J Ornithol (2011) 152:93–101
DOI 10.1007/s10336-010-0553-5

ORIGINAL ARTICLE

Variation in deuterium (δD) signatures of Yellow Warbler *Dendroica petechia* feathers grown on breeding and wintering grounds

Sam P. Quinlan · David J. Green

Received: 17 November 2009 / Revised: 3 May 2010 / Accepted: 15 June 2010 / Published online: 3 July 2010

Abstract Stable isotope analysis of feathers may help track populations of migratory birds throughout their annual cycle. We use deuterium isotope ratios in feathers (δD_f) to confirm that Yellow Warblers *Dendroica petechia* go through both a prebasic molt on or near their breeding grounds and a prealternate molt on their wintering grounds, and evaluate whether δD analysis of different feather types can help assign birds to breeding and winter origins. We show that primary coverts and tail feathers have δD_f values that reflect long-term average deuterium isotope ratios in precipitation (δD_P) on the breeding grounds. Most greater coverts and crown feathers, however, have δD_f values that are more enriched than predicted based on the δD_P of their wintering distribution. We also found significant interannual variation in the δD_f values of tail feathers, greater coverts and crown feathers. Interannual variation in δD_f of winter-grown feathers may be explained by El Niño/La Niña conditions that influence rainfall and thus δD_P; feathers were more depleted following an El Niño year (2005) than a La Niña year (2006). Gender had no effect on the δD_f values of any feathers sampled. Age influenced the δD_f values of crown feathers but not greater coverts. This study therefore confirms that δD_f of summer-grown feathers can be used to identify breeding locations, but suggests that the ability to use δD_f of winter-grown feathers to assign individuals to winter locations is limited by weak spatial gradients and temporal variation in δD_P.

Communicated by F. Bairlein.

S. P. Quinlan · D. J. Green (✉)
Centre for Wildlife Ecology, Department of Biological Sciences, Simon Fraser University, Burnaby, BC V5A 1S6, Canada
e-mail: djgreen@sfu.ca

Keywords Stable isotope analysis · Migratory connectivity · Yellow Warbler · Moult

Introduction

Migratory bird populations may be influenced by events that take place on breeding grounds, on wintering grounds, or along migration routes, and there has consequently been considerable debate about when, and where, migratory bird populations are limited (Holmes 2007; Newton 2004). Long-term studies have demonstrated that, in some cases, changes in population size can be explained solely by events on breeding grounds (e.g., Swainson's Thrush *Catharus ustulatus* Johnson and Geupel 1996; Black-throated Blue Warbler *Dendroica caerulescens* Sillet and Holmes 2005), or events on wintering grounds (e.g., Willow Warbler *Phylloscopus trochilus* Baillie and Peach 1992; Barn Swallow *Hirundo rustica* Moller 1989). However, recent work suggests that events at every stage of the annual cycle can affect productivity and survival and contribute to changes in the size of migratory bird populations (Holmes 2007; Norris et al. 2004a; Sillett and Holmes 2002). Identification of the links between breeding areas, migratory stopover sites and wintering areas is therefore critical for effective conservation of migratory birds (Webster and Marra 2005).

Over the last decade, stable isotope analysis of animal tissues has become one of the most widely used tools to track the movement of migratory animals (Hobson and Wassenaar 2008). Deuterium isotope analysis has been particularly useful because there are strong latitudinal gradients in the amount of deuterium in precipitation (δD_P) (Rozanski et al. 1993, Bowen et al. 2005) that are reflected in the isotopic signatures of tissue grown at a particular location (Hobson 1999). Deuterium isotope ratios in feathers ($\delta D_{f)}$ have informed studies of avian movement because feathers are grown at well-defined periods of the annual cycle after which they become metabolically inert locking in the isotopic signature of the habitat where they were grown (Hobson and Clark 1992; Bearhop et al. 2002). Pioneering studies by Hobson and Wassenaar (1997) and Chamberlain et al. (1997) showed how Neotropical migrants captured on their wintering grounds could be traced to their breeding origins using δD_f values of feathers grown during the previous breeding season, continental scale base maps of δD_P, and an estimate of the difference in the δD of precipitation and feathers grown at a site (the discrimination factor). More recently, studies have begun to use δD_f of other feather types, such as crown feathers grown prior to leaving wintering areas, to estimate the wintering origins of birds captured during the breeding season (e.g., Jones et al. 2008; Oppel and Powell 2008) or δD_f of multiple feather types to estimate both the wintering and breeding locations of birds captured on migration (e.g., Mazerolle et al. 2005).

Despite the increasing use of δD_f and isoscape maps of $\delta D_{P,}$ now available for all continents (Bowen et al. 2005), to track migratory birds, there are limits to the accuracy of spatial assignments. Accurate assignment is dependent on the existence of geographic separation in $\delta D_{P,}$ and error will be introduced if annual δD_P deviates from the 40-year averages used to produce isoscape maps, when data from fixed points are interpolated over a large area, as a result of variation in the precipitation–feather discrimination factor, and due to measurement error (Farmer et al. 2008; Wunder and Norris 2008). Year to year variation in δD_P is expected due to interannual variation in climatic (rainfall, temperature) or hydrological processes (e.g., snowmelt runoff). Considerable variation in δD_f has also been noted among feathers known to originate from the same site (Hobson and Wassenaar 1997; Langin et al. 2007; Wunder et al. 2005). Langin et al. (2007) documented differences in the δD_f of feathers produced by hatch-year and adult American Redstarts *Setophaga ruticilla* that could be explained by differences in their diet, differences in the timing of molt that are related to temporal change in δD in local food webs, or because diet–tissue discrimination factors vary with individual age. Greater understanding of factors that lead to interannual variation in $\delta D_{P,}$ and variation in δD_f among individuals would allow these factors to be incorporated into models producing δD isoscapes and increase the accuracy of spatial assignments (Hobson et al. 2009).

In this study, we first examine whether stable isotope analysis of different feather types could help track the annual movements of Yellow Warblers *Dendroica petechia*, and then investigate interannual, sex, and age-related variation in δD_f. Yellow Warblers are documented as going through a complete molt on the breeding grounds before fall migration (the preformative molt for the young and a prebasic molt for the adults) and a partial prealternate molt on the wintering grounds prior to spring migration (Pyle 1997). If molt in Yellow Warblers has been described accurately, we expected that the δD_f of primary coverts and tail rectrices would be depleted compared to the δD_f of crown feathers and greater coverts, and that the δD_f for each feather type would reflect the δD_P of the location in which they were grown. Deuterium isotope ratios of the four feather types may vary from year to year because of variation in global climatic conditions, such as ENSO, that influences rainfall and thus δD_P, or local conditions that impact δD in riparian foodwebs. We collected feathers grown in the summer of 2004 or the winter of 2004/2005 in the 2005 breeding season and feathers grown in the summer of 2005 or the winter of 2005/2006 in the 2006 breeding season. Since feathers grown during the summer of 2004, the winter of 2004/2005 and the summer of 2005 were all grown during an El Niño period while feathers grown during the winter of 2005/2006 were grown during a La Niña period, we predicted that there would be greater interannual variation in the δD_f of greater covert and crown feathers than primary covert and tail feathers.

Methods

Study species and study area

Yellow Warblers have one of the largest distributions of all wood warblers (Parulidae), breeding across most of North America and overwintering in Mexico, Central America and northern South America (Lowther et al. 1999). Yellow Warblers are restricted to relatively low elevations on both breeding and wintering grounds (breeding grounds: <1,450 m in British Columbia; Campbell et al. 1990; wintering grounds: <600 m; Greenberg and Salgado-Ortiz 1994; Greenberg et al. 1996; Lynch 1989). Mitochondrial DNA and stable hydrogen analysis of tissues sampled during migration and on wintering grounds suggest that western and eastern lineages of Yellow Warblers are geographically segregated throughout the annual cycles. The two lineages have a parallel migration with western lineages found from Alaska/California to Alberta/Colorado migrating to Mexico and Panama, and eastern lineages found from Manitoba/Kansas to Newfoundland/Virginia migrating to the Yucatan, Panama, and Venezuela (Boulet et al. 2006).

We have monitored a marked population of Yellow Warblers that breed in riparian habitat near Revelstoke, British Columbia, since 2004. The study site is situated on a floodplain on the upper reaches of the Upper Arrow

Lakes Reservoir (49.088°N, 115.678°W; elevation 435–442 m).

Feather sampling

We collected feather samples from territorial birds captured in May through July of 2005 and 2006. Males were lured into mistnets using call playback shortly after their arrival at the study site, while females were typically captured passively moving to and from their nests. Any unbanded birds captured were marked with a Canadian Wildlife Service aluminium band and a unique combination of three color bands. We determined the gender and age (SY: second-year; or ASY: after-second-year) of all birds using morphological and plumage characteristics. Males and females can be distinguished based on plumage coloration and the presence of an enlarged cloacal protuberance or a brood patch. SY and ASY birds can be distinguished based on feather wear and color of the primary coverts, the presence of secondary molt limits, and tail feather shape (Pyle 1997). We collected feathers from four feather blocks: sampling the third outer right tail feather (R4) and the innermost primary covert (PC1) which are thought to be replaced on the breeding grounds during the prebasic molt, and 5–6 crown feathers and one greater covert that are thought to be replaced on the wintering grounds during the prealternate molt between December and April (Pyle 1997). We ensured that the greater covert feather collected had broad, uniform yellow edging, and avoided sampling greater coverts with dull olive edges that may not have been replaced during the pre-alternate molt. Feathers were placed in individually labelled paper envelopes and stored in a freezer prior to being transported to a laboratory for cleaning and analysis. The numbers of feather blocks sampled per individual varied because greater coverts were not sampled at the start of the 2005 breeding season and a few birds were released before sampling was complete because they showed signs of stress. We subsequently monitored the breeding of all pairs at our study site (ca. 30 pairs per year) and restricted analysis to feather samples collected from birds known to breed in the area.

Laboratory methods and stable isotope analysis

Feather samples were soaked in 2:1 chloroform:methanol solution for 24 h, drained and air-dried in a fume hood for an additional 24 h to remove excess solvent. Prior to isotope analysis, we cut and weighed 350 ± 10 µg of feather material into 3.5 × 5-mm elemental analyzer silver capsules. We ensured that the sample was cut from the distal tip of the feather to minimize bias related to intra-feather (vane vs. rachis) variation in δD composition (Wassenaar and Hobson 2006). Samples collected from the 2005 and 2006 field seasons were analyzed at the National Water Research Institute in Saskatoon, Canada, in May and December of 2006, respectively. The deuterium composition of the nonexchangeable component of a feather sample was measured using the online pyrolysis and continuous-flow isotope-ratio mass spectrometry (CFIRMS) techniques described by Wassenaar and Hobson (2003). During analysis, samples of similar feather types were run together to eliminate potential bias from drift in feather δD values. Repeated analysis of in-house hydrogen isotope intercomparison material was routinely included as a check to eliminate variation owing to isotope exchange with ambient water vapor. Stable-hydrogen isotopes are reported in per mil notation (‰) relative to Vienna Standard Mean Ocean Water–Standard Light Antarctic Precipitation (VSMOW–SLAP). The standard deviation for repeated measurement of an in-house standard was 1.8‰ ($n = 30$). Duplicates of the same feather sample ($n = 18$; crown and tail feathers) showed that δD values had a repeatability of ±3‰.

Data analysis

We used general linear mixed models (GLMM) to evaluate whether δD_f values varied with feather type. Individual identity was included as a random term in models because individuals contributed up to four feather samples per year and 14 birds were sampled in both years. GLMMs were also used to examine whether variation in the δD values of feathers grown on breeding grounds (primary coverts and tail feathers) and wintering grounds (greater coverts and crown) varied between years or with the sex and age of the individual. Significance of the explanatory variable was tested using the Wald statistic when that variable was dropped from a more complete model including only significant terms. Wald statistics approximate a chi-square distribution. All analyses were conducted in Genstat Version 12 (VSN International, Hemel Hempstead, UK).

Relationship between δD_P and δD_f

We tested whether feathers purported to be grown in either the breeding or wintering grounds have deuterium signatures consistent with those expected based on interpolated isotopic base maps for North and South America available at (http://www.waterisotopes.org). We derived expected mean and 95% CI values of δD_P from an equal-area grid of long-term average growing season δD_P (Bowen et al. 2005) for the breeding and wintering region using ARCGIS software (ESRI, Redlands, California). We defined the breeding region as being within a 400-km buffer centered on Revelstoke, BC, but constrained the region to include only areas west of the continental divide, and areas below 1,450 m elevation where breeding birds are concentrated (Campbell et al. 1990). We employed a 400-km buffer because latitudinal gradients in δD_P across North America impose limits on the ability to accurately assign individual samples to their origins (Farmer et al. 2008), and studies are unlikely to attempt to assign individuals to sites separated by less than 7° of latitude. We defined the wintering range based on the distribution map of Ridgely et al. (2003), but constrained the region to elevations below 600 m that are occupied by wintering Yellow Warblers. We subsequently derived expected mean and 95% CI values of δD_P for three areas within the potential winter range; mainland areas of Mexico, Central America, and northern South America. We compared the observed δD_f with the expected δD_P for the breeding and wintering regions assuming a discrimination factor of −19‰ to account for isotopic fractionation of deuterium when it is transferred and propagated from precipitation into animal tissues (Hobson and Wassenaar 1997; Langin et al. 2007; Mazerolle et al. 2005).

Results

We analyzed the stable hydrogen isotope ratio of 222 feathers sampled from 71 individuals breeding near Revelstoke, BC, in 2005 and/or 2006. Fourteen individuals were sampled in both years. The 85 sets of feather samples included 39 where the bird had been banded and known to breed in the area in the previous year and 46 birds whose breeding or natal origin in the previous year were unknown. The sample included feathers from 38 females (SY = 11, ASY = 27) and 47 males (SY = 12, ASY = 35). However, we only obtained δD_f values for primary coverts and tail feathers from ASY birds.

Variation in δD_f across feather blocks

There were large differences in the δD_f of Yellow Warbler feathers collected from different feather blocks ($\chi^2_3 = 1{,}877$, $P < 0.001$), with tail and primary covert feathers having depleted values compared to crown and greater coverts (Fig. 1). Two (5%) of the 42 tail feathers analyzed were highly enriched compared to the rest of the sample, suggesting that some tail feathers may be molted on migration. Three (4%) of the 81 crown feather samples had extremely depleted values (Fig. 1). The δD_f of the two feathers thought to be replaced on the breeding grounds were only weakly correlated ($r_p = 0.32$, $n = 40$, $P = 0.04$), and the correlation did not improve if the one extreme tail value included in this analysis was removed ($r_p = 0.25$, $n = 39$, $P = 0.11$). The δD_f of the two feathers thought to be replaced on the wintering grounds were more strongly correlated ($r_p = 0.46$, $n = 58$, $P < 0.001$), and this correlation improved if the three extreme crown values included in this analysis were removed ($r_p = 0.56$, $n = 55$, $P < 0.001$).

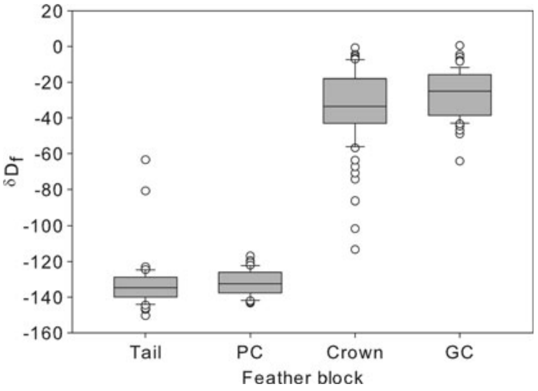

Fig. 1 *Box plot* (median, interquartile range, values within 10th and 90th percentile and outliers) comparing δD_f of feather blocks collected from Yellow Warblers *Dendroica petechia* captured at a breeding site near Revelstoke, British Columbia, Canada, during the spring of 2005 and 2006

Variation in δD_f within feather blocks

Analyses were performed after excluding the two tail feather and three crown feather samples with extreme δD_f values. The δD_f of the primary coverts did not vary between years (Table 1). There was also no difference in the δD_f of primary coverts sampled from males and females (model predictions ± SE, males = −132.4 ± 1.4‰, females = −131.4 ± 1.8‰, $\chi^2_1 = 0.2$, $P = 0.68$). In contrast, the δD_f of the tail feathers did vary between years (Table 1), but again δD_f did not vary with gender (model predictions ± SE after controlling for year, males = −134.8 ± 1.1‰, females = −135.9 ± 1.5‰, $\chi^2_1 = 0.3$, $P = 0.57$).

As predicted, if El Niño conditions result in more precipitation and lower δD_P, the δD_f of the greater coverts and the crown were significantly more depleted in 2005 than 2006 (Table 1). This pattern was also observed in all 14 individuals where crown feathers were sampled in both 2005 and 2006 [mean (δD_{f2005}–δD_{f2006}) ± SD = −23.6 ± 6.7‰, paired $t_{13} = -13.6$, $P < 0.001$]. Deuterium isotope values of the greater coverts did not vary with either the gender or age of the individual sampled (model predictions ± SE after controlling for year; males = −21.1 ± 2.8‰, females = −27.4 ± 2.9‰, $\chi^2_1 = 2.1$, $P = 0.16$; SY = −26.9 ± 3.2‰, ASY = −31.5 ± 2.7‰, $\chi^2_1 = 1.7$, $P = 0.20$). The δD_f of crown feathers also did not vary with gender (model predictions ± SE controlling for significant terms, males = −37.0 ± 2.3‰, females = −34.5 ± 2.5‰, $\chi^2_1 = 0.6$, $P = 0.44$), but crown feathers from SY birds were more depleted than those from ASY

Table 1 Interannual variation in the δD values (‰) of four feathers collected from Yellow Warblers *Dendroica petechia* breeding in Revelstoke, British Columbia, in 2005 and 2006

Feather	2005			2006			Statistic	
	Mean	Range	*n*	Mean	Range	*n*	χ^2_1	*P*
Primary covert	−131.3	−142.9, −117.0	22	−132.8	−143.3, −120.5	20	0.7	0.41
Tail	−139.2	−150.4, −129.1	19	−131.2	−139.7, −123.0	21	21.2	<0.001
Greater covert	−34.3	−47.0, −22.4	8	−25.2	−64.2, 0.5	51	4.0	0.05
Crown	−43.7	−74.3, −28.1	27	−23.6	−70.9, −0.8	51	43.2	<0.001

Two tail feather and three crown feather samples with extreme δD_f values were excluded from these analyses

birds (model predictions ± SE controlling for significant terms, $SY = -40.3 \pm 3.1$‰, $ASY = -31.3 \pm 1.9$‰, $\chi^2_1 = 6.2$, $P = 0.02$).

Relationship between long term averaged δD_P and predicted and observed δD_f

The long-term growing season δD_P for the area surrounding our study population in Revelstoke, southeast British Columbia, based on an interpolated base maps for North and South America (Bowen et al. 2005) was -114 ± 9.4 ‰. Assuming a fixed discrimination factor of −19‰, flight feathers grown in the Revelstoke region or southeast British Columbia would be expected to have mean δD_f of −133.4‰. The observed mean δD_f for both primary coverts and tail feathers was −132.0‰, and all primary coverts and 91% of tail feathers fell within the 95% confidence intervals of the expected δD_f (Table 2).

The long-term growing season δD_P for the area covering the known wintering distribution of Yellow Warblers was -29 ± 6.3 ‰, and there was relatively little difference between the δD_P expected for Mexico, Central and South America (Table 2). Assuming a fixed discrimination factor of −19‰, winter-grown feathers would be expected to have a mean δD_f of −48.1‰. The observed mean δD_f for the greater covert and crown feathers sampled was more enriched than expected, being −23.1‰ for greater coverts and −33‰ for crown feathers. Furthermore, only 28% of greater coverts and 33% of the crown feathers sampled fell within the 95% confidence intervals of the expected δD_f for feathers grown anywhere in the winter distribution (Table 2). However, since the observed values were more enriched than expected, and δD_P values become more depleted as you move from Mexico to Canada, these feathers are unlikely to have been grown on migration.

Table 2 Summary of long-term average growing season δD_P (± SD) for the area surrounding Revelstoke, BC

Region	Expected δD_f		
	δD_P ± SD (‰)	Mean (‰)	95% CI (‰)
Summer			
BC	−114.4 ± 9.4	−133.4	−151.8, −115.0
Winter			
Entire distribution	−29.1 ± 6.3	−48.1	−60.4, −35,8
Mexico	−29.7 ± 5.3	−48.7	−59.0, −38.3
Central America	−35.2 ± 3.7	−54.2	−61.5, −46.9
South America	−27.6 ± 6.0	−46.6	−58.3, −34.9

δD_P (± SD) for the known wintering distribution of Yellow Warblers in its entirety and broken down into regions, and the expected δD_f of feathers grown in these areas assuming a precipitation to tissue discrimination factor of −19‰

Discussion

Yellow Warblers, and several other species in the Parulidae, have been documented to have a biannual molting strategy in which different feather blocks are replaced in different seasons (Pyle 1997; Voelker and McFarland 2002). This study found that the δD_f of primary coverts and tail feathers are depleted compared to the δD_f of greater coverts and crown feathers. The δD_f values documented confirm that Yellow Warblers complete their preformative or prebasic molt on or close to their breeding grounds and undergo a prealternate molt, which involves the replacement of some body and flight feathers, on their wintering grounds. The ability to use deuterium isotope ratios of different feather blocks and isoscapes of δD_P to assign individual Yellow Warblers to their breeding and wintering regions is, however, limited by interannual variation in δD_f of some feather blocks and the weak spatial gradient in δD_P across the wintering distribution. Nevertheless, the consistent seasonal molting patterns observed among multiple feather tracts means that additional insights into the migratory connectivity and habitat use of Yellow Warblers on their breeding and wintering grounds could be obtained using other stable isotopes or trace elements.

Variation in δD_f across feather blocks

Stable isotope analysis of δD values in feathers has become a widely applied tool to link birds captured on the wintering grounds (or en route during migration) to their previous breeding origins (Hobson and Wassenaar 2008). The success of this approach has been supported by isotope base maps created to represent the known latitudinal gradient of spatially distinct δD patterns expressed in precipitation (Bowen et al. 2005) and confirmed for feathers grown in these regions (Hobson and Wassenaar 1997). More recently, studies have begun to examine the utility of using winter-grown feathers sampled from birds captured on breeding grounds to identify their wintering grounds (e.g., Jones et al. 2008; Kelly et al. 2008). Kelly et al. (2008) found that discriminant functions based on hydrogen, nitrogen and carbon isotope ratios in feathers were only able to accurately assign 30–50% of Willow Flycatchers (*Empidomax traillii*) to five regions within their winter range. Our study confirms that deuterium isotope analysis of summer-grown feathers sampled from Yellow Warblers provides information about their breeding origins. We found that the δD_f of the vast majority of primary coverts and tail feathers fell within the range expected from the long-term average δD_P for the area surrounding Revelstoke. However, despite showing that Yellow Warblers also undergo a prealternate molt on their wintering grounds, we found that deuterium isotope analysis of winter-grown feathers provided little information about their wintering location. Winter-grown feathers had more enriched δD_f signatures than expected, and only 30% of crown and greater coverts fell within the range expected given the long-term average δD_P for their winter distribution.

There are several possible explanations for why the δD_f of most crown and greater covert feathers fall outside the expected range based on long-term average growing season δD_P. First, the isotope base map for Central and South America is based on data on rainfall over the entire growing season from relatively few fixed points interpolated over a large geographic area that may not reflect finer scale temporal or geographic variation in δD_P. This explanation is supported by δD_P data from single sites in Vera Cruz, Mexico, and the Panama Canal, Panama (available on the GNIP/ISOHIS database, IAEA 2007), where δD_P values for the wintering period (October–March) align more closely with the observed δD_f values in winter grown feathers (Vera Cruz = 0.9 ± 20‰; Panama Canal = −17.9 ± 15.2‰). This highlights the need for a greater understanding of the timeframe over which δD_P is incorporated into the diet and then feather tissue (see Coulton et al. 2009). Second, El Niño events that are associated with increased winter rainfall in Mexico would be expected to result in more depleted δD_f values than those predicted using isoscapes based on long-term averaged δD_P. This would explain the interannual variation in δD_f (see below) but does not explain why δD_f values are more enriched than expected in both 2005 and 2006. Third, δD_f values may be more enriched than expected because diet–tissue discrimination factors vary with latitude, with habitats used at different times of the year, or with the season tissues are produced. Lott and Smith (2006), for example, found that the relationship between estimates of δD_P and δD_f in raptor feathers varied across regions of North America.

We found that there was greater variation in the δD_f of some feather blocks than others, with extreme values being more likely in tail and crown feathers. Tail feathers with relatively enriched signatures could be evidence that a small percentage of Yellow Warblers complete their molt on migration (Norris et al. 2004b). Molt migration has been argued to be more common in western populations of Neotropical migrants than eastern populations (Rohwer et al. 2005; Carlisle et al. 2005). Alternatively, it is possible that enriched values result because tail feathers are occasionally lost inadvertently and replaced during migration or on wintering grounds (Reudink et al. 2008). Crown feathers with relatively depleted δDf values compared to other winter-grown feathers may indicate that some birds complete their prealternate molt after leaving their wintering grounds. However, it is also possible that individuals do not replace all their crown feathers during the prealternate molt and that extreme values are produced when one or more of the five crown feathers sampled for deuterium isotope analysis was grown at the end of the breeding season. If ASY birds replaced a higher proportion of their crown feathers in their prealternate molt, this argument would also explain why SY birds have, on average, more depleted δD_f than ASY birds. Regardless of the mechanism, the greater variability in the δD_f of tail and crown feathers may mean they provide less reliable information about the breeding and wintering locations than primary and greater coverts, respectively.

Interannual variation in δD signatures

Interannual variation in δD is a fundamental source of uncertainty for stable isotope studies attempting to assign migratory animals to their geographic origins (Farmer et al. 2008). In this study, there was considerable annual variation in the δD_f of feathers replaced on the wintering grounds and in the δD_f of one of the feathers grown on the breeding grounds. Interannual variation in the δD_f of the crown and greater coverts could arise because individuals sampled in 2005 had over-wintered in different locations to those sampled in 2006 or because of annual variation in the δD values of the diet and hence tissue synthesized in the 2 years. The former appears unlikely because year to year differences in the entire dataset were also observed in the feathers collected from individuals sampled in both years, and Yellow Warblers have been documented as showing winter site fidelity (Greenberg and Salgado-Ortiz 1994; Warkentin and Hernandez 1996). The latter appears more likely. Interannual variation in the δD_f of the crown and greater coverts was expected because the winters of 2004/2005 and 2005/2006 were classified as El Niño and La Niña events, respectively (as defined by SST anomalies where 5-month running averages are consistently above or below 0.5°C; NOAA), and El Niño events are associated with increased winter–spring rainfall across Mexico (Caso et al. 2007), and greater precipitation is associated with more depleted δD_P (Panarello and Dapeña 2009). Atkinson et al. (2005) have also reported interannual differences in δD values of Red Knot *Calidris canutus* feathers grown on their Caribbean and South America wintering grounds and related these differences to broad-scale changes in climatic patterns across the Knot wintering range. Given that global scale climate events have predictable, but different, effects on rainfall in different regions, interannual variation in δD_f may provide information that allows the geographic origins of migratory birds to be assigned more accurately.

Recent work documented interannual variation in the δD_f of feathers from Mallards *Anas platyrynchos* grown on breeding grounds in north-central North America that reflected the dynamics of water entering the wetlands and variation in δD_P dating back more than 12 months (Coulton et al. 2009). We might therefore have expected interannual variation in the δD_f of both primary coverts and tail feathers because Yellow Warblers in Revelstoke breed in riparian habitat within the upper reaches of Upper Arrows Lake Reservoir, and water levels vary depending on snowpack, the timing of snowmelt, and the water use decisions in the reservoir system that reflect demands for hydro-electric power. However, snowpack, the timing of snowmelt, precipitation, and water levels in the Upper Arrows Reservoir were similar in 2004 and 2005, when the primary coverts and tail feathers sampled in 2005 and 2006, respectively, were grown (Environment Canada 2009; B.C. Hydro, unpublished data). Since interannual variation in evapotranspiration rates and the source of water entering the riparian system would also be expected to lead to variation in the δD_f values of all feathers grown at the end of the breeding season, it is unclear why the δD_f of tail feathers, but not primary coverts, varied between years. Further work is needed to understand how annual variation in δD_P and the source of water entering riparian systems influence seasonal variation in dietary δD and the δD_f of different feather blocks.

Sex differences in δDf of winter grown feathers

In several species of Neotropical migratory birds, including Yellow Warblers, females are argued to overwinter at more southerly locations than males (Komar et al. 2005). For populations of Yellow Warblers breeding in western Canada that are thought to overwinter across Mexico and as far south as Panama (Boulet et al. 2006), females might then be expected to have more enriched δD_f signatures than males. We did not detect any differences in the δD_f of winter-grown feathers collected from male and female Yellow Warblers. However, this is not that surprising since, despite differences in the sex ratio of Yellow Warblers in Mexico and southern Central America, both males and females are found in both locations (Komar et al. 2005) and differences in long-term average δD_P between Mexico, Central and northern South America are small.

In summary, while δD analysis of feather samples and isotopic base maps of δD_P have been used successfully as spatial references for studying movement patterns in migratory species, the strength of latitudinal gradients in δD_f and temporal variation in δD_P can limit the accuracy of assignment to breeding or wintering grounds. This study confirms that δD analysis of summer-grown feathers and isotope base maps can be used to assign Yellow Warblers captured on wintering grounds to their breeding origins. However, the weak gradients in long-term average δD_P across Mexico and Central America combined with climatic events that influence δD_P and lead to interannual variation in δD_f of winter-grown feathers do not allow this approach to be used to assign birds to their wintering grounds. Our study therefore supports the suggestion made by Farmer et al. (2008) that greater consideration should be given to spatial and temporal variation in δD_P gradients before using isotopic base maps of δD_P to infer the wintering locations of Neotropical migrants.

Zusammenfassung

Schwankungen in den Deuterium(δD)signaturen von im Brutgebiet und im Überwinterungsgebiet gewachsenen Goldwaldsängerfedern *Dendroica petechia*

Eine stabile Isotopenanalyse von Federn könnte dabei helfen, die Populationen von Zugvögeln im Jahreszyklus zu verfolgen. Wir verwenden Deuteriumisotop-Verhältnisse in Federn (δD_f), um zu bestätigen, dass Goldwaldsänger sowohl eine Postnuptialmauser in oder nahe ihrem Brutgebiet als auch eine Pränuptialmauser in ihrem Überwinterungsgebiet durchmachen, und schätzen ab, ob eine δD-Analyse unterschiedlicher Federtypen dabei helfen kann, Vögel einem Brut- oder Überwinterungsgebiet zuzuordnen. Wir zeigen, dass die Handdecken und Schwanzfedern δD_f-Werte aufweisen, welche die langfristigen durchschnittlichen Deuteriumisotop-Verhältnisse im Niederschlag (δD_P) im Brutgebiet widerspiegeln. Die meisten großen Decken und Kronenfedern haben jedoch δD_f-Werte, die höher sind als auf der Basis der δD_P-Werte im Überwinterungsgebiet vorhergesagt. Wir fanden außerdem signifikante jährliche Schwankungen in den δD_f-Werten von Schwanzfedern, großen Decken und Kronenfedern. Jährliche Schwankungen der δD_f-Werte von im Winter gewachsenen Federn könnten mit den El Niño-/La Niña-Bedingungen erklärt werden, welche die Niederschlagsmenge und daher δD_P beeinflussen; Federn hatten niedrigere δD_f-Werte nach einem El Niño-Jahr (2005) als nach einem La Niña-Jahr (2006). Das Geschlecht hatte keinerlei Einfluss auf die δD_f-Werte beprobter Federn. Das Alter beeinflusste die δD_f-Werte von Kronenfedern, nicht jedoch von großen Decken. Diese Studie bestätigt daher, dass die δD_f-Werte von im Sommer gewachsenen Federn verwendet werden können, um Brutgebiete zu identifizieren, deutet jedoch darauf hin, dass die Möglichkeit, die δD_f-Werte von im Winter gewachsenen Federn heranzuziehen, um Individuen ihren Überwinterungsgebieten zuzuordnen, durch schwache räumliche Gradienten und zeitliche Schwankungen in δD_P begrenzt ist.

Acknowledgments We would like to thank Julian Hudson and Christine Croton for initiating the monitoring of this population in 2004. Pauline Riding and Danny O'Farrell worked long hours mist-netting birds. Ryan Norris provided valuable comments on several early versions of this paper. Marylène Boulet provided valuable advice. Funding for the research came from the Columbia Basin Fish and Wildlife Program, BC Hydro, a NSERC Discovery grant to DJG and a Friends of Mount Revelstoke and Glacier National Parks grant to SPQ. SPQ was supported by an NSERC Industrial Scholarship sponsored by BC Hydro. All field protocols were approved by the Simon Fraser University Animal Care Committee and conducted under a Federal Scientific Permit.

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