

USING ISOTOPIC VARIANCE TO DETECT LONG-DISTANCE DISPERSAL AND PHILOPATRY IN BIRDS: AN EXAMPLE WITH OVENBIRDS AND AMERICAN REDSTARTS

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Abstract. Understanding movements of individual birds between breeding sites (breeding dispersal) or between natal sites and the site of first breeding (natal dispersal) is crucial to the modeling of population dynamics. Unfortunately, these aspects of demography are poorly understood for avian species in general, and for migratory songbirds in particular. This is because it is often impossible to sample broadly enough to relocate marked birds that have moved. We used stable-hydrogen (δD) and carbon ($\delta^{13}C$) isotope analyses of the feathers of 139 American Redstarts (*Setophaga ruticilla*) and 193 Ovenbirds (*Seiurus aurocapillus*) to evaluate evidence for individuals molting feathers at locations other than their breeding sites from the previous year. We sampled outer rectrices from breeding populations at three extensive boreal forest sites (Prince Albert National Park and Duck Mountain, Saskatchewan, and Lac La Biche, Alberta) and at three isolated forest tracts (Cypress Hills, and Moose Mountain, Saskatchewan, and Turtle Mountain, Manitoba) in western Canada. Based on outlier analysis of δD measurements, we found evidence for long-distance dispersal ranging from 0–29% of individuals. For both species, second-year birds had higher variance in δD values suggesting they had a higher probability of originating from elsewhere compared to after-second-year birds.

Key words: carbon-13, deuterium, dispersal, feathers, philopatry, source-sink populations, stable isotopes.

Utilización de la Variación Isotópica para Detectar Dispersión de Larga Distancia y Filopatría en las Aves: Un ejemplo con *Seiurus aurocapillus* y *Setophaga ruticilla*

Resumen. Entender los movimientos de aves individuales entre sitios de cría (dispersión reproductiva) o entre el sitio de nacimiento y el sitio del primer evento reproductivo (dispersión natal) es crucial para modelar la dinámica de poblaciones. Desafortunadamente, estos aspectos demográficos están poco entendidos para las especies de aves en general y para las aves canoras migratorias en particular. Esto se debe a que es usualmente imposible realizar muestreos lo suficientemente amplios como para relocalizar a las aves marcadas que se desplazaron. Usamos análisis de isótopos estables de hidrógeno (δD) y carbono ($\delta^{13}C$) de las plumas de 139 individuos de *Setophaga ruticilla* y de 193 individuos de *Seiurus aurocapillus* para evaluar la presencia de individuos que han mudado sus plumas en localidades distintas a las de sus sitios reproductivos del año anterior. Muestreamos las rectrices externas en poblaciones reproductivas de tres sitios extensos de bosque boreal (Parque Nacional Prince Albert y Duck Mountain, Saskatchewan, y Lago La Biche, Alberta) y de tres parches de bosque aislados (Cypress Hills y Moose Mountain, Saskatchewan, y Turtle Mountain, Manitoba) en el oeste de Canadá. Basados en análisis de datos extremos (outliers) de medidas de δD , encontramos evidencia de dispersión de larga distancia que comprendió entre el 0–29% de los individuos. Para ambas especies, las aves del segundo año de vida presentaron mayor varianza en los valores de δD , sugiriendo que poseen una mayor probabilidad de haberse originado en algún otro lugar comparado con aves de más de dos años de vida.

INTRODUCTION

The dispersal of birds from natal and breeding locations has long been a subject of great inter-

est among avian ecologists (Greenwood and Harvey 1982, Walters 2000). More recently, approaches to the conservation and management of migratory birds, and particularly Neotropical migrants, have emphasized the importance of knowing whether birds move between breeding sites and how they disperse from natal sites. This

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fundamental information is required in order that habitats can be protected and managed more effectively (Holmes and Sherry 1992, Hobson et al. 2001, Webster et al. 2001). Unfortunately, it is tremendously difficult to follow marked individual birds between years, and to document the movement of birds that may never return to areas where they can be recovered. This is less of a problem for movements on the order of several territories (Lemon et al. 1996) or for birds with severely restricted distributions (Daniels and Walters 2000). However, mark-recapture approaches are less suitable when attempting to understand large-scale geographical movements, information that is crucial to evaluating source-sink and metapopulation dynamics (Donovan, Thompson, et al. 1995, Donovan, Lamberson, et al. 1995).

The successful demonstration that naturally occurring deuterium in the feathers of birds can be used to infer geographical origin of molt in North America raises the prospect that isotope approaches may shed new light on the movement of individuals, particularly across zones of latitude (Hobson and Wassenaar 1997, Hobson 1999a, Hobson et al. 2001, Graves et al. 2002). Additionally, the measurement of other naturally occurring stable isotopes (e.g., ^{13}C , ^{15}N) in bird feathers shows promise as a means of delineating biome characteristics in which the feathers were grown. These factors may include the photosynthetic pathway of dominant vegetation, ambient growing conditions (e.g., mesic vs. xeric) and land-use practices (Marra et al. 1998, Hobson 1999b, Chamberlain et al. 2000, Hebert and Wassenaar 2001). It is difficult to make *a priori* expectations of geographical pattern of $\delta^{13}\text{C}$ in feathers. However, several studies have shown this isotope to manifest geographical and altitudinal structure in food webs in North America (Graves et al. 2002, Hobson et al. 2003, Rubenstein et al. 2002), and variance in feather $\delta^{13}\text{C}$ values at the population level could still provide *minimum* estimates of dispersal.

In North America, hydrogen isotope ratios in rainfall change in a predictable fashion with latitude. These hydrogen isotope patterns are thereafter reflected in local food webs and ultimately in the feathers grown by birds at those locations (see figure in Hobson and Wassenaar 1997, Wassenaar and Hobson 2001). Since most adult songbirds in North America molt flight feathers on or about their breeding sites prior to fall mi-

gration, and hatch-year (HY) birds maintain the flight feathers they grew on natal sites until their second year (SY), the hydrogen isotope values of flight feathers the following spring should provide information on (1) the latitude of natal origin (in the case of 1-year old birds) or (2) previous breeding latitude in the case of birds over 1 year in age (Wassenaar and Hobson 2001). Thus, it should be possible to determine north-south dispersal of birds using hydrogen isotope measurements of feathers at least to the order of 1 to 1.5 degrees of latitude (Meehan et al. 2001, Hobson 2004).

We investigated this possibility by examining the stable-isotope values of the outer rectrices of territorial male Ovenbirds (*Seiurus aurocapillus*) and American Redstarts (*Setophaga ruticilla*) in isolated forest areas and continuous boreal forest at sites across the western Canadian Prairie provinces. Both species molt their flight feathers on the breeding ground before migrating south and retain these feathers until the following year (Van Horn and Donovan 1994, Sherry and Holmes 1997). We analyzed feathers from after-second-year (ASY) males possibly breeding for at least the second time and SY males breeding for the first time. We hypothesized that ASY birds would show lower hydrogen isotope variability consistent with higher breeding philopatry over younger birds that may have dispersed long distances from their natal sites. In addition, we expected higher isotope variance among birds using isolated forest patches compared with continuous forest as we assumed isolated forest patches represented more of a habitat sink than the continuous forest habitat (Andr n 1995, Bayne and Hobson 1997, 2002a, 2002b), although Weatherhead and Forbes (1994) concluded that natal philopatry was higher in birds raised in fragmented habitats. Our goal was to provide minimum estimates of the proportion of male birds returning to the sampling area to breed and to determine whether there was evidence for greater natal dispersal than breeding dispersal.

METHODS

FIELD COLLECTIONS

We obtained feathers from male Ovenbirds and American Redstarts that responded to song playback. During June 2000 and 2001, birds were mist-netted on their territories in the aspen (*Po-*

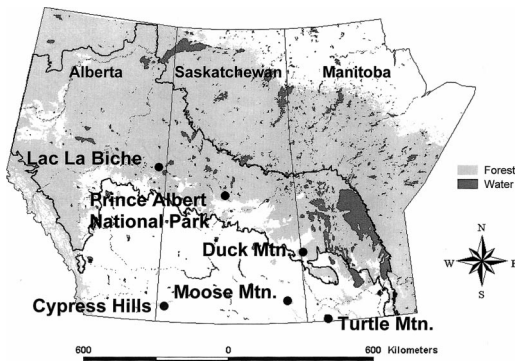


FIGURE 1. Location of Ovenbird and American Redstart study sites in deciduous mixedwood forest of Canada. Dark shading represents water bodies, light shading is forest, and no shading is agriculture or tundra.

pulus tremuloides)-dominated forests of Saskatchewan, Manitoba, and Alberta, Canada. However, our data for Prince Albert National Park were based on collections made during June 1997.

The continuous-forest sampling sites (sites consisting of at least 1000 km²) were located in Prince Albert National Park, Saskatchewan (53°57'N, 106°22'W; elevation 500–750 m), Duck Mountain Provincial Park (51°38'N, 101°38'W; 655 m), Saskatchewan, and near Lac La Biche, Alberta (54°46'N, 111°58'W, 660 m). The Prince Albert National Park site is a long-term study site for Ovenbird research (Bayne and Hobson 2002a, 2002b) and several of these Ovenbirds were previously banded, allowing for an independent test of philopatry information obtained from isotope data (Wassenaar and Hobson 2001).

Populations sampled in isolated forest tracts were located at Cypress Hills, Saskatchewan (49°40'N, 109°30'W; 1200–1350 m; 288 km² of forest), Moose Mountain, Saskatchewan (49°13'N, 102°12'W; 730–800 m; 532 km² of forest) and Turtle Mountain, Manitoba (49°00'N, 100°14'W; 180–245 m; 196 km² of forest; Fig. 1). Both species of birds were present at all sites with the exception of the Cypress Hills, where only Ovenbirds were found. Insufficient numbers of American Redstarts were captured in Lac La Biche to include in this study. Ovenbirds were classed as ASY if they were banded one year before as SY or older, or aged as SY or ASY based on outer rectrix wear patterns (Don-

ovan and Stanley 1995). American Redstart males were aged as SY or ASY based on their plumage coloration (Pyle 1997).

ISOTOPIC METHODS

Feathers were cleaned in a 2:1 chloroform:methanol solvent rinse and prepared for stable-hydrogen and carbon isotope analysis at the National Water Research Institute in Saskatoon, Canada. Stable-hydrogen isotope analyses of feathers are complicated compared to $\delta^{13}\text{C}$ measurements due to the problem of uncontrolled isotopic exchange between samples and ambient water vapor (Wassenaar and Hobson 2000). Elsewhere we describe how we use keratin standards as a means of correcting for this effect so that the values reported here are equivalent to nonexchangeable feather hydrogen (Wassenaar and Hobson 2003). Briefly, the process involves the simultaneous measurement of unknowns with several replicates of three different keratin standards whose nonexchangeable δD values are known and which span the range of expected feather values. Algorithms generated from each run that relate δD values of unknowns to their expected nonexchangeable values are then used on a run-by-run basis.

Stable-hydrogen isotope measurements on feathers and keratin standards were performed on H₂ derived from high-temperature flash pyrolysis of feathers and continuous-flow isotope-ratio mass spectrometry (CF-IRMS). Pure H₂ was used as the sample analysis gas and the isotopic reference gas. A Eurovector 3000TM (Milan, Italy) high temperature elemental analyzer (EA) with autosampler was used to automatically pyrolyze feather samples to a single pulse of H₂ gas (and N₂ and CO gas). The resolved H₂ sample pulse was then introduced to the isotope ratio mass spectrometer (Micromass IsoprimeTM with electrostatic analyzer, Micromass, Manchester, UK) via an open split capillary. All δD results are expressed in the typical delta notation, in units of per mil (‰), and normalized on the Vienna Standard Mean Ocean Water–Standard Light Antarctic Precipitation (VSMOW–SLAP) standard scale. Repeated analyses of hydrogen isotope intercomparison material IAEA-CH-7 (–100‰), routinely included as a check, yielded an external repeatability of better than $\pm 1.0\text{‰}$. This method eliminates variation due to isotope exchange with ambient water vapor, but because not all laboratories follow this recom-

mended standardization technique, our δD values may not be comparable to those reported by others. Our $\delta^{13}C$ analyses were made using a Micromass Optima[®] dual-inlet isotope-ratio mass spectrometer interfaced with a Carlo Erba (Milan, Italy) elemental analyzer. Stable-isotope results were compared with the Vienna Pee Dee Belemnite (VPDB) Standard for $\delta^{13}C$. Based on long-term measurements of intercomparison material, we estimate our laboratory error to be $\pm 1.5\%$ for δD and $\pm 0.2\%$ for $\delta^{13}C$ analyses, respectively.

STATISTICAL ANALYSES

To determine whether there were significant differences in the average isotopic values between species, region, and age classes, we used a three-way ANOVA. All two-way interactions were considered. Tukey's test was used for *post-hoc* multiple comparisons among groups.

Although we tested for differences in the mean, our main interest was in the variance between age classes. Our *a priori* expectation was that SY birds would be more likely to disperse over large distances than ASY birds. Thus, we predicted variance in deuterium signatures would be greater for SY than ASY birds. To test for these differences we used one-tailed *F*-tests for homogeneity of variance (i.e., variance-ratio test, Zar 1984). We first compared whether SY American Redstarts from all regions combined showed greater variation in isotope signature than ASY birds. To determine if the patterns we observed were consistent among regions, we repeated our variance-ratio testing for each region separately. We then used a meta-analytical approach to combine the probabilities from each regional test to create an omnibus test of significance (Sokal and Rohlf 1997). Separate tests were done for Ovenbirds. Box and whisker plots were used to quantify those individuals outside the whisker limit (defined as 1.5 times the length of the box defining the 25% and 75% quartiles). This approach assumes that most of the birds in the population are not from elsewhere and that the mean feather δD value for the population is close to that expected for that location (Wassenaar and Hobson 2001). All results are expressed as means \pm SD. The degrees of freedom in our statistical tests differ between carbon and hydrogen isotopes because of missing values for some feather samples.

RESULTS

From 332 birds captured (193 Ovenbirds and 139 American Redstarts), we obtained 323 deuterium values and 332 carbon values (Table 1).

HYDROGEN ISOTOPES

Mean deuterium values differed among locations (Fig. 2; $F_{5,306} = 31.3$, $P < 0.001$) but not between ASY (mean $\delta D = -112.7 \pm 1.8\%$) and SY birds (mean $\delta D = -114.4 \pm 1.3\%$; $F_{1,306} = 0.3$, $P = 0.57$). American Redstarts (mean $\delta D = -120.3 \pm 1.1\%$) had lower deuterium values than Ovenbirds (mean $\delta D = -108.2 \pm 1.5\%$; $F_{1,306} = 88.6$, $P < 0.001$). However, the site \times species interaction was significant ($F_{3,306} = 14.3$, $P < 0.001$). Ovenbirds from the Turtle Mountains and the Duck Mountains differed from all other locations (all $P < 0.001$). Turtle Mountain birds had the highest mean δD values followed by the Duck Mountain sample. Ovenbirds from Prince Albert National Park were not significantly different from those sampled at Moose Mountain ($P = 0.34$) and Lac La Biche ($P = 0.52$), but were lower than those at Cypress Hills ($P = 0.02$). Cypress Hills birds did not differ from those at Moose Mountain ($P = 0.95$) or Lac La Biche ($P = 0.67$). Feathers of American Redstarts from Turtle Mountain had significantly higher δD values than those from birds at Moose Mountain or Prince Albert National Park (all $P < 0.005$). No other pairwise comparisons were significant.

Although our global model provided a reasonable fit to the data (adjusted $r^2 = 0.43$), the assumptions of ANOVA were violated. White's general test for heteroscedasticity was significant ($\chi^2_{19} = 35.3$, $P = 0.01$) while an interquartile range test on the residuals from this model indicated there were 15 severe outliers and 12 mild outliers.

Pooling data across regions, we observed greater variability for SY (SD = 14.9) than ASY (SD = 11.5) American Redstarts ($F_{58,79} = 1.67$, $P = 0.02$). Within each region, American Redstarts consistently had deuterium values that were more variable for SY birds than ASY birds. These differences were significant for the Moose Mountains (SD = 22.9 vs. 15.5; $F_{14,28} = 2.1$, $P = 0.04$) and Prince Albert National Park (SD = 8.0 vs. 4.0; $F_{12,11} = 4.0$, $P = 0.01$). The combined probability test also demonstrated that the pattern of higher variance for SY American

TABLE 1. Stable-hydrogen and carbon isotope values (mean \pm SD) measured in feathers of male American Redstarts and Ovenbirds sampled on breeding territories in Canada. Sample size corresponds to number of birds captured, but not every individual was tested for both isotopes. ASY = after second year, SY = second year.

Location	Species (age)	n	δD (‰)			$\delta^{13}C$ (‰)			Outliers (%)
			Mean \pm SD	Range	Outliers (%)	Mean \pm SD	Range	Outliers (%)	
Prince Albert National Park									
	Ovenbird (ASY)	20	-122.5 \pm 16.5	-138.0 to -77.7	15.0	-23.3 \pm 0.6	-24.4 to -22.1	0	
	Ovenbird (SY)	20	-123.9 \pm 12.7	-137.2 to -78.3s	10.0	-23.6 \pm 0.6	-24.8 to -22.7	0	
	American Redstart (ASY)	12	-128.1 \pm 4.0	-135.0 to -123.0	0	-22.8 \pm 0.9	-23.9 to -21.3	0	
	American Redstart (SY)	13	-126.0 \pm 8.3	-140.0 to -112.0	0	-23.2 \pm 0.7	-24.3 to -22.0	0	
Duck Mtn.									
	Ovenbird (ASY)	23	-99.4 \pm 6.8	-110.7 to -87.3	0	-23.6 \pm 0.8	-26.2 to -22.5	4.5	
	Ovenbird (SY)	16	-90.0 \pm 28.1	-116.5 to -33.0	20.0	-23.5 \pm 1.0	-24.6 to -20.3	6.6	
	American Redstart (ASY)	11	-121.7 \pm 3.9	-127.7 to -115.0	0	-23.8 \pm 0.9	-25.5 to -22.6	0	
	American Redstart (SY)	14	-119.7 \pm 5.3	-127.1 to -106.7	7.1	-23.3 \pm 0.7	-24.4 to -21.3	7.1	
Lac La Biche									
	Ovenbird (ASY)	17	-115.6 \pm 13.1	-130.0 to -90.4	11.8	-22.9 \pm 0.5	-23.7 to -22.3	0	
	Ovenbird (SY)	16	-118.4 \pm 16.6	-136.5 to -70.5	12.5	-23.3 \pm 0.7	-24.5 to -21.9	0	
Cypress Hills									
	Ovenbird (ASY)	20	-108.8 \pm 17.2	-132.0 to -72.0	0	-22.5 \pm 1.0	-24.0 to -20.9	5.0	
	Ovenbird (SY)	8	-116.8 \pm 21.5	-139.0 to -87.0	0	-22.5 \pm 0.6	-23.1 to -21.2	12.5	
Moose Mtn.									
	Ovenbird (ASY)	16	-114.0 \pm 17.0	-144.0 to -76.0	15.0	-23.0 \pm 0.6	-24.0 to -22.0	0	
	Ovenbird (SY)	9	-116.7 \pm 3.0	-120.0 to -111.0	14.3	-23.0 \pm 0.5	-23.5 to -22.4	0	
	American Redstart (ASY)	29	-121.3 \pm 15.5	-139.0 to -69.0	11.5	-23.6 \pm 1.0	-25.6 to -21.3	0	
	American Redstart (SY)	15	-125.9 \pm 229.0	-145.0 to -87.0	28.6	-22.6 \pm 0.6	-23.8 to -21.6	21.4	
Turtle Mtn.									
	Ovenbird (ASY)	17	-81.3 \pm 6.6	-132.0 to -72.0	0	-23.5 \pm 0.6	-24.8 to -22.3	0	
	Ovenbird (SY)	11	-82.9 \pm 10.3	-139.0 to -87.0	0	-23.7 \pm 0.7	-25.3 to -23.1	22.2	
	American Redstart (ASY)	28	-115.5 \pm 8.6	-122.7 to -116.6	7.1	-24.3 \pm 1.0	-26.2 to -22.0	0	
	American Redstart (SY)	17	-111.2 \pm 11.1	-125.2 to -83.5	11.8	-23.4 \pm 1.2	-24.9 to -19.6	5.9	

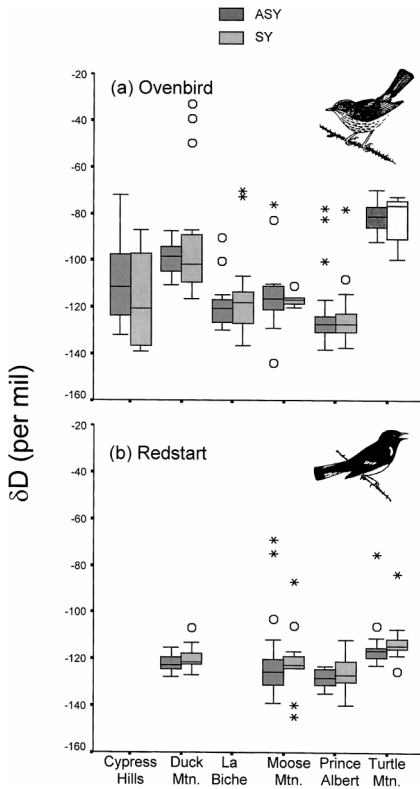


FIGURE 2. Distribution of feather deuterium values for male (a) Ovenbirds and (b) American Redstarts sampled on their breeding territories in Canada. Outliers more than 1.5 box-lengths from the lower and upper box limits (25th and 75th percentiles, respectively) are depicted with unfilled circles; those more than 3 box-lengths from these limits are depicted with asterisks. Dark-gray boxes indicate after-second-year birds (ASY); light gray indicates second-year birds (SY).

Redstarts was significant ($\chi^2_8 = 23.4$, $P = 0.003$).

For Ovenbirds, we found that SY birds ($SD = 23.1$) had significantly greater variability in deuterium values than ASY birds ($SD = 18.7$; $F_{74,108} = 1.5$, $P = 0.02$) when all data were pooled. However, increased variability in SY birds was driven by birds from the Duck Mountains ($SD = 27.5$ vs. 6.8 ; $F_{14,21} = 16.2$, $P < 0.001$) and Turtle Mountains ($SD = 10.3$ vs. 6.6 ; $F_{8,15} = 2.4$, $P = 0.07$). Contrary to expectation, ASY Ovenbirds in Prince Albert Park and Moose Mountain had significantly greater variability than SY birds. This made a summed probability test invalid for this species.

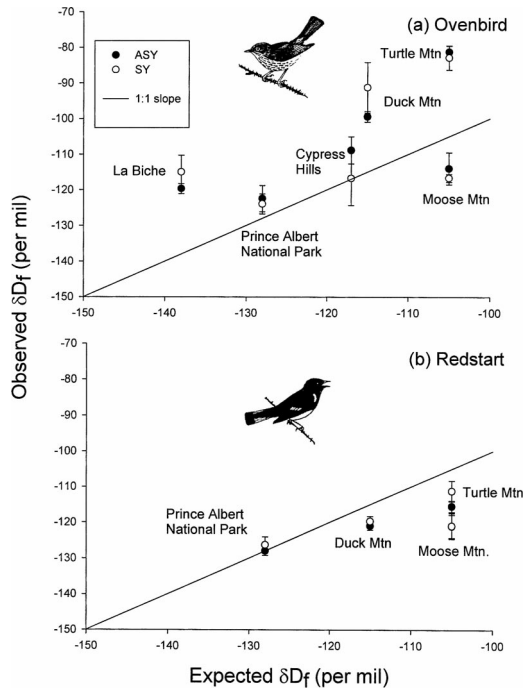


FIGURE 3. Relationship between deuterium isotope values measured in feathers (δD_f) of male (a) Ovenbirds and (b) American Redstarts, and values expected based on the continental relationship shown in Wassenaar and Hobson (2001).

We compared the mean feather deuterium values for each age class of American Redstart and Ovenbird at each location with that expected from latitudinal position according to the continent-wide relationship depicted in Wassenaar and Hobson (2001, Fig. 3). Here we interpolated kriged mean feather deuterium values for our sites based on growing-season average values. For Ovenbirds, populations at Lac La Biche and Duck and Turtle Mountains showed higher than expected mean feather δD values. In contrast, the smaller set of sites available for redstarts showed more depleted isotope values only for Moose Mountain. For deuterium, we detected Ovenbird outliers at Prince Albert National Park, Duck Mountain, Lac La Biche, and Moose Mountain. Among these sites, the highest percentage (25%) of outliers was recorded for SY individuals at Moose Mountain. All but one outlier showed higher than average δD values suggesting they grew their feathers south of the sites.

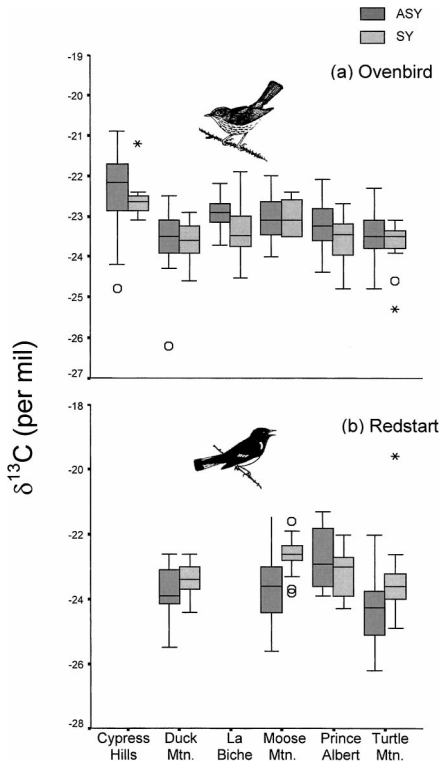


FIGURE 4. Distribution of feather $\delta^{13}\text{C}$ values for male (a) Ovenbirds and (b) American Redstarts sampled on their breeding territories in Canada. Outliers more than 1.5 box-lengths from the lower and upper box limits (25th and 75th percentiles, respectively) are depicted with unfilled circles; those more than 3 box-lengths from these limits are depicted with asterisks. Dark gray boxes indicate after-second-year birds (ASY); light gray indicates second-year birds (SY).

CARBON ISOTOPES

Similar to our deuterium results, $\delta^{13}\text{C}$ values differed among locations (Fig. 4; $F_{5,315} = 10.5$, $P < 0.001$) but not between species ($F_{1,315} = 0.01$, $P = 0.94$). There was a significant difference between ASY and SY birds ($F_{1,315} = 4.9$, $P = 0.03$). However, the age \times species interaction was also significant ($F_{1,315} = 8.0$, $P = 0.005$) with no difference between ages for Ovenbirds but lower values for ASY (mean $\delta^{13}\text{C} = -23.8 \pm 0.9\text{‰}$) than for SY American Redstarts (mean $\delta^{13}\text{C} = -23.1 \pm 1.1\text{‰}$). Ovenbirds from Cypress Hills had higher $\delta^{13}\text{C}$ values than birds from all other locations except Moose Mountain ($P = 0.06$). Birds from Turtle Mountain, Duck Mountain, and Prince Albert National Park did not differ (all $P > 0.2$). Moose Mountain birds differed from Duck Mountain and Turtle Moun-

tain ($P < 0.03$), an effect driven by lower feather $\delta^{13}\text{C}$ values from Turtle Mountain compared with Moose Mountain ($P < 0.001$) or Prince Albert National Park ($P = 0.003$). No other pairwise comparisons were significant.

The variance explained by our model for $\delta^{13}\text{C}$ values (adjusted $r^2 = 0.21$) was considerably lower than the model for deuterium. However, the carbon model met the assumptions of ANOVA as White's general test for heteroscedasticity was not significant ($\chi^2_{19} = 15.7$, $P = 0.68$) and an interquartile range test on the residuals from this model indicated there was only one severe outlier and nine mild outliers. Controlling for site and species differences, we found no difference in the variance for SY birds ($\text{SD} = 0.79\text{‰}$) relative to ASY birds ($\text{SD} = 0.83\text{‰}$; $P = 0.47$).

Distributions of $\delta^{13}\text{C}$ values indicated outliers for Ovenbirds at Duck Mountain, Cypress Hills, and Turtle Mountain. Of these sites, the highest levels (22.2‰) were found for SY individuals at Turtle Mountain, which contrasted notably with our deuterium results that showed no outliers for this species at that location. American Redstarts showed outliers at all sites except Prince Albert National Park with the highest level for SY birds at Moose Mountain, a result consistent with our deuterium results.

DISCUSSION

USING ISOTOPIC VARIANCE AND OUTLIERS

An analysis of the distributions of stable-isotope values in feathers of migratory passerines revealed considerable variation, which suggests that many individuals grew their feathers at locations outside the isotopic range of the local breeding site. Based on the assumption that individuals grew their flight feathers at or near their previous breeding or natal site, our method provides a new means of estimating minimum levels of dispersal. The use of δD in particular provides a useful means of detecting such movement patterns since this isotope is a robust indicator of latitudinal origins of molt in North America. Our results provide the first quantification of this phenomenon in migratory birds, and indicate that dispersal varies among age classes.

Although data are sparse, it has been generally assumed that philopatry among adult migratory passerines is high (Greenwood and Harvey 1982, Holmes and Sherry 1992), despite a va-

riety of individual and population-level factors such as previous reproductive success, sex, and density (Porneluzi and Faaborg 1999, Bayne and Hobson 2002a, 2002b). Our isotopic analysis and interpretation supports this general notion, although many adult birds showed evidence of long-distance dispersal. Based on banding, Bayne and Hobson (2002b) found that 30% of the Ovenbirds recruited into the breeding population in Prince Albert National Park were ASY males that presumably had attempted to breed elsewhere in the previous year. By contrast, virtually nothing is known about natal dispersal or recruitment of locally produced individuals into other populations, because conventional approaches to estimating such parameters typically would involve the mark and recapture of an impossibly large number of HY birds (Weatherhead and Dufour 2000). Our δD results generally showed that higher proportions of SY than ASY birds had dispersed from elsewhere. This trend was also evident in distributions of $\delta^{13}C$ values, but both isotopes were not always concordant. Such decoupling of the two isotopes was expected since there is no *a priori* reason to expect food web $\delta^{13}C$ and δD values to be correlated.

We anticipated higher levels of dispersal to be evident in populations of birds occupying isolated tracts of forest in the southern regions compared to those from the northern continuous forest sites. We reasoned that isolated patches might represent population sinks, and so be maintained through higher levels of immigration than in "better" continuous boreal forest habitats (Bayne and Hobson 2000, Hoover 2003). No such pattern was evident for either species. We suspect that our isolated forest patches were of sufficient size (all $>195 \text{ km}^2$) to escape such fragmentation effects. In addition, as isolated forest tracts, such sites may be less likely to be discovered by dispersing birds. Further research designed to evaluate whether these sites are population sources or sinks would be invaluable. Interestingly, as indicated by higher δD values, birds identified as outliers were generally from south of the sites where they were captured. This suggests that recruits into our study populations may well have been from birds dispersing from more fragmented forests in the continental United States. Considering the breeding range of Ovenbirds, corresponding feather δD values could be associated with latitudes as far south as the southern Great Lakes in the East, or the Midwest

regions of Iowa and Missouri (Wassenaar and Hobson 2001). The only situation where recruitment from the north was not expected was the case of Ovenbirds breeding in the Cypress Hills. This population is the *cinereus* subspecies, and that location represents the northernmost limit of its range in our area. All other ovenbirds were the *aurocapillus* subspecies. For the particular situation of natal philopatry, Weatherhead and Forbes (1994) reviewed the literature for passerine birds and found that individuals from isolated habitat patches generally had higher natal philopatry than those from less isolated patches. Our results tended to support their finding but again, further isotopic studies designed to discriminate between patch size and patch isolation effects are now required.

For American Redstarts, feather deuterium values identified outliers at all sites except the continuous forest site of Prince Albert National Park. As with Ovenbirds, the highest degree of dispersal (29%) was recorded for the SY age category at Moose Mountain. Of 12 redstart outliers, 9 had higher than expected δD values indicating again that the majority originated from sites to the south of their respective capture sites. Among these outliers, and considering the breeding range of redstarts to the south and east of our study sites, individuals could have originated as far south as the precipitation contour extending from Maryland through Missouri (Wassenaar and Hobson 2001).

Stable-carbon isotope values are expected to be a poor indicator of movement patterns since there is little *a priori* reason to suggest spatial patterns across the landscape, which typically tends to be C-3 dominated forests for these insectivorous passerines. Hobson et al. (2003) recently showed that large changes in altitude can cause changes in both $\delta^{13}C$ and δD values in feathers; however, with the exception of Cypress Hills, our study sites were elevationally similar. The more enriched $\delta^{13}C$ values at Cypress Hills compared to other sites were consistent with the pattern found by Hobson et al. (2003). It is also possible that dietary differences among individuals during molt could result in corresponding variation in feather $\delta^{13}C$ values. Insect prey may differ trophically (e.g., Lepidoptera vs. predatory beetles) and this can change feather $\delta^{13}C$ values (Bennett and Hobson, unpubl. data). The difference in $\delta^{13}C$ values between ASY and SY

redstarts in this study may also reflect different prey selection or habitat differences.

Because feather δD values are strongly linked to latitude of origin in North America, we suggest focusing on δD measurements as an indicator of dispersal. Although the feather δD values we measured departed from the values we expected based on the latitude of our sites (especially for Ovenbirds at Lac La Biche, Duck Mountain, and Turtle Mountain), this may be due to the fact that our study area generally experienced drought conditions during our study (Environment Canada, unpubl. data) and local food web δD values were more likely to be influenced by synoptic weather events than by long-term average patterns as depicted in Hobson and Wassenaar (1997).

The Cypress Hills site was considerably higher in elevation than the other sites. Based on altitudinal effects alone, we expected Cypress Hills and Moose Mountain to be 9‰ and 1.5‰, respectively, depleted, and Turtle Mountain to be 6‰ more enriched in feather deuterium content relative to Lac La Biche, Prince Albert National Park, and Duck Mountain (see relationships in Poage and Chamberlain 2001, Bowen and Wilkinson 2002). These are relatively negligible effects compared to the latitudinal effects on feather δD depicted in Figure 3. In general, birds occupying sites in regions of high elevational change represent specific cases where dispersal of individuals from various altitudes can be estimated (Graves et al. 2002, Hobson et al. 2003). Regardless, we used the stable-isotope approach only to examine patterns within sites in order to identify potential individuals recruited into each local breeding population and were not concerned with possible annual departures from the long-term growing-season average δD precipitation relationship *per se*.

Interestingly, at both Duck Mountain and Turtle Mountain, redstarts showed expected feather δD values for those latitudes, but Ovenbirds had higher δD than expected. In general, where both species were sampled, Ovenbirds tended to have higher feather δD values than redstarts. We have no explanation for this difference, since both species were sampled simultaneously at each site. It is unlikely that the entire Ovenbird population moved into these sites from more southern (i.e., more deuterium-enriched) locations. Another possible explanation is that Ovenbirds delayed their molt until migrating south follow-

ing the breeding season. Wassenaar and Hobson (2001) found isotopic evidence for molt migration in Swainson's Thrush (*Catharus ustulatus*). If this is the case here, it would suggest the intriguing possibility that molt patterns are population specific in some years (see also Hemborg et al. 2001). Alternatively, unexpected partitioning of feather δD values by microhabitat may be responsible for the interspecific differences we measured. Clearly, more research is required to decipher these possibilities. Again, we stress that the identification of outliers using an examination of the distributions of stable-isotope patterns *within* sites and *within* species presents the most parsimonious means of detecting dispersal and philopatry in migratory birds.

FUTURE WORK

Our goal was to employ stable-hydrogen and carbon isotope measurements of redstarts and Ovenbirds to test the hypothesis that dispersal would differ between age classes. We recognize some of the inherent problems of the stable-isotope approach. First, without an isotopic benchmark for feather values in a given year at a given site we could only detect outliers in each population, and thereby only obtain minimum estimates of dispersal. Second, by using δD measurements we were only able to obtain information on birds that moved over considerable latitudinal distance. Because feather δD contours are largely parallel throughout most of North America (Hobson and Wassenaar 1997), birds moving eastward or westward typically cannot be distinguished. Currently, feather δD measurements allow resolution of populations across the continental United States (i.e., corresponding to a 95% confidence interval) to about 3–5‰ (Meehan et al. 2001). In our study area, this corresponds to about 1 degree of latitude (Hobson 2004). Third, this method assumes we accurately aged all birds. Differences in plumage coloration make this distinction absolute for male American Redstarts. However, for Ovenbirds we relied on the degree of feather wear to identify the different age classes. While this method has been shown to be accurate for individuals with rectrix tip angles $<78^\circ$ and $>90^\circ$ (Donovan and Stanley 1995), individuals with intermediate tip angles could have been incorrectly classified and may explain some of the inconsistency in our results for this species. Finally, if an individual accidentally lost and regrew a flight feather on the

wintering grounds, or delayed its molt until the migration period, that individual would appear to be an outlier if sampled on the breeding grounds prior to molt the following year. Generally, this should represent a relatively small source of error for species other than those known to delay their molt (Butler et al. 2002) but more information is required for these higher-latitude breeding populations in North America since birds may be faced with trade-offs regarding timing of molt, breeding effort, and migration (Hemborg et al. 2001).

Long-term studies of specific populations of migratory birds may greatly benefit by coupling stable isotopes to measure philopatry and dispersal. It would be straightforward to monitor the stable-isotope values of feathers from local birds at key sites in any given year. This would provide site-specific baseline isotopic distributions for any subsequent year in question and so would be amenable to the kind of modeling suggested by Powell (2004). General populations of birds at a site could then be sampled and compared with the expected isotopic distributions for a particular year using data from the Canadian Network for Isotopes in Precipitation and the Global Network for Isotopes in Precipitation. Such an approach was used by Wassenaar and Hobson (1998) in a study of the natal origins of monarch butterflies (*Danaus plexippus*) wintering in Mexico. These authors created a North American δD and $\delta^{13}C$ isotopic base map appropriate for the birth year preceding the wintering year when migrant monarchs were sampled.

Isotope studies of bird populations need not be limited to δD and $\delta^{13}C$ measurements. Other isotopes show some promise in providing additional geospatial information, including those of lead, strontium, and nitrogen (Hobson 1999a, Hebert and Wassenaar 2001, Hobson 2002, 2004). In addition, the inclusion of trace-element analyses to describe bird study populations in a true multivariate sense has the potential to increase the resolution in identifying individuals from outside study areas. Szép et al. (2003) used trace-element approaches to identify different African wintering subpopulations of Sand Martins (*Riparia riparia*) breeding at sites in Europe. While they could not predict where birds wintered in Africa, they could identify different wintering sites based on different trace-element profiles. Finally, the approach we have demonstrated here is not specific to birds but can be

applied to several taxa of migratory organisms moving across isotopic isoclines (Hobson 1999a).

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LITERATURE CITED

- ANDRÉN, H. 1995. Effects of landscape composition on predation rates at habitat edges, p. 225–255. *In* L. Hansson, L. Fahrig, and G. Merriam [EDS.], *Mosaic landscapes and ecological processes*. Chapman and Hall, New York.
- BAYNE, E. M., AND K. A. HOBSON. 1997. Comparing the effects of landscape fragmentation by forestry and agriculture on predation of artificial nests. *Conservation Biology* 11:1418–1429.
- BAYNE, E. M., AND K. A. HOBSON. 2000. Effects of habitat fragmentation on pairing success of Ovenbirds: the importance of male age and floater behavior. *Auk* 118:380–388.
- BAYNE, E. M., AND K. A. HOBSON. 2002a. Annual survival of adult American Redstarts and Ovenbirds in the southern boreal forest. *Wilson Bulletin* 114: 358–367.
- BAYNE, E. M., AND K. A. HOBSON. 2002b. Apparent survival of male Ovenbirds in fragmented and forested boreal landscapes. *Ecology* 83:1307–1316.
- BOWEN, G. J., AND B. WILKINSON. 2002. Spatial distribution of $\delta^{18}O$ in precipitation. *Geology* 30:315–318.
- BUTLER, L. K., M. G. DONAHUE, AND S. ROHWER. 2002. Molt-migration in Western Tanagers (*Piranga ludoviciana*): age effects, aerodynamics, and conservation implications. *Auk* 119:1010–1023.
- CHAMBERLAIN, C. P., S. BENSCH, X. FENG, S. AKESSON, AND T. ANDERSSON. 2000. Stable isotopes examined across a migratory divide in Scandinavian Willow Warblers (*Phylloscopus trochilus trochilus* and *Phylloscopus trochilus acredula*) reflect African winter quarters. *Proceedings of the Royal Society of London Series B* 267:43–48.
- DANIELS, S. J., AND J. R. WALTERS. 2000. Inbreeding depression and its effects on natal dispersal in Red-cockaded Woodpeckers. *Condor* 102:482–491.
- DONOVAN, T. M., R. H. LAMBERSON, A. KIMBER, F. R. THOMPSON, AND J. FAABORG. 1995. Modeling the effects of habitat fragmentation on source and sink demography of Neotropical migrant birds. *Conservation Biology* 9:1396–1407.
- DONOVAN, T. M., AND C. M. STANLEY. 1995. A new method of determining Ovenbird age on the basis

- of rectrix shape. *Journal of Field Ornithology* 66: 247–252.
- DONOVAN, T. M., F. R. THOMPSON, J. FAABORG, AND J. R. PROBST. 1995. Reproductive success of migratory birds in habitat sources and sinks. *Conservation Biology* 9:1380–1395.
- GRAVES, G. R., C. S. ROMANEK, AND A. R. NAVARRO. 2002. Stable isotope signature of philopatry and dispersal in a migratory songbird. *Proceedings of the National Academy of Sciences* 99:8096–8100.
- GREENWOOD, P. J., AND P. H. HARVEY. 1982. The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics* 13:1–21.
- HEBERT, C., AND L. I. WASSENAAR. 2001. Stable nitrogen isotopes in waterfowl feathers reflect agricultural land use in western Canada. *Environmental Science and Technology* 35:3482–3487.
- HEMBORG, C., J. J. SANZ, AND A. LUNDBERG. 2001. Effects of latitude on the trade-off between reproduction and moult: a long-term study with the Pied Flycatcher. *Oecologia* 129:206–212.
- HOBSON, K. A. 1999a. Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia* 120:314–326.
- HOBSON, K. A. 1999b. Stable-carbon and nitrogen isotope ratios of songbird feathers grown in two terrestrial biomes: implications for evaluating trophic relationships and breeding origins. *Condor* 101: 799–805.
- HOBSON, K. A. 2002. Making migratory connections with stable isotopes, p. 379–392. *In* P. Berthold, E. Gwinner, and E. Sonnenschein [EDS.], *Avian migration*. Springer-Verlag, Berlin.
- HOBSON, K. A. 2004. Flying fingerprints: making connections with stable isotopes and trace elements. *In* P. Marra and R. Greenberg [EDS.], *Birds of two worlds*. Johns Hopkins University Press, Baltimore, MD.
- HOBSON, K. A., K. P. MCFARLAND, L. I. WASSENAAR, C. C. RIMMER, AND J. E. GOETZ. 2001. Linking breeding and wintering grounds of Bicknell's Thrushes using stable isotope analyses of feathers. *Auk* 118:16–23.
- HOBSON, K. A., AND L. I. WASSENAAR. 1997. Linking breeding and wintering grounds of Neotropical migrant songbirds using stable hydrogen isotopic analysis of feathers. *Oecologia* 109:142–148.
- HOBSON, K. A., L. I. WASSENAAR, B. MILÁ, I. LOVETTE, C. DINGLE, AND T. B. SMITH. 2003. Stable isotopes as indicators of altitudinal distributions and movements in an Ecuadorean hummingbird community. *Oecologia* 136:302–308.
- HOLMES, R. T., AND T. W. SHERRY. 1992. Site fidelity of migratory warblers in temperate breeding and Neotropical wintering areas: implications for population dynamics, habitat selection, and conservation, p. 563–578. *In* J. M. Hagan and D. W. Johnston [EDS.], *Ecology and conservation of Neotropical migrant landbirds*. Smithsonian Institution Press, Washington, DC.
- HOOVER, J. P. 2003. Decision rules for site fidelity in a migratory bird, the Prothonotary Warbler. *Ecology* 84:416–430.
- LEMON, R. E., S. PERREAULT, AND G. A. LOZANO. 1996. Breeding dispersions and site fidelity of American Redstarts (*Setophaga ruticilla*). *Canadian Journal of Zoology* 74:2238–2247.
- MARRA, P. P., K. A. HOBSON, AND R. T. HOLMES. 1998. Linking winter and summer events in a migratory bird using stable carbon isotopes. *Science* 282: 1884–1886.
- MEEHAN, T. D., C. A. LOTT, Z. D. SHARP, R. B. SMITH, R. N. ROSENFELD, A. C. STEWART, AND R. K. MURPHY. 2001. Using hydrogen isotope geochemistry to estimate the natal latitudes of immature Cooper's Hawks migrating through the Florida Keys. *Condor* 103:11–20.
- POAGE, M. A., AND C. P. CHAMBERLAIN. 2001. Empirical relationships between elevation and the stable isotope composition of precipitation and surface waters: considerations for studies of paleoelevation change. *American Journal of Science* 301: 1–15.
- PORNELUZI, P. A., AND J. FAABORG. 1999. Season-long fecundity, survival, and viability of Ovenbirds in fragmented and unfragmented landscapes. *Conservation Biology* 13:1151–1161.
- POWELL, L. A. 2004. A multistate capture-recapture model using a *posteriori* classification to enhance estimation of movement rates. *Condor* 106:761–767.
- PYLE, P. 1997. Identification guide to North American birds. Slate Creek Press, Bolinas, CA.
- RUBENSTEIN, D. R., C. P. CHAMBERLAIN, R. T. HOLMES, M. P. AYRES, J. R. WALDBAUER, G. R. GRAVES, AND N. C. TUROSS. 2002. Linking breeding and wintering ranges of a migratory songbird using stable isotopes. *Science* 295:1062–1065.
- SHERRY, T. W., AND R. T. HOLMES. 1997. American Redstart (*Setophaga ruticilla*). *In* A. Poole and F. Gill [EDS.], *The birds of North America*, No. 277. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.
- SOKAL, R. R., AND F. G. ROHLF. 1997. *Biometry*. 3rd ed. W. H. Freeman and Company, New York.
- SZÉP, T., A. P. MØLLER, J. VALLNER, B. KOVACS, AND D. NORMAN. 2003. Use of trace elements in feathers of Sand Martins *Riparia riparia* to identify molting areas: effects of molting origin and age on the composition of elements. *Journal of Avian Biology* 34:307–320.
- VAN HORN, M. A., AND T. M. DONOVAN. 1994. Ovenbird (*Seiurus aurocapillus*). *In* A. Poole and F. Gill [EDS.], *The birds of North America*, No. 88. The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.
- WALTERS, J. R. 2000. Dispersal behavior: an ornithological frontier. *Condor* 102:479–481.
- WASSENAAR, L., AND K. A. HOBSON. 1998. Natal origins of migratory monarch butterflies at wintering colonies in Mexico: new isotopic evidence. *Proceedings of the National Academy of Sciences* 95: 15436–15439.
- WASSENAAR, L. I., AND K. A. HOBSON. 2000. Improved method for determining the stable-hydrogen iso-

- topic composition (δD) of complex organic materials of environmental interest. *Environmental Science and Technology* 34:2354–2360.
- WASSENAAR, L. I., AND K. A. HOBSON. 2001. A stable-isotope approach to delineate geographical catchment areas of avian migration monitoring stations in North America. *Environmental Science and Technology* 35:1845–1850.
- WASSENAAR, L. I., AND K. A. HOBSON. 2003. Comparative equilibration and online technique for determination of non-exchangeable hydrogen of keratins for use in animal migration studies. *Isotopes in Environment and Health studies* 39:1–7.
- WEATHERHEAD, P. J., AND K. W. DUFOUR. 2000. Fledging success as an index of recruitment in Red-winged Blackbirds. *Auk* 117:627–633.
- WEATHERHEAD, P. J., AND M. R. L. FORBES. 1994. Natal philopatry in passerine birds: genetic or ecological influences? *Behavioral Ecology* 5:426–433.
- WEBSTER, M. S., P. P. MARRA, S. H. HAIG, S. BENSCH, AND R. T. HOLMES. 2001. Links between worlds: unraveling migratory connectivity. *Trends in Ecology & Evolution* 17:76–83.
- ZAR, J. H. 1984. *Biostatistical analysis*. 2nd ed. Prentice-Hall, Englewood Cliffs, NJ.