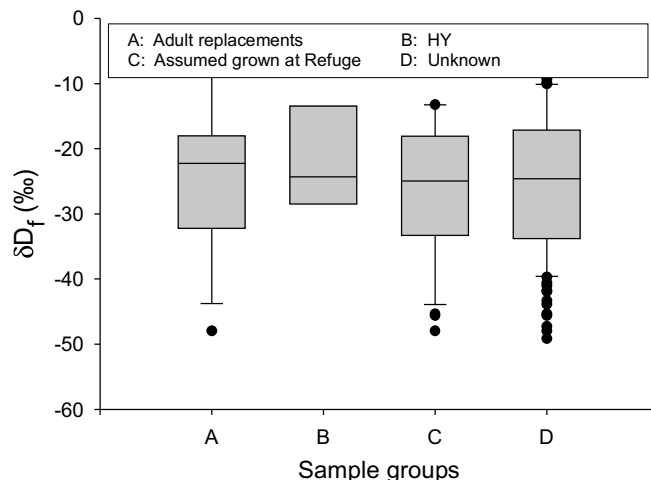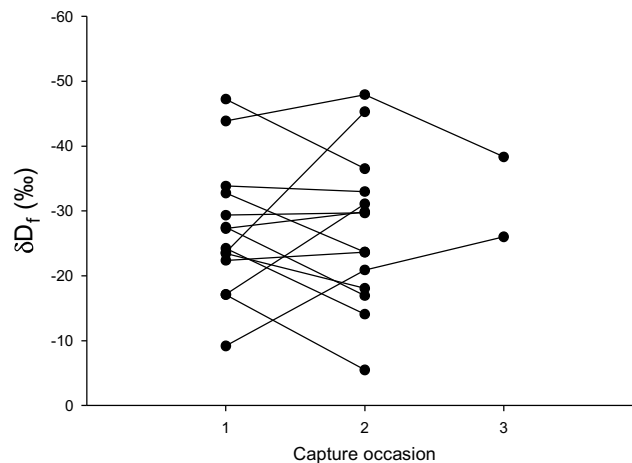

Fig. 3. Variation in stable hydrogen isotope values (‰; δD_f) measured in feathers of Wood Thrushes sampled during the breeding season at the Piedmont National Wildlife Refuge and Oconee National Forest in Georgia. Each line indicates repeated sample of the same individual across two or three capture occasions within and (or) between years during 1994–1996.

model was the annual variance model (Table 3), but δD_f values did not differ among growth years (AIC$_c$ = 1042.3, ΔAIC = 14.0, Table 3; 1993: −24.1‰ ± 12.1‰, $n = 66$; 1994: −25.8‰ ± 8.6‰, $n = 82$; 1995: −16.3‰ ± 4.7‰, $n = 3$).

δD_f values did not differ between samples from birds assumed to have molted at the study site and birds with unknown molting locations (AIC$_c$ = 1049.7, ΔAIC = 21.4,

Table 2. Stable hydrogen isotope values (‰; mean ± SD) measured in feathers of Wood Thrush sampled during the breeding season in different forest management compartments at the Piedmont National Wildlife Refuge and Oconee National Forest (ONF) in Georgia.

Management compartment(s)	All samples		Duncan's test	Restricted sample	
	n	δD_f		n	δD_f
5, ONF-118	8	−34.0±5.0	C	0	—[a]
8	10	−27.5±7.4	B, C	1	−29.9
11, 12	60	−25.3±8.9	A, B	15	−24.4±9.4
25	39	−25.7±11.7	A, B	12	−28.6±12.0
19, 23, 31	31	−19.2±10.6	A	4	−23.0±12.0

Note: Sample size corresponds to the number of individuals tested for isotopes; feathers in the restricted sample were thought to have been grown at the study site. Results of Duncan's test for the entire sample are shown; compartment groups that share letters (A, B, or C) do not have different stable hydrogen isotope values.

[a]No sample from this group.

Fig. 4. Variation in stable hydrogen isotope values (‰; δD_f) from Wood Thrush feathers among geographic sample locations at the Piedmont National Wildlife Refuge and Oconee National Forest in Georgia. Box plots indicate mean, 25th and 75th percentiles, and outliers. Sample sizes are listed in Table 2.
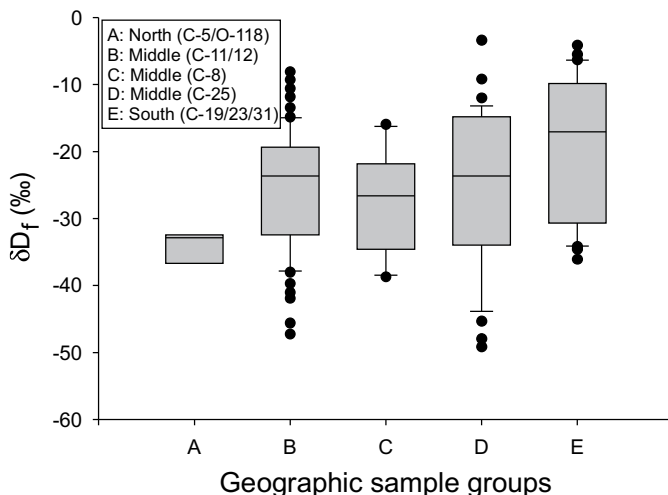

Table 3; assumed Refuge molters: −25.9‰ ± 10.5‰, $n = 31$; unknown molters: −24.6‰ ± 10.3‰, $n = 120$). Also, variance did not differ between the two groups ($F_{[1,149]} = 0.03$, $P = 0.968$). δD_f values did not differ between males and females (males: −25.7‰ ± 10.7‰, $n = 84$; females: −23.5‰ ± 10.1‰, $n = 58$; Table 3). A portion of our sample of feathers were either known (HY and replacement feathers) or assumed (captures from previous years) to have been molted at the study site. δD_f values tended to differ between samples that were known to be replacement feathers (and HY birds) and those from birds assumed to have grown their feathers at the Refuge at the end of the previous year (known to have been at the Refuge the previous year; replacement/HY: −23.5‰ ± 9.7‰, $n = 19$; "assumed": −29.7‰ ± 11.0‰, $n = 12$; $F_{[1,28]} = 2.76$, $P = 0.107$). Variance did not differ among the two groups ($F_{[1,28]} = 0.17$, $P = 0.679$).

Discussion

Variation in the sample

Our attempt to use the stable hydrogen isotope method to predict fidelity to the region was unsuccessful, as we found significant variation in the δD_f values in our sample. Even the sample of feathers known to have been grown at the study site (mean: −23.5‰) varied significantly in δD_f values (Fig. 2); unlike the study of Hobson et al. (2004) for Ovenbirds and American Redstarts from forests in Saskatchewan, we did not discover a narrow, Refuge-specific signature for δD_f.

Although variation of δD_f values in our sample was high, within-individual variation during the same year was low. This suggests that interindividual differences in δD_f values was a good indicator of real differences in either location of molt or physiology of individuals. Geographic location was an important criteria to explain variation in δD_f values. The AIC analysis allowed us to assess the strength of multiple hypotheses, but we emphasize that our inferences are limited to the set of hypotheses which we proposed (Burnham and Anderson 2002).

Powell et al. (2000a) reported an apparent survival rate (return rate) of 57.9% from a mark–recapture analysis of band returns for the same population of Wood Thrushes that we sampled. Powell et al. (2000b) and Lang et al. (2002) also reported significant within-year breeding dispersal for adults in our sample. Most within-year movements were within forest management compartments (≤1 km; Lang et al. 2002). We have no information to substantiate that small-scale variation in δD values exists at our study site. However, if δD values in the food web vary at small spatial scales, the movement dynamics documented by Lang et al. (2002) could create the variability we observed. We gathered our feather samples before stable-isotope analyses of feathers were common and we encourage biologists to gather samples of diet organisms in concert with feather samples (Smith et al. 2003).

The ability to accurately determine the prior location of an individual with stable-isotope analyses is critical to most analyses. For example, Powell's (2004) multistate model structure assumed that stable-isotope analyses could provide error-free information with regard to the prior state of an individual. Our analyses suggest that δD_f values do not provide the necessary level of precision for Wood Thrushes to be used in Powell's (2004) model.

Enriched deuterium values

Our δD_f values were higher than expected and included some highly enriched values. Based on the long-term Inter-

Table 3. Comparison of models developed to explain variation in stable hydrogen isotope values measured in feathers of Wood Thrushes sampled during the breeding season in different forest management compartments at the Piedmont National Wildlife Refuge and Oconee National Forest in Georgia.

Model	k	AIC_c	ΔAIC_c	w_i
Local geographic variation	5	1028.3	0.0	0.9988
Annual variation	3	1042.3	14.0	0.0009
Refuge-specific signature + sex-related variation	4	1045.4	17.1	0.0002
Refuge-specific signature	2	1049.7	21.4	0.0000
Sex-related variation	2	1049.9	21.6	0.0000
Null	1	1054.3	26.0	0.0000

Note: Models correspond to the set of hypotheses listed in the text; k represents the number of sample means estimated by the model. Models were ranked by Akaike's information criterion corrected for small sample size (AIC_c) values. Akaike weight (w_i) is the weight of evidence in favor of the given model from the set of models considered. The number of parameters estimated for each model deviation from the best model (row 1) is shown by ΔAIC_c for each alternative model.

national Atomic Energy Association (IAEA) data set, corrected for altitude (Meehan et al. 2004), the interpolated growing-season mean δD_p value for our site is –28‰. This value was reasonably close to the mean annual δD_p value for the site (–34.1‰, 95% CI = 10.9‰) using methods of Bowen and Revenaugh (2003) and Bowen (2005). Assuming that the local food web supporting Wood Thrushes was based on H_2 derived from precipitation, both values suggest that feathers grown at these sites were expected to have a value of the order of –53‰ to –59‰, far lower than those of feathers presumably grown at our site (i.e., using a discrimination factor of –25‰; Wassenaar and Hobson 2001). Feather δD values would be more enriched in deuterium if water driving the food web depended preferentially (i.e., more than by weighted mass balance considerations) on May precipitation, which had the most positive precipitation δD value (–6.4‰). To validate patterns suggested by interpolation of precipitation data (Bowen and Revenaugh 2003; Bowen 2005), we were able to access a 2-year monthly precipitation δD data set from the nearby Savannah River site (34.43°N, 82.85°W; C. Romanek, unpublished data). That analysis showed mean (±SD) annual δD_p values of –16.9‰ ± 9.1‰ in 2003 and –21.9‰ ± 11.5‰ in 2004, and again reported May as having both the highest annual monthly precipitation and among the most positive-weighted mean δD_p values (–11.1‰ in 2003 and –6.4‰ in 2004).

A review of all of the available δD_p values for our region suggests at least six possible explanations for the high Wood Thrush δD_f values: (1) birds grew tail feathers at sites distant (and much farther south) from our site, (2) the food web supporting birds at our site during feather growth was much more enriched in deuterium owing to differential influence of May rainfall than previously suspected, (3) Wood Thrushes sampled a food web that did not reflect mean δD_p values, (4) physiological processes related to heat stress during molt resulted in high body and feather δD values, (5) the current precipitation base map is inaccurate, and (6) the isotopic discrimination factor between precipitation and Wood Thrush feathers is close to 0‰ vs. –25‰. We examine each of these possibilities in turn.

Birds assumed to have molted at the Refuge (banded in previous year at the Refuge) had just as much variance in δD_f values as birds with unknown molt locations (no prior captures). One explanation for this pattern is that assumptions of molt location may be incorrect. As suggested by Cherry (1985) and Vega Rivera et al. (1998), some Wood Thrushes may travel to molt locations away from their breeding site prior to migration. Stable-isotope analyses of breeding site fidelity may be limited in species, as in the case of the Wood Thrush that may molt away from their breeding location. Field data from Vega Rivera et al. (1998) contradicts this explanation; radio-marked adult Wood Thrushes in Virginia began to molt immediately following fledgling independence or last-clutch predation, and birds in their sample routinely molted their rectrices simultaneously. All adults in Vega Rivera et al.'s (1998) sample completed their flight feather molt before leaving the study area. In addition, Wood Thrush captured during fall migration in southern Mississippi (K.A. Hobson, S. Van Wilgenburg, L. Wassenaar, and F. Moore, unpublished data) showed much more depleted δD_f values, which corresponded more to their expected breeding range (median HY δD_f values of –58.7‰ in 2000, n = 58, and –56.1‰ in 2001, n = 37). Thus, there does not seem to be anything particularly unusual about this species per se in terms of molt location. Nonetheless, it is possible that some populations of Wood Thrush change their molt strategies from 1 year to the next. However, in our case, this would have involved birds molting outer tail feathers likely in Central America (Bowen et al. 2005).

Our second explanation seems to be possible since May precipitation tended to be quite enriched in deuterium compared with those in other months. This could be tested by examining isotopically known prey items of Wood Thrushes throughout the season and especially during the purported molt period. However, other species from Georgia have shown the expected δD_f values. Chamberlain et al. (1997) reported a value for δD_f of –68‰ (SD = 10‰) for Black-throated Blue Warblers (*Dendroica caerulescens* (J.F. Gmelin, 1789)) from Cooper Creek, Georgia. Cooper Creek is in the north Georgia mountains (higher elevation than our study site), near the border of Georgia with Tennessee and North Carolina. Additionally, even May precipitation could not account for such positive feather values, since the predicted δD_p value based on the feather data was of the order of 0‰.

It is possible that Wood Thrushes sampled a food web that was more enriched than expected based on δD_p values

at our site. Unfortunately, nothing is known about the isoptopic composition of Wood Thrush diet here or elsewhere.

We feel that the fourth possibility, i.e., Wood Thrush experienced heat stress at our site during feather molt, is a possible explanation for their enriched δD_f values. McKechnie et al. (2004) demonstrated experimentally that pigeons became enriched in deutrerium because of heat stress. Recently, Smith and Dufty (2005) similarly suggested that unusually high δD_f values in accipiters was due to their unusual molt during breeding when they were more energetically taxed.

The fifth explanation is unlikely because of the significant success other researchers have had in placing birds to origin based on the deuterium base map for North America (Hobson 2005). However, as demonstrated recently by Lott and Smith (2006), the reliability of the δD_f vs. δD_p values may indeed vary regionally and clearly further ground truthing is desirable. As for the sixth explanation, i.e., the precipitation – feather isotopic discrimination factor for deuterium, it is almost certainly true that a single factor does not apply to all birds (Bowen et al. 2005). Unfortunately, deriving such factors will require captive studies of birds throughout the molt period and under a variety of ambient conditions.

Acknowledgements

References

Bowen, G.J. 2005. Online isotopes in precipitation calculator: global estimated mean annual δD and $\delta^{18}O$ of precipitation. Available from http://wateriso.eas.purdue.edu/waterisotopes/pages/data_access/oipc.html [accessed 17 February 2006].

Bowen, G.J., and Revenaugh, J. 2003. Interpolating the isotopic composition of modern meteoric precipitation. Water Resour. Res. 39: 1299. doi:10.1029/2003WR002086.

Bowen, G.J., Wassenaar, L.I., and Hobson, K.A. 2005. Application of stable hydrogen and oxygen isotopes to wildlife forensic investigations at global scales. Oecologia (Berl.), 143: 337–348. doi:10.1007/s00442-004-1813-y. PMID:15726429.

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theorectic approach. 2nd ed. Springer-Verlag, New York.

Chamberlain, C.P., Blum, J.D., Holmes, R.T., Feng, X., Sherry, T.W., and Graves, G.R. 1997. The use of isotope tracers for identifying populations of migratory birds. Oecologia (Berl.), 109: 132–141. doi:10.1007/s004420050067.

Cherry, J.D. 1985. Early autumn movements and prebasic molt of Swainson's Thrushes. Wilson Bull. No. 97. pp. 368–370.

Clarke, A.L., Saether, B.E., and Roskaft, E. 1997. Sex biases in avian dispersal: a reappraisal. Oikos, 79: 429–438.

Donovan, T.M., Thompson, F.R., Faaborg, J., and Probst, J.R. 1995. Reproductive success of migratory birds in habitat sources and sinks. Conserv. Biol. 9: 1380–1395. doi:10.1046/j.1523-1739.1995.09061380.x.

Grubb, T.C., Jr. 1989. Ptilochronology: feather growth bars as indicators of nutritional status. Auk, 106: 314–320.

Hobson, K.A. 1999. Tracing origins and migration of wildlife using stable isotopes: a review. Oecologia (Berl.), 120: 314–326. doi:10.1007/s004420050865.

Hobson, K.A. 2005. Stable isotopes and the determination of avian migratory connectivity and seasonal interactions. Auk, 122: 1037–1048. doi:10.1642/0004-8038(2005)122[1037:SIATDO]2.0.CO;2.

Hobson, K.A., Wassenaar, L.I., and Bayne, E. 2004. Using isotopic variance to detect long-distance dispersal and philopatry in birds: an example with Ovenbirds and American Redstarts. Condor, 106: 732–743. doi:10.1650/7631.

Lang, J.D., Powell, L.A., Krementz, D.G., and Conroy, M.J. 2002. Wood thrush movements, habitat use, and effects of forest management for red-cockaded woodpeckers. Auk, 119: 109–124. doi:10.1642/0004-8038(2002)119[0109:WTMAHU]2.0.CO;2.

Lott, C.A., and Smith, J.P. 2006. A GIS approach to estimating the origins of migratory raptors in North America using hydrogen stable isotope ratios in feathers. Auk, 123: 822–835.

McKechnie, A.E., Wolf, B.O., and Martinez del Rio, C. 2004. Deuterium stable isotope ratios as tracers of water resource use: an experimental test with rock dove. Oecologia (Berl.), 140: 191–200. PMID:15185137.

Meehan, T.D., Giermakowski, J.T., and Cryan, P.M. 2004. GIS-based model of stable hydrogen isotope ratios in North American growing-season precipitation for use in animal movement studies. Isotopes Environ. Health Stud. 40: 291–301. doi:10.1080/10256010410001731404. PMID:15621747.

Powell, L.A. 2004. A multi-state capture–recapture model using stable isotope data to enhance estimation of movement rates. Condor, 106: 761–767. doi:10.1650/7633.

Powell, L.A., Lang, J.D., Conroy, M.J., and Krementz, D.G. 2000a. Effects of forest management on density, survival, and population growth of wood thrushes. J. Wildl. Manag. 64: 11–23.

Powell, L.A., Conroy, M.J., Hines, J.E., Nichols, J.D., and Krementz, D.G. 2000b. Simultaneous use of mark–recapture and radio telemetry to estimate survival, movement, and capture rates. J. Wildl. Manag. 64: 302–313.

Pyle, P., Howell, S.N.G., Yunick, R.P., and DeSante, D.F. 1987. Identification guide to North American passerines. Braun-Brumfield, Ann Arbor, Mich.

Roth, R.R., Johnson, M.S., and Underwood, T.J. 1996. Wood thrush (Hylocichla mustelina). In The birds of North America. No. 246. Edited by A. Poole and F. Gill. Academy of Natural Sciences, Philadelphia, Pa., and American Ornithologists' Union, Washington, D.C.

SAS Institute Inc. 2000. SAS® OnlineDoc. Version 8. SAS Institute Inc., Cary, N.C.

Sauer, J.R., Hines, J.E., Gough, G., Thomas, I., and Peterjohn, B.G. 1997. The North American Breeding Bird Survey, results and analysis. Version 96.2. US Geological Survey, Patuxent Wildlife Research Center, Laurel, Md.

Simons, T.R., Farnsworth, G.L., and Shriner, S.A. 2000. Evaluating Great Smoky Mountains National Park as a population source for the Wood Thrush. Conserv. Biol. **14**: 1133–1144. doi:10.1046/j.1523-1739.2000.98606.x.

Smith, A.D., and Dufty, A.M., Jr. 2005. Variation in the stable-hydrogen isotope composition of Northern Goshawk feathers: relevance to the study of migratory origins. Condor, **107**: 547–558. doi:10.1650/0010-5422(2005)107[0547:VITSIC]2.0.CO;2.

Smith, T.B., Marra, P.P., Webster, M.S., Livette, I., Gibbs, H.L., Holmes, R.T., Hobson, K.A., and Rohwer, S. 2003. A call for feather sampling. Auk, **120**: 218–221. doi:10.1642/0004-8038 (2003)120[0218:ACFFS]2.0.CO;2.

Vega Rivera, J.H., McShea, W.J., Rappole, J.H., and Haas, C.A. 1998. Pattern and chronology of prebasic molt for the wood thrush and its relation to reproduction and migration departure. Wilson Bull. No. 110. pp. 384–392.

Wassenaar, L.I., and Hobson, K.A. 2001. A stable-isotope approach to delineate geographical catchment areas of avian migration monitoring stations in North America. Environ. Sci. Technol. **35**: 1845–1850. doi:10.1021/es0010204. PMID:11355202.

Wassenaar, L.I., and Hobson, K.A. 2003. Comparative equilibration and online technique for determination of non-exchangeable hydrogen of keratins for use in animal migration studies. Isotopes Environ. Health Stud. **39**: 1–7.

Webster, M.S., Marra, P.P., Haig, S.M., Bensch, S., and Holmes, R.T. 2002. Links between worlds: unraveling migratory connectivity. Trends Evol. Ecol. **17**: 76–83. doi:10.1016/S0169-5347 (01)02380-1.