Oecologia (2002) 130:216–221
DOI 10.1007/s004420100789

**Jeffrey F. Kelly · Viorel Atudorei · Zachary D. Sharp
Deborah M. Finch**

Insights into Wilson's Warbler migration from analyses of hydrogen stable-isotope ratios

Received: 26 March 2001 / Accepted: 17 July 2001 / Published online: 6 September 2001

Abstract Our ability to link the breeding locations of individual passerines to migration stopover sites and wintering locations is limited. Stable isotopes of hydrogen contained in bird feathers have recently shown potential in this regard. We measured hydrogen stable-isotope ratios (δD) of feathers from breeding, migrating, and wintering Wilson's Warblers. Analyses of feathers from museum specimens collected throughout the western portion of the breeding range indicate that δD values are significantly negatively related to latitude of collection (R^2=0.52), which is an indication that δD values are a good descriptor of breeding latitude. Analyses of feathers collected from birds migrating through the Bosque del Apache National Wildlife Refuge, New Mexico (USA), revealed a significantly positive relationship between δD values and the timing of autumn migration (R^2=0.34), but not the timing of spring migration. This pattern indicates that Wilson's Warblers that bred furthest north migrated earliest in the autumn. Finally, analysis of feathers collected on the wintering grounds indicate that the hydrogen isotope ratio is significantly positively related to wintering latitude (R^2=0.80), which indicates that birds that bred furthest north wintered furthest south. In combination, these patterns suggest that in the western portion of their range, Wilson's Warblers have a leapfrog migration system in which the northern-most breeding birds pass through New Mexico early in the autumn to arrive on the wintering grounds in southern Central America, the southern edge of the Wilson's Warblers winter range. We know of no other literature documenting or suggesting that Wilson's Warbler engage in leapfrog migration. We think the novelty of these results is a reflection of the potential for stable-isotope techniques to revise our understanding of bird migration.

Keywords Leapfrog migration · Hydrogen-isotope ratio · *Wilsonia pusilla* · Wilson's Warbler · Stopover biology

Introduction

Recent field studies have improved our understanding of Nearctic-Neotropic songbird migration (Parrish 1997; Woodrey and Moore 1997; Yong et al. 1998). Despite these advances, large gaps remain in our knowledge of how birds migrate. In particular, our ability to understand migration is limited by our scant knowledge of the origin and destination of migrating individuals. Passive tracking of individuals (e.g., banding) has produced notoriously little data in this regard and active tracking (e.g., radio telemetry) still has severe limitations when applied to small birds traveling large distances.

Filling this void is recent evidence that the ratio of stable isotopes of hydrogen (^{2}H/^{1}H) can be used to identify the latitude at which feathers were grown (Chamberlain et al. 1997, 2000; Hobson and Wassenaar 1997; Hobson et al. 2000; Kelly and Finch 1998; Meehan et al. 2001). The majority of passerines, including Wilson's Warblers (*Wilsonia pusilla*), undergo a post-breeding molt in the vicinity of their breeding territory prior to fall migration. Since feathers grown during this molt are retained throughout the year (Pyle 1997), they are useful in tracing the breeding latitude of migrating and wintering birds (Chamberlain et al. 1997; Hobson and Wassenaar 1997).

The utility of hydrogen isotopes in this regard relies on two patterns. First, hydrogen isotope ratios of feathers reflect closely those of the growing-season (monthly average temperatures >0°C) precipitation of the locality where they were grown (Chamberlain et al. 1997; Hobson and Wassenaar 1997). Second, fractionation of hydrogen isotopes in rainfall creates a gradient in the hydrogen isotope ratio (δD) in growing-season precipitation associated

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J.F. Kelly (✉) · D.M. Finch
Rocky Mountain Research Station, 333 Broadway SE, Suite 115,
Albuquerque, NM 87102, USA
e-mail: jfkelly@fs.fed.us
Fax: +1-505-7243688

V. Atudorei · Z.D. Sharp
Department of Earth and Planetary Sciences,
University of New Mexico, Albuquerque, NM 87131, USA

primarily with latitude, but also with continental (distance from the coast) and altitudinal effects (Cormie et al. 1994; Rozanski et al. 1993). This gradient is characterized by precipitation at southern latitudes being more enriched in deuterium than that at northern latitudes.

In the western United States the breeding distribution of the Wilson's Warbler ranges from 35° to 70° north latitude. The species breeds in riparian vegetation and is restricted to high elevation in the southern portions of its range. Wilson's Warbler is the most abundant wood warbler during autumn migration in the middle Rio Grande Valley, New Mexico (Kelly et al. 1999, 2000), and individual Wilson's Warblers can differ in the timing of their migration by months (Yong et al. 1998). One potential explanation for the large variation in the timing of migration is that birds from different breeding latitudes migrate at different times.

In the study presented here we used recently developed techniques for measuring stable isotope ratios of hydrogen in bird feathers to further our understanding of the relationships among breeding latitudes, timing of migration, and wintering locations of Wilson's Warblers. Specifically, we sought to: (1) verify that breeding latitude was related to stable hydrogen isotope ratio in Wilson's Warbler feathers, (2) determine if feathers collected during migration could be used to assess the breeding latitude of migrants, (3) determine if stable hydrogen isotope ratios indicated a relationship between breeding location and migration timing, and (4) determine if a relationship exists between breeding and wintering latitudes.

Materials and methods

The ratio of stable hydrogen isotopes ($^{2}H/^{1}H$) is expressed in delta notation (δD), where $\delta D=[(\text{hydrogen isotope ratio}_{\text{sample}}/\text{hydrogen isotope ratio}_{\text{standard}}) - 1] \times 1{,}000$. Consequently, δD is parts per thousand (‰) deviation from the standard, that is, standard mean ocean water (vSMOW).

Feathers were washed in detergent and thoroughly rinsed to remove oil, dirt, and residual detergent. To address problems with exchangeable hydrogen in feather keratin (Chamberlain et al. 1997), feathers were stored in sealed vials with water of known isotopic composition (–95.5‰ vs vSMOW) for at least 10 days prior to isotopic measurements. Feathers were oven dried at 100°C prior to analysis to remove water. A small piece (0.1–0.2 mg) of the distal end of a feather was removed and wrapped in a silver capsule. The feather was then dropped into a high-temperature reduction furnace (Finnigan TC/EA) interfaced through an open split (Finnigan MAT Conflo II) with a mass spectrometer (Finnigan MAT Delta plus XL). The reduction furnace was used to pyrolize feather samples at 1,450°C. Hereafter this technique is referred to as on-line pyrolysis. We verified that on-line pyrolysis techniques provide accurate values for international isotopic water standards with a standard deviation of ±2‰ (Sharp et al. 2001) as well as for feathers. Comparisons of on-line and off-line analyses (i.e., methods of Chamberlain et al. 1997) of the same Western Gull (*Larus occidentalis*) feather indicate close agreement between these techniques (on-line mean±SD=–25.8±3.8‰, n=4; off-line=–28.4±2.5‰, n=4). Repeated on-line pyrolysis of the same European Starling (*Sturnus vulgaris*) feather indicated that the precision of the technique was ±4‰ (mean±SD=–78.8±3.7‰, range –84.9 to –74.5‰, n=10).

To test the ability of stable isotopes of hydrogen to detect latitudinal differences between breeding locations of birds captured during migration, we compared δD values of feathers from ten birds for each of two subspecies of White-crowned Sparrows (*Zonotrichia leucophrys*) collected during autumn migration. Because Gambel's White-crowned Sparrows (*Z. l. gambelii*) breed nearly entirely north of Mountain White-crowned Sparrows (*Z. l. leucophrys*; Pyle 1997), feathers of Gambel's White-crowned Sparrows should have lower δD values than the Mountain subspecies. We collected feathers from these two subspecies, which can be distinguished by plumage differences in the field, during autumn migration 1998 at the Bosque del Apache National Wildlife Refuge (NWR), New Mexico, USA (33° 48′N, 106° 52′W).

While the plumage characters of White-crowned Sparrow subspecies made them useful for testing the efficacy of hydrogen isotope ratios in distinguishing breeding latitudes, they would not be useful for examining the relationship between breeding latitude and the timing of migration in New Mexico. Because White-crowned Sparrows of both subspecies (primarily *gambelii*) winter in the study area, comparing capture dates for the subspecies could be very misleading. That is, the date on which a White-crowned Sparrow is captured may have little to do with when it arrived. Moreover, the range of dates over which we captured these subspecies overlap nearly entirely in both spring and fall, which precludes the use of range of capture dates as an indication of migration timing.

Wilson's Warblers occur at our study site only as migrants and are therefore useful for examining the relationship between breeding latitude and timing of migration. Because Wilson's Warblers replace their flight and body feathers only once during the year immediately post-breeding on the breeding grounds (Pyle 1997), these feathers carry the isotope signature from the breeding site throughout the year. A primary feather and body feathers were removed from Wilson's Warblers caught during migration through the Bosque del Apache NWR in spring and autumn 1998. Pairs of flight and body feathers were analyzed to confirm that these types of feathers contained similar stable hydrogen isotope ratios. To de-

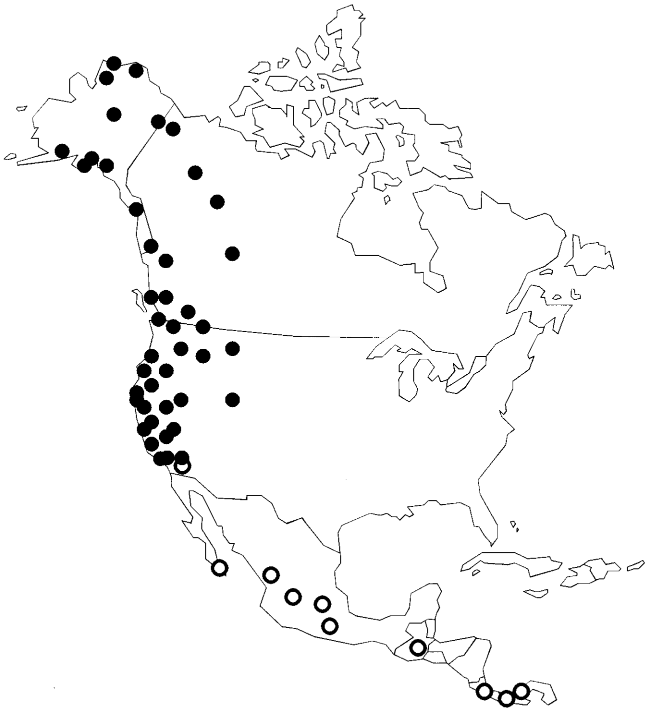

Fig. 1 Map of collection locations of Wilson's Warbler feathers. *Solid circles* indicate feathers collected between June 3 and August 3 and *open circles* indicate feathers collected between November and February

termine the relationship between hydrogen isotope ratio and breeding latitude, body feathers from adult Wilson's Warblers provided by the Museum of Vertebrate Zoology and the National Museum of Natural History were analyzed. These specimens had been collected on the breeding grounds between 3 June and 3 August (Fig. 1). Similarly, body feathers of Wilson's Warblers that had been collected between November and February in Mexico and Central America were used to evaluate patterns in hydrogen isotope ratios on the wintering grounds (Fig. 1). The significance of all statistical tests was evaluated with a critical value of 0.05 and data are reported as means±SD unless noted otherwise.

Results

Analyses of pairs of body and primary feathers from migrating Wilson's Warblers indicate that there is a linear correspondence between the hydrogen isotope ratios in body feathers and flight feathers (Fig. 2). There was also a consistent depletion in the hydrogen isotope ratio of flight feathers relative to body feathers (difference=9.6±7.6‰, t=4.3, P=0.002). Because the difference between flight and body feathers was consistent across the range of values, we concluded that the hydrogen isotope ratio of body feathers would be as useful as those of flight feathers in assessing the geographic location feather growth.

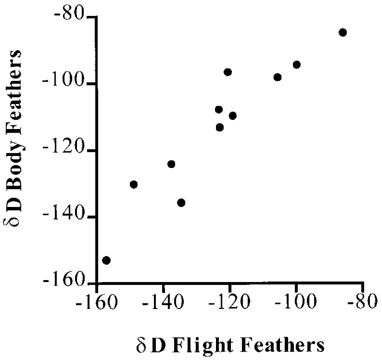

Fig. 2 Hydrogen isotope ratios (*δD*) of pairs of body and flight feathers from 11 Wilson's Warblers. Feathers were collected during migration

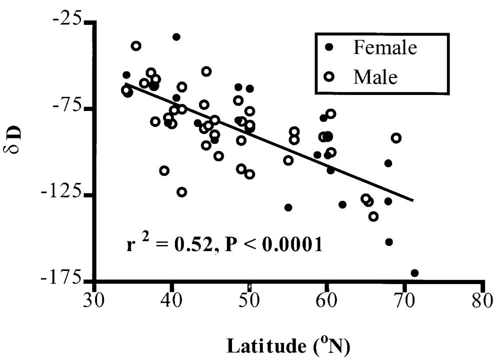

Fig. 3 Hydrogen isotope ratios of Wilson's Warbler feathers from the breeding season plotted against the latitude at which the feathers were collected. The slope of the regression line (mean±SE) is –1.8±0.24 and the intercept is 0.1±11.9

Isotopic analysis of body feathers from 63 Wilson's Warblers (21 female, 42 male) collected during the breeding season indicated that there was a strong negative relationship between the latitude of the collection site and hydrogen isotope ratio that explained 52% of the variation in hydrogen isotope ratios (Fig. 3). The latitudinal pattern was evident in both females (R^2=0.59, $F_{1,19}$=27.1, P<0.0001) and males (R^2=0.46, $F_{1,40}$=17.6, P<0.0001). The relationship between hydrogen isotope ratio and latitude did not differ between the sexes (analysis of covariance, $F_{1,60}$=0.2, P=0.6)

The ability to predict breeding latitude of an individual from a hydrogen isotope measurement is still limited. For instance, by using inverse 95% prediction intervals we predict that an individual with a δD value of –120‰ probably did not breed south of 46°N latitude. Conversely, an individual with a δD value of – 70‰ probably did not breed north of 60°N latitude. An individual with a δD value of –100‰, however, could have bred anywhere in the range. At the population level the prediction intervals are considerably smaller; 36–42 N latitude, 52–60°N latitude and 63–71°N latitude for individuals with δD values of –70‰, –100‰ and – 120‰, respectively.

δD values segregated subspecies of White-crowned Sparrows (Fig. 4b). Specifically, Mountain White-crowned Sparrows (*Zonotrichia leucophrys oriantha*), which breed primarily in the western continental United

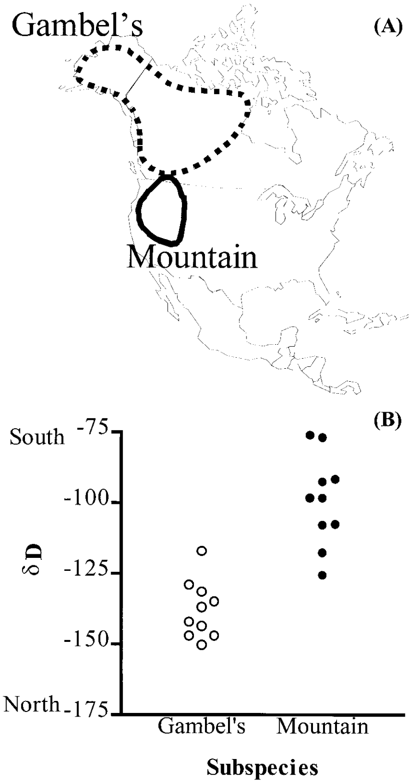

Fig. 4 Map of the breeding ranges of two subspecies of White-crowned Sparrows (**A**) and hydrogen isotope ratios of feathers from these two subspecies (**B**). Note that the subspecies have disjunct breeding ranges and have little overlap in stable isotope ratios

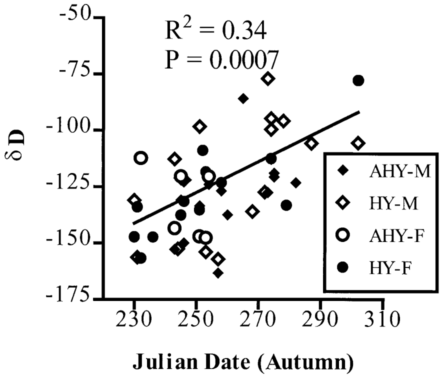

Fig. 5 Hydrogen isotope ratios of feathers collected from Wilson's Warblers migrating through the Bosque del Apache National Wildlife Refuge in autumn. *Symbols* refer to the age and sex classes of the birds. (*AHY* After-hatch-year, *HY* hatch year, *M* male, *F* female)

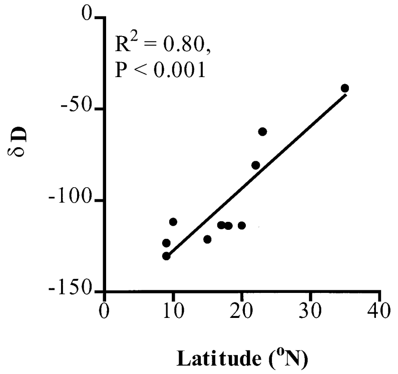

Fig. 6 Stable hydrogen isotope ratios of Wilson's Warbler feathers collected between November and February plotted against latitude of the collection site. The slope of the regression line (mean±SE) is 3.4±0.6 and the intercept is –161±11.5

States had higher δD values, as predicted, than Gambel's White-crowned Sparrows (*Z. l. gambelii*), which breed in Alaska and northern Canada (Fig. 4a; Pyle 1997).

There was a positive relationship between the δD values of 50 Wilson's Warblers captured in autumn migration though the Bosque del Apache NWR and capture date (Fig. 5). Thus, birds breeding at high latitudes migrated through the Middle Rio Grande Valley prior to birds that grew their feathers at lower latitudes. This pattern was evident in after-hatch-year males (R^2=0.29, $F_{1,12}$=5.0, P<0.05), hatch-year males (R^2=0.31, $F_{1,15}$=6.7, P<0.03) and hatch-year females (R^2=0.67, $F_{1,11}$=22.7, P<0.001). The number of after-hatch-year females sampled (n=6) was probably too small to detect any pattern. The δD values of 20 birds (10 female and 10 male) showed no relationship with the timing of their migration in spring (R^2=0.06, $F_{1,18}$=1.2, P=0.3), nor was there any relationship when sexes were analyzed separately. Finally, there was a positive relationship between the latitude of winter collection sites and stable hydrogen isotope ratio (Fig. 6), indicating that birds that bred at the northern edge of the breeding range wintered at the southern end of the winter range.

Discussion

Our analyses of paired flight and body feathers demonstrated that body feathers and flight feathers contain similar hydrogen isotope information. This evidence justifies, at least in the Wilson's Warbler, the use of stable hydrogen isotope ratios from the body feathers of museum specimens to examine relationships among breeding latitude, migration timing and wintering latitude. Our analysis of body feathers from throughout the western breeding range of the Wilson's Warbler support the findings of Chamberlain et al. (1997) and Hobson and Wassenaar (1997) that hydrogen isotope ratio alone provides a good description of breeding latitude.

The strong relationship we found between hydrogen isotope ratio and latitude is also important because it demonstrates that potential confounding factors, particularly continental and altitudinal effects, are not large enough to obscure the latitudinal pattern. There are well-known and relatively strong negative relationships between distance from the coast, altitude and hydrogen isotope ratios of precipitation. For this reason, it is likely that bird feathers collected in a small geographic area across an altitudinal gradient would vary systematically in their hydrogen isotope ratios. It is also possible for birds from low latitudes and high elevations (e.g., southern Rocky Mountains) to have hydrogen stable-isotope ratios that are similar to those from high latitudes and low elevations (e.g., the arctic tundra). In our data, however, these effects did not override the relationship between latitude and hydrogen isotope ratio. Moreover, analysis of 18 samples for which the elevation of the collection site was known indicated no correlation between hydrogen isotope ratio and altitude. Similarly, adding distance from the west coast to our analyses did not explain more of the variation in hydrogen isotope ratios. Despite these findings, we still suspect that the scatter of points in Fig. 3 is impacted by these factors. For instance, the northern samples that fall well below the regression line in Fig. 5 were collected in the continental interior (east of the Rocky Mountains). It is likely that the relatively depleted hydrogen isotope ratios of these samples are a result of the continental effect.

The robustness of the relationship between latitude and hydrogen isotope ratio was further evident in the δD values of White-crowned Sparrow feathers. These data also demonstrate that feathers collected from migrants and wintering birds will be useful for delineating their breeding locations. Gambel's White-crowned Sparrows breed as far south as southern British Columbia, whereas Mountain White-crowned Sparrows breed only as far north as southern Alberta (Pyle 1997). As expected from these breeding distributions, there was limited overlap in the stable hydrogen isotope ratios of feathers between these subspecies.

Wilson's Warblers that grew feathers further north (i.e., had lower δD values) migrated through the Bosque Del Apache earlier in the autumn than those whose feathers were grown further south. It is not clear why a pattern that was so clear in autumn was non-existent in the spring. This seasonal difference does not appear to be the result of a restricted subset of birds migrating through our banding site in either season, as the δD values of birds in each season range from about –75‰ to –150‰. In our view it is more likely that different constraints on the timing and pace of migration between seasons may account for these differences. For instance, males migrate earlier than females in the spring and stopover for shorter time periods, whereas in autumn these sex-based differences are minimal and the differences among age classes are more pronounced (Yong et al. 1998).

There was also a strong relationship between wintering location and stable hydrogen isotope ratios in feathers. This relationship suggests that migrants from the northern portion of the breeding range leapfrog individuals from the more southern portion of the species range to winter in the southern portion of the winter range. To our knowledge there is no previous indication in the literature that Wilson's Warblers are leapfrog migrants. This interpretation is also bolstered by the autumn relationship between δD values and the timing of migration. In particular, it seems reasonable to speculate that birds migrating from northern latitudes are arriving at the Bosque del Apache first in the autumn because they have the furthest to travel to arrive at their wintering grounds.

These patterns are inconsistent with one of the commonly purported explanations for leapfrog migration. That is, birds that have only short distances to migrate get to the best (northern most) wintering grounds first and later arrivals are forced through competition to migrate further south (Alerstam 1990). This explanation predicts a pattern of earlier passage of southern compared to northern breeders in the autumn, which contrasts with our finding. Another common explanation for leapfrog migration is that the timing of spring arrival is more critical for southern breeding birds than northern conspecifics, and therefore wintering in close proximity to the breeding ground is of more value to birds that breed at the southern edge of the range (Alerstam 1990). Thus, these southern breeders are willing to endure heavier costs to winter further north. Because it does not lead to clear predictions about the timing of either spring or fall migration, our results neither confirm nor conflict with this explanation.

Leapfrog migration in Wilson's Warblers may have broad implications for their migration patterns, breeding ecology, and morphology. If birds that winter in Baja California migrate only as far as California, Nevada, Utah and Colorado to breed, then these individuals will travel less than half the distance of birds that winter in Panama and breed in the Arctic. Although the inverse prediction intervals indicate that our ability to assign a particular migrant exactly to its breeding latitude is still quite limited, stable isotopes of hydrogen still appear to be useful in advancing our understanding of migration. For example, the affect of a bird's body condition (i.e., stored energy) and time of arrival at a stopover site on its length of stay and behavior could be examined in light of the distance already traveled during autumn migration or the distance that remains to be traveled in spring. In addition, populations of Wilson's Warblers that migrate from the Arctic to southern Central America might be expected to differ predictably in morphology (e.g., have longer wings) from those that migrate from Sonora to Utah, as has been shown in both Old World and New World Warblers (Gaston 1974; Wiedenfeld 1991).

These types of questions have been very difficult to address, but the advances in stable-isotope technology have made them practical to answer. Our results indicate that stable isotopes of hydrogen can be a powerful tool for furthering our understanding of the links between breeding regions, migration timing and wintering locations of small songbirds.

Acknowledgements We thank M.D. Means, D.L. Hawksworth, S. Allerton, and G. Bodner for operating the banding station and collecting feathers in 1998. John Taylor at Bosque del Apache NWR provided access to field sites and logistical support. The Museum of Vertebrate Zoology and the National Museum of Natural History provided feather samples. Tim Meehan, Mark Chappell, and Gary Graves provided comments that improved the manuscript. Linda Delay helped with mapping feather collection sites.

References

Alerstam T (1990) Bird migration. Cambridge University Press, Cambridge

Chamberlain CP, Blum JD, Holmes RT, Feng X, Sherry TW, Graves GR (1997) The use of isotope tracers for identifying populations of migratory birds. Oecologia 109:132–141

Chamberlain CP, Bensch S, Feng X, Akesson S, Andersson T (2000) Stable isotopes examined across a migratory divide in Scandinavian willow warblers (*Phylloscopus trochilus trochilus* and *Phylloscopus trochilus acredula*) reflect their African winter quarters. Proc R Soc Lond 267:43–48

Cormie AB, Schwarcz HP, Gray J (1994) Relation between hydrogen isotopic ratios of bone collagen and rain. Geochim Cosmochim Acta 58:377–391

Gaston AJ (1974) Adaptation in the genus Phylloscopus. Ibis 116:432–450

Hobson KA, Wassenaar LI (1997) Linking breeding and wintering grounds of neotropical migrant songbirds using stable hydrogen isotopic analysis of feathers. Oecologia 109:142–148

Hobson KA, Brua RB, Hohman WL, Wassenaar LI (2000) Low frequency of double molt of remiges in Ruddy Ducks revealed by stable isotopes: implication for tracking migratory waterfowl. Auk 117:129–135

Kelly JF, Finch DM (1998) Tracking migrant songbirds with stable isotopes. Trends Ecol Evol 13:48–49

Kelly JF, Smith R, Finch DM, Moore FR, Yong W (1999) Influence of summer biogeography on wood warbler stopover abundance. Condor 101:76–85

Kelly JF, Finch DM, Yong W (2000) Vegetative associations of wood warblers migrating along the Middle Rio Grande Valley, New Mexico. Southwest Nat 45:159–168

Meehan TD, Lott CA, Sharp ZD, Smith RB, Rosenfield RN, Stewart AC, Murphy RK (2001) Using hydrogen isotope geochemistry to estimate the natal latitudes of immature Cooper's Hawks migrating through the Florida Keys. Condor 103:11–20

Parrish JD (1997) Patterns of frugivory and energetic condition in Nearctic landbirds during autumn migration. Condor 99:681–697

Pyle P (1997) Identification guide to North American Birds. Slate Creek, Bolinas, Calif.

Rozanski K, Araguas-Araguas L, Gonfiantini R (1993) Isotopic patterns in modern global precipitation. Geophys Monogr 78: 1–36

Sharp ZD, Atudorei V, Durakiewicz T (2001) A rapid method for the determination of hydrogen and oxygen isotope ratios from water and hydrous minerals. Chem Geol 178:197–210

Woodrey MS, Moore FR (1997) Age-related timing differences in stopover of fall landbird migrants on the coast of Alabama. Auk 114:695–707

Wiedenfeld DA (1991) Geographical morphology of male Yellow Warblers. Condor 93:712–723

Yong W, Finch DM, Moore FR, Kelly JF (1998) Stopover ecology and habitat use of migratory Wilson's Warblers. Auk 115:829–841