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SPATIAL AND TEMPORAL MIGRATION PATTERNS OF WILSON'S WARBLER (*WILSONIA PUSILLA*) IN THE SOUTHWEST AS REVEALED BY STABLE ISOTOPES

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ABSTRACT.—We used stable hydrogen isotopes (δD) to identify the breeding locations of Wilson's Warbler (*Wilsonia pusilla*) migrating through five sites spanning a cross-section of the species' southwestern migration route during the springs of 2003 and 2004. Determining the temporal and spatial patterns of migration and degree of population segregation during migration is critical to understanding long-term population trends of migrant birds. At all five migration sites, we found a significant negative relationship between the date Wilson's Warblers passed through the sampling station and δD values of their feathers. These data were consistent with a pattern of "leap-frog" migration, in which individuals that bred the previous season at southern latitudes migrated through migration stations earlier than individuals that had previously bred at more northern latitudes. We documented that this pattern was consistent across sites and in multiple years. This finding corroborates previous research conducted on Wilson's Warbler during the fall migration. In addition, mean δD values became more negative across sampling stations from west to east, with the mean δD values at each station corresponding to different geographic regions of the Wilson's Warblers' western breeding range. These data indicate that Wilson's Warblers passing through each station represented a specific regional subset of the entire Wilson's Warbler western breeding range. As a result, habitat alterations at specific areas across the east–west expanse of the bird's migratory route in the southwestern United States could differentially affect Wilson's Warblers at different breeding areas. This migration information is critical for management of Neotropical migrants, especially in light of the rapid changes presently occurring over the southwestern landscape. Received 1 June 2005, accepted 25 January 2006.

Key words: deuterium, migration, migratory connectivity, Neotropical migrant, stable isotopes, *Wilsonia pusilla*, Wilson's Warbler.

Patrones Espaciales y Temporales de la Migración de *Wilsonia pusilla* en el Sudoeste Detectados Mediante Isótopos Estables

RESUMEN.—Usamos isótopos estables de hidrógeno (D) para identificar las localidad de cría de individuos de *Wilsonia pusilla* que se encontraban migrando a través de cinco sitios abarcando una sección de la ruta migratoria del sudoeste de la especie durante las primaveras de 2003 y 2004. Determinar los patrones

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temporales y espaciales de migración y el grado de segregación poblacional durante la migración es esencial para entender las tendencias poblacionales a largo plazo de las aves migratorias. En los cinco sitios de migración encontramos una relación negativa significativa entre la fecha en la que los individuos pasaron por la estación de muestreo y los valores de D de sus plumas. Estos datos fueron consistentes con un patrón migratorio del tipo "salto de rana", en donde los individuos que crían en la estación previa a latitudes más meridionales migraron más temprano a través de las estaciones migratorias que los individuos que criaron en latitudes más septentrionales. Documentamos que este patrón fue consistente a través de los sitios y en múltiples años. Este hallazgo corrobora investigaciones previas realizadas con *W. pusilla* durante la migración de otoño. Adicionalmente, los valores medios de D se volvieron más negativos a lo largo de las estaciones de muestreo desde el oeste hacia el este, correspondiendo los valores medios de D de cada estación a diferentes regiones geográficas del rango oeste de cría de *W. pusilla*. Estos datos indican que los individuos de *W. pusilla* que pasaron por cada estación representaron un subconjunto específico regional de la parte oeste del rango de cría de *W. pusilla*. Como resultado, las alteraciones de hábitat en áreas específicas a lo largo de la extensión este-oeste de la ruta migratoria de la especie en el sudoeste de Estados Unidos podrían afectar de modo diferencial a *W. pusilla* en las diferentes áreas de cría. Esta información es crucial para el manejo de las aves migratorias neotropicales, especialmente a la luz de los cambios actuales rápidos que se presentan en el paisaje del sudoeste.

THE MIGRATION PERIOD, when birds move between their wintering and breeding grounds, has not received attention proportional to the role that it plays in the population dynamics of Neotropical migrants (Gauthreaux 1979). Only within the past 10 years attention has been given to the importance of conservation of migrants along migration pathways. This is in spite of the fact that migration represents a critical period when birds can be at the edge of their physiological limits (Blem 1980) and may suffer the largest amount of annual mortality (Ketterson and Nolan 1982, Moore et al. 1995, Sillett and Holmes 2002). Both the spatial and temporal patterns of migration have important implications for understanding the ecology and evolution of migrants and factors influencing overall population dynamics (Moore and Simons 1992, Moore et al. 1995, Sherry and Holmes 1995). Whether breeding populations use distinctive migratory routes or mix across a broad migratory front directly determines how alteration of habitat along the route could potentially affect breeding populations. Likewise, differences in the timing of migration by different populations could suggest that different selective forces are acting on those populations (Cox 1985).

Research examining the dynamics of migration in the United States has primarily

focused on migration systems in the eastern part of the country (Moore and Simons 1992, Moore et al. 1995, Simons et al. 2000), whereas our understanding of migration in the west remains rudimentary (Kelly and Hutto 2005). Increasing habitat alterations and loss of critical stopover habitat in the southwestern United States (Rosenberg et al. 1991) make it essential that we begin to understand the temporal and spatial distribution patterns of Neotropical migrants across southwestern migration routes and how habitat alterations might affect different breeding populations. Traditional methods, such as banding, have yielded little data to answer these questions, but recent studies have shown that naturally occurring stable isotopes in animal tissues can be used to delineate geographically distinct populations (Chamberlain et al. 1997, Hobson and Wassenaar 1997, Marra et al. 1998). Specifically, stable hydrogen isotopes (δD) are a powerful research tool in connecting different parts of migratory birds' annual cycle, because predictable continental patterns of δD in precipitation are highly correlated with δD in body tissues of birds, owing to trophic-level interactions (Chamberlain et al. 1997, Hobson and Wassenaar 1997, Hobson et al. 2001, Meehan et al. 2001, Kelly et al. 2002, Rubenstein et al. 2002). This relationship is

primarily associated with latitude, given that southern latitudes are more enriched in δD than northern latitudes, but elevation and continental factors can also influence δD values (Ingraham 1998).

Most studies examining migratory connectivity (e.g., links between breeding and non-breeding areas; Webster et al. 2002) using stable isotopes have focused on linking the breeding and wintering grounds of Neotropical migrant birds (see review by Hobson 2003), with few studies focusing on migration (Meehan et al. 2001, Wassenaar and Hobson 2001, Kelly et al. 2002, Mazerolle et al. 2005). Yet determining how the migration period is linked to other stages of the annual cycle and the degree of population segregation during migration is also critical to understanding long-term population trends of migrants (Moore et al. 1995, Sherry and Holmes 1995). This is especially important in light of evidence of population declines of migratory passerine birds in recent decades (Robbins et al. 1989, Askins et al. 1990, Hagan and Johnston 1992, DeSante and George 1994).

Using stable hydrogen isotopes, we examined temporal and spatial migration patterns of Wilson's Warblers (*Wilsonia pusilla*; hereafter "warblers") during spring migration at multiple migration stations spanning their southwestern migration route. Warblers molt their flight feathers once on the breeding grounds before migration (Pyle 1997). Because the feathers' δD value reflects the diet of the bird only during the period of growth (Mizutani et al. 1990), the isotope value of the warbler feathers collected during migration should represent the isotopic signature of its breeding location. The two western subspecies of Wilson's Warbler (*W. p. pileolata* and *W. p. chryseola*) are abundant migrants throughout the southwestern United States, migrating north to breeding locations across western North America (Ammon and Gilbert 1999), and have a wide range of δD values. Kelly et al. (2002) and Clegg et al. (2003) showed that there is a strong negative relationship between δD values of warbler feathers collected on their breeding grounds and the latitude of the collection site. On the basis of this information, Kelly et al. (2002) found that during fall migration of warblers at one site in New Mexico, the northernmost breeders passed through first,

ahead of more southern-breeding warblers, but the same temporal pattern was not found for this site during spring migration.

Our study expands on the earlier work by Clegg et al. (2003) and Kelly et al. (2002) by examining the relationship between δD values of warbler feathers collected across their breeding range and the δD values of local precipitation at the collection site. This allows for a more precise connection between δD values of feathers collected during migration and their breeding locations. We also examined the temporal pattern of spring migration for warblers at multiple sites and in multiple years to determine whether a similar "leap-frog" migration pattern found during the fall (Kelly et al. 2002) is exhibited during the spring migration, and whether such a pattern is consistent across sites. In addition, we examined spatial patterns of warbler migration by comparing δD values among multiple migration stations spanning a cross-section of the species' southwestern migration route. This information provides insight into whether warblers migrate in broad fronts across the southwest or whether different breeding populations use distinctive migratory routes. Finally, both spatial and temporal migration patterns were tested in multiple years to determine the consistency of the patterns.

METHODS

Study areas.—To determine the relationship between δD values of warbler feathers collected on the breeding grounds and local precipitation where they were captured, δD values were determined from a single rectrix collected from 63 warblers across their western breeding grounds (Fig. 1) between 1996 and 2002 (feathers were supplied by the University of California at Los Angeles [UCLA] Conservation Genetics Resource Center). All feathers were from adult male and female birds. To ensure that feathers were from breeding individuals and not potential migrants, only warblers captured between 15 June and 1 August (15 August for sites in Alaska) were included. A geographic-information-system (GIS) derived map of δD values for growing-season precipitation across North America (Meehan et al. 2004) was used to obtain δD values of local precipitation where breeding warblers were sampled. In addition, we

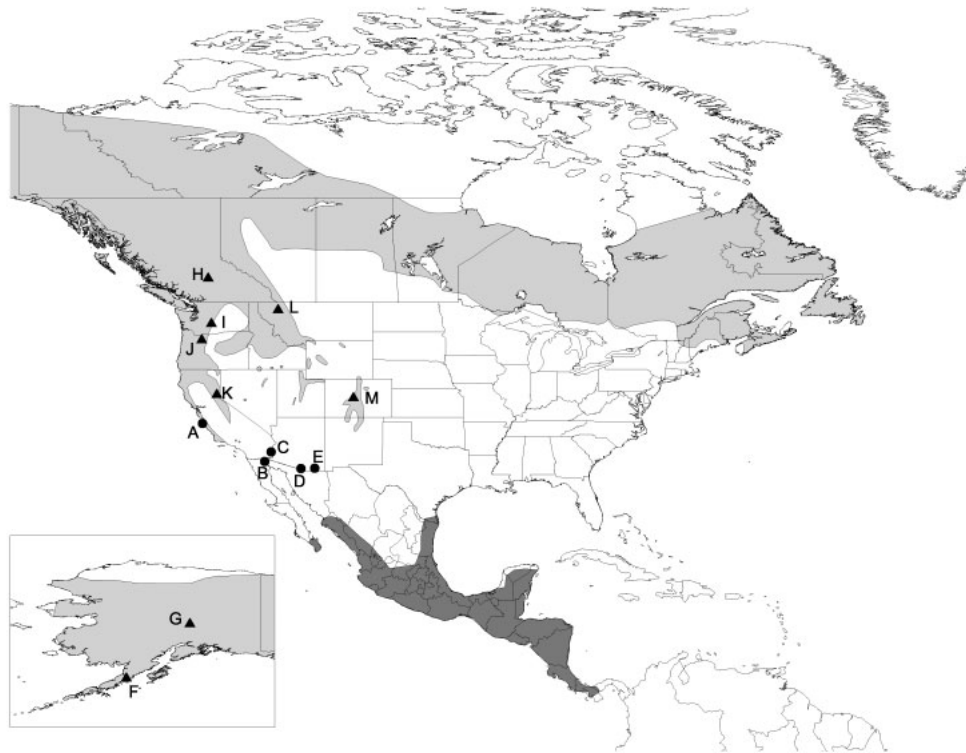


FIG. 1. Location of breeding and migration stations where Wilson's Warblers' feathers were collected (see Table 1 for site information). Light- and dark-gray shaded regions indicate Wilson's Warblers' breeding and wintering ranges, respectively. Triangles indicate sites where feathers were collected on the breeding ground, and circles indicate migration collection sites.

examined the relationship between δD values of the feathers collected on breeding grounds and collection site latitude, distance from coast, and elevation, all of which affect precipitation δD values in North America (Ingraham 1998).

Warblers were captured during spring migration between 15 March and 1 June 2003 at four sites: Colorado River Delta in Baja California, Mexico; Lower Colorado River at Cibola National Wildlife Refuge (NWR) in southwestern Arizona; Arivaca Creek at Buenos Aires NWR in southeastern Arizona; and San Pedro River at San Pedro Riparian National Conservation Area in southeastern Arizona. In 2004, warblers were again captured during the same period at the Lower Colorado River and Arivaca Creek sites, and at an additional site, Big Sur, California (Fig. 1 and Table 1). Warblers were caught by passive mist netting and banded. Standard morphological measurements were

taken, and an outer rectrix from each side of the tail was pulled for stable isotope analysis. Feathers were stored in labeled, sealed envelopes until analyzed.

Stable isotope analysis.—Feathers were washed in detergent and thoroughly rinsed to remove oil, dirt, and residual detergent (Chamberlain et al. 1997, Kelly et al. 2002) and then air dried at room temperature. Feather material from the distal end (0.33–0.37 mg) was removed and wrapped in a silver capsule for isotopic analysis. Because of the problem of uncontrolled isotopic exchange between ~13% of noncarbon-bound hydrogen in feathers and ambient water vapor (Chamberlain et al. 1997), we used a comparative equilibrium approach with calibrated keratin standards to correct for this effect. As a result, values presented here are nonexchangeable feather hydrogen only. Details of this method and standards used are described in

TABLE 1. Feather collection sites sampled during the breeding and spring migration of Wilson's Warblers. Letters correspond to those in Figure 1. Mean stable hydrogen isotope values for feathers (δD_f) and stable hydrogen isotope values for precipitation (δD_p) are given for each breeding site. Mean predicted stable hydrogen isotope values for feathers (δD_x) are given for each migration station.

Sampling site	Latitude, longitude	<i>n</i>	δD_x (mean \pm SD)	δD_p
Migration sites				
A. Big Sur, California	36°16'N, 121°49'W	112	-62.9 \pm 15.9	
B. Colorado River Delta, Mexico	32°18'N, 115°20'W	99	-77.7 \pm 24.7	
C. Lower Colorado River, Arizona	33°18'N, 114°41'W	186	-95.9 \pm 24.7 ^a	
D. Arivaca Creek, Arizona	31°33'N, 111°33'W	77	-92.7 \pm 22.4 ^b	
E. San Pedro River, Arizona	31°34'N, 110°07'W	113	-102.7 \pm 24.5	
Breeding sites				
F. Mother Goose Lake, Alaska	57°12'N, 157°19'W	4	-111.2 \pm 9.1	-90
G. Denali National Park, Alaska	63°25'N, 150°26'W	8	-151.7 \pm 8.4	-118
H. 100 Mile House, British Columbia	51°39'N, 121°17'W	6	-148.8 \pm 6.0	-113
I. Wenatchee National Forest, Washington	46°56'N, 121°04'W	10	-115.3 \pm 9.4	-96
J. Willamette National Forest, Oregon	44°15'N, 122°00'W	14	-84.5 \pm 5.6	-72
K. Tahoe National Forest, California	39°37'N, 120°31'W	5	-87.5 \pm 4.8	-64
L. Flathead National Forest, Montana	48°23'N, 114°02'W	5	-123.7 \pm 3.3	-97
M. Grand Mesa, Colorado	39°02'N, 107°57'W	6	-103.8 \pm 3.6	-88

^a 2003 value; for 2004, $\delta D_x \pm$ SD = -106.9 \pm 36.6.

^b 2003 value; for 2004, $\delta D_x \pm$ SD = -99.9 \pm 34.3.

Wassenaar and Hobson (2003). Briefly, several replicates of three keratin standards whose nonexchangeable δD values were known and that spanned the range of expected feather values were measured within the same analytical run as the unknown feather samples. A least-squares regression was generated for each run, relating measurements of raw δD values of the standards to their expected nonexchangeable δD values. This regression equation was then applied to all unknown samples within that run. Unlike past methods to control for non-exchangeable feather hydrogen, this method allows for comparisons of δD values between years and among laboratories.

All stable isotope analyses were conducted at the Colorado Plateau Stable Isotope Laboratory at Northern Arizona University, Flagstaff. Stable hydrogen isotope ratios for both feathers and keratin standards were determined on H_2 gases, produced by high-temperature flash pyrolysis of feathers using a Thermo Finnigan high-temperature conversion elemental analyzer (1,400°C) interfaced through an open split (Finnigan Conflo II, Thermo Electron Corporation, Waltham, Massachusetts), with a continuous-flow isotope-ratio mass-spectrometer (Finnigan Delta Plus

XL). Stable hydrogen isotope ratios ($^2H/^1H$) are reported in delta (δ) notation, in per-mil units (‰), where $\delta D_{\text{sample}} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1,000$, relative to a standard (Vienna standard mean ocean water [VSMOW]). Repeat analyses of internal hydrogen isotope standards yielded an external repeatability of $\pm 2.3\%$. Duplicates of the same feather sample ($n = 23$) and comparison of values from two rectrices from the same warbler ($n = 23$) had mean standard deviations of $\pm 2.3\%$ and $\pm 1.5\%$, respectively.

Statistical analysis.—To determine where warblers migrating through the migration stations occurred within their breeding range, we used the regression equation that expressed the relationship between δD of feathers collected on the breeding grounds (δD_f) and δD of local precipitation (δD_p) to estimate the δD of warblers caught at the migration stations (δD_x). Values of δD_x were used for all analyses.

We used linear regression to examine the relationship between timing of migration and putative breeding location based on δD_x . Analysis of covariance (ANCOVA) was used to test whether the same pattern was exhibited in 2003 and 2004 at the Lower Colorado River and Arivaca Creek sites. We examined differences in

the mean δD_x values for each sampling station using ANOVA.

To determine where migrating warblers molted (and most likely bred) the previous year, from a GIS-derived map of δD values of precipitation across North America (Meehan et al. 2004), we clipped out the warbler's breeding range (breeding range from Ridgley et al. 2003), so that δD values only within this geographical area could be queried. To be conservative and account for error within the regression model and the deuterium map, δD values were queried from the GIS map within 20‰ ranges, which creates six 20‰ categories, with each category representing distinct geographic regions within the warbler's western breeding range. Values of δD between -41 ‰ and -60 ‰ occur only along the California Coast, whereas values between -61 ‰ and -80 ‰ correspond to the Pacific Slope Region and a small portion of the range in the high-elevation mountains of New Mexico and Colorado. The Sierra Nevada Mountains and Intermountain West Region have δD values predominantly between -81 ‰ and -100 ‰, whereas δD values between -101 ‰ and -140 ‰ occur within the western Canadian provinces and Alaska, and δD values between -141 ‰ and -160 ‰ are found only within the Yukon Territory of Canada (δD values within this category are not included in analyses because they represent $<2\%$ of the total warblers sampled for all sites combined). We used a chi-square test of independence to evaluate associations between migration sampling sites and the frequency of δD values within the five categories.

All GIS analyses were done with ARCGIS, version 8.2 (ESRI, Redlands, California). All statistical analyses were conducted in SPSS, version 12.0 (SPSS, Chicago, Illinois), and significance for statistical tests was accepted at $P < 0.05$.

RESULTS

Relationship between δD of feathers and precipitation.—We found a significant positive relationship between the δD_f of warbler feathers and the δD_p where the warblers were captured ($F = 610.78$, $df = 1$ and 61 , $P < 0.001$, $r^2 = 0.91$; Table 1; Fig. 2), which is consistent with field data indicating that warblers molt their feathers on or near their breeding grounds.

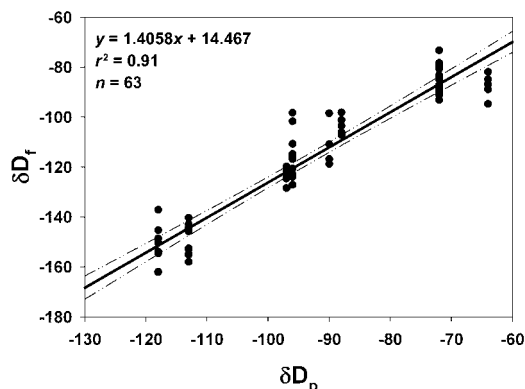


FIG. 2. Regression showing the positive relationship between stable hydrogen isotopes of warbler feathers (δD_f) collected on the breeding grounds and growing-season precipitation (δD_p) of those sites where warblers were captured. Dashed lines represent 95% confidence intervals (1.29 to 1.52).

The relationship between δD of warbler feathers and parameters such as latitude, distance from coast, and elevation where the feathers were collected was best explained by a regression model that incorporated both latitude and elevation ($F = 161.38$, $df = 2$ and 60 , $P < 0.001$, $r^2 = 0.84$). This model indicated a strong negative relationship between the δD of warbler feathers and latitude of collection ($t = -17.38$, $P < 0.001$, $\beta = -3.49/1,000 \text{ m} \pm 0.2$) and elevation ($t = 11.12$, $P < 0.001$, $\beta = -0.018/1000 \text{ m} \pm 0.002$). A model using latitude alone had an r^2 value of 0.52. These data support past research (Chamberlain et al. 1997, Hobson and Wassenaar 1997, Kelly et al. 2002, Rubenstein et al. 2002) that showed a strong relationship between δD of bird feathers and latitude but also indicate that, in mountainous western North America, elevation must also be taken into account when developing δD models, as has been demonstrated for carbon isotopes (Graves et al. 2002).

Timing of migration with respect to breeding location.—We found a significant negative relationship between the date when migrating warblers passed through our collection stations and δD_x values of their feathers (Fig. 3). These data indicate that warblers that bred the previous season at southern latitudes migrated earlier than warblers that previously bred at more northern latitudes. Four out of the five migration stations that we sampled showed a significant

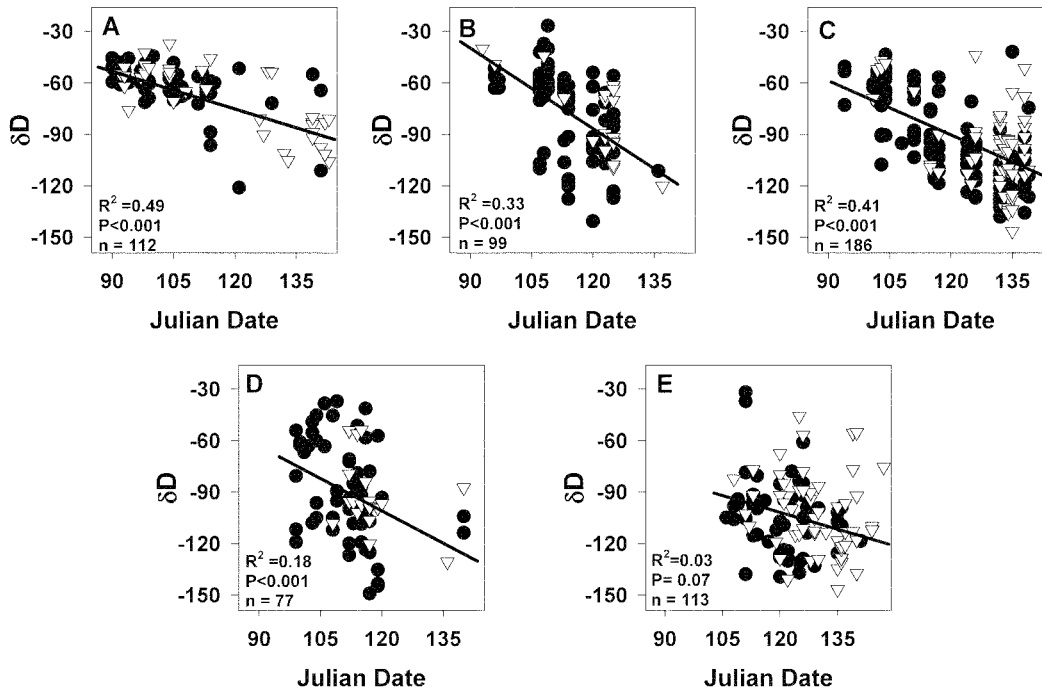


FIG. 3. Regression of δD_x of migrating Wilson's Warblers by date, for each site, showing a negative relationship between timing of migration and δD_x of migrating warblers. This pattern was the same for both males (black circles) and females (white triangles). Migration sites are (A) Big Sur (2004), (B) Colorado River Delta (2003), (C) Lower Colorado River (2003), (D) Arivaca Creek (2003), and (E) San Pedro River (2003). All sites were sampled during the same period, 15 March to 1 June, corresponding to Julian dates 74 to 152, respectively. The δD_x values that are more negative or depleted indicate more northern breeding locations, whereas more positive or enriched δD_x values indicate more southern breeding locations.

relationship: Big Sur ($F = 104.37$, $df = 1$ and 110 , $P < 0.001$, $r^2 = 0.49$), Colorado River Delta ($F = 48.03$, $df = 1$ and 97 , $P < 0.001$, $r^2 = 0.33$), Lower Colorado River ($F = 128.47$, $df = 1$ and 183 , $P < 0.001$, $r^2 = 0.41$), and Arivaca Creek ($F = 15.95$, $df = 1$ and 75 , $P < 0.001$, $r^2 = 0.18$). Although the regression at the San Pedro River was only marginally significant ($F = 3.31$, $df = 1$ and 101 , $P = 0.07$), the same trend was evident.

Differential migration strategies between age and sex classes of warblers contributed variation to the overall relationship between the date when captured and feather δD_x value. Males had a significantly earlier mean arrival date than females at all sites (overall mean difference = 9.97 days, 95% CI: 7.7–12.21). Comparison of the regressions between sexes at each site indicated that the same temporal pattern was exhibited in males and females. At the Lower Colorado River

site, we had sufficient sample size to examine the relationship between date of passage and the δD_x values for different age and sex classes (Fig. 4). There were significant decreasing δD_x values for both after-second-year (ASY) males ($F = 104.91$, $df = 1$ and 86 , $P < 0.001$, $r^2 = 0.55$) and females ($F = 11.44$, $df = 1$ and 24 , $P = 0.002$, $r^2 = 0.32$) that were captured throughout most of the migration season. Second-year (SY) males and females had a truncated migration that occurred only toward the end of the migration season, but still covered a large range of δD values. This truncated migration pattern may have contributed to the nonsignificant pattern for both SY males ($F = 2.78$, $df = 1$ and 31 , $P = 0.11$) and females ($F = 1.50$, $df = 1$ and 26 , $P = 0.23$).

A significant negative relationship between date of passage and δD_x values of feathers was also found in 2004 at the Lower Colorado River

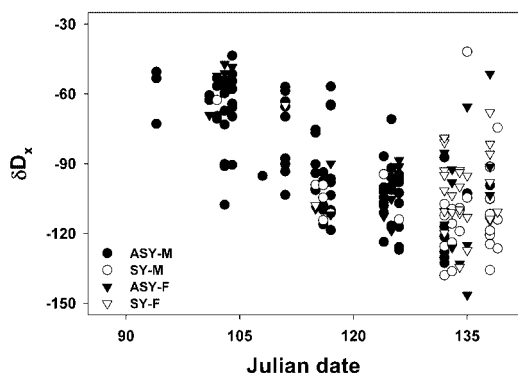


FIG. 4. Regression of δD_x values of migrating Wilson's Warblers by date, for different age-sex classes, at the Lower Colorado River site, 2003. After-second-year (ASY) males (solid black circles) and ASY females (solid black triangles) are captured throughout the entire migration season, whereas second-year (SY) males (open white circles) and SY females (open white triangles) have a truncated migration occurring at the end of the migration season. The differences in migration strategies between the age classes may contribute to the variation in the overall temporal pattern for this site.

($F = 276.71$, $df = 1$ and 170 , $P < 0.001$, $r^2 = 0.62$) and Arivaca Creek ($F = 35.48$, $df = 1$ and 37 , $P < 0.001$, $r^2 = 0.49$) sites. Comparison of the relationship between δD_x values and date of capture between 2003 and 2004 at both sites revealed that the temporal pattern was not significantly different between years for either site (ANCOVA: Lower Colorado River: $F = 0.40$, $df = 1$ and 353 , $P = 0.53$; Arivaca Creek: $F = 0.476$, $df = 1$ and 112 , $P = 0.49$), demonstrating that the pattern of warbler migration was consistent from year to year.

Differences in δD among the migration stations.—Differences in mean δD_x values among our collection sites showed a shift toward more negative δD_x values from the western to the eastern migration stations sampled in the present study (Fig. 5). There was a significant difference in the mean δD_x values among all sites, except the Lower Colorado River and Arivaca Creek (Tukey's *post-hoc* test: $F = 55.61$, $df = 4$ and 565 , $P < 0.001$). The range of δD_x values was also consistent from one year to the next when tested at two sites (Lower Colorado River: $t = -2.069$, $P = 0.30$; Arivaca Creek: $t = -1.414$, $P = 0.16$).

The frequency of δD_x values within the five 20‰ categories found within the warbler's western breeding range were not randomly distributed among the migration sampling stations ($\chi^2 = 202.90$, $P < 0.001$). The range of δD_x values at each of the migration stations corresponded to δD values in different geographic regions of the range. For example, at the most westerly migration station (Big Sur), the range of δD_x values represented a very limited geographic area within the warbler's breeding range, with >80% of migrating warblers with δD_x values (−41‰ to −80‰) consistent with those along the California coast and Pacific slope region. Warblers migrating through the Colorado River Delta had a larger breadth of δD_x values than at the Big Sur site, with 55% of the warblers migrating through this station having δD_x values that are consistent with those along the California coast and Pacific slope region and ~23% of the warblers having δD_x values (−81‰ to −100‰) like that of the intermountain west. By contrast, at the easternmost sampling site, San Pedro River, most of the δD_x values were restricted to highly depleted values that corresponded to more northerly breeding locations within the warbler's breeding range. Thirty-percent of the warblers at this site had values expected in the intermountain west, whereas >60% of the warblers had δD_x values (−101‰ to 140‰) consistent with those in western Canadian provinces and Alaska. The Lower Colorado River and Arivaca Creek represented intermediate sites, with warblers migrating through these stations having values corresponding to breeding locations in the interior of the warbler's breeding range. Most (80%) of δD_x values (−61‰ to 120‰) at these migration stations were consistent with those along the Pacific slope region, intermountain west, and lower regions of the western Canadian Provinces.

DISCUSSION

Relationship between the δD of feathers and precipitation.—The strong relationship between δD of warbler feathers collected on the breeding grounds and that of the local precipitation at the sites where they were collected supports past research showing the utility of using stable hydrogen isotopes to delineate breeding origins of certain Neotropical migrant birds (Chamberlain et al. 1997, Hobson and

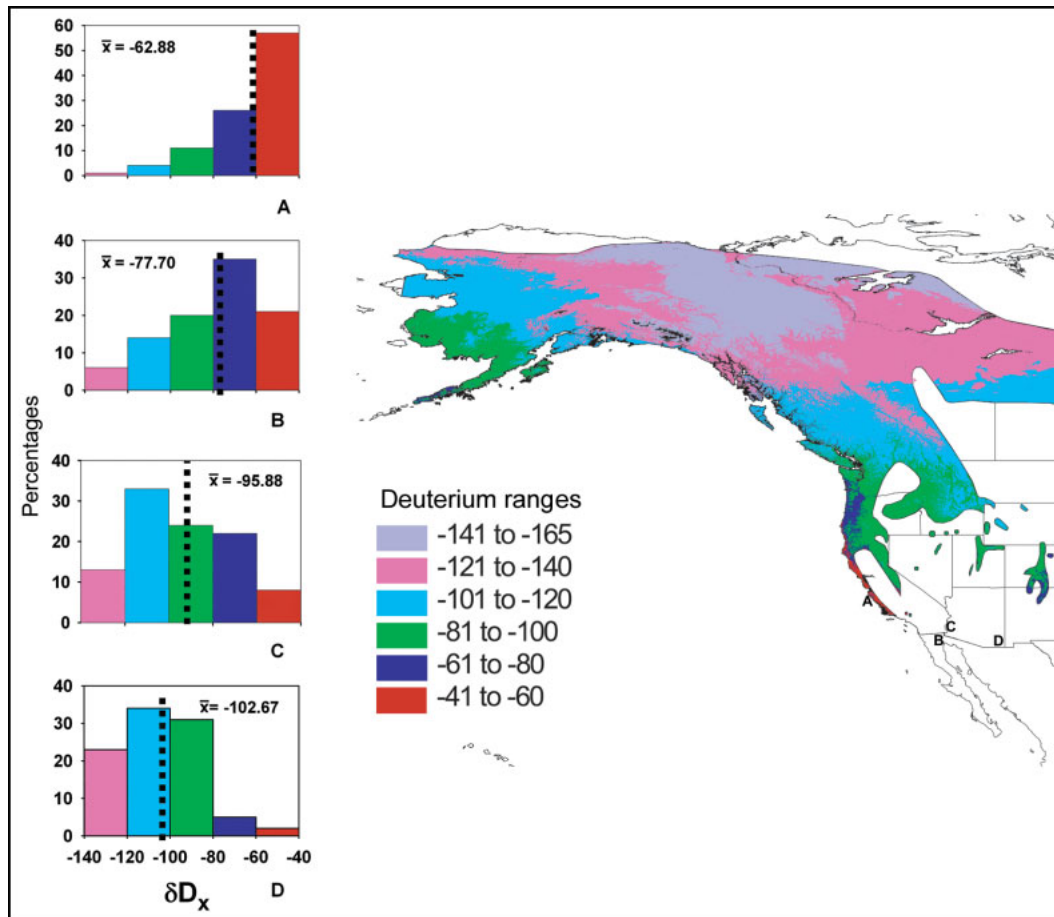


FIG. 5. Map representing δD values within the Wilson's Warbler's western breeding range (modified from Meehan et al. 2004). Colors on map correspond to histograms of δD_x values for (A) Big Sur (2004), (B) Colorado River Delta (2003), (C) Lower Colorado River (2003), and (D) San Pedro (2003) migration stations. Mean δD_x values (dotted lines) were significantly different among all sites, except Lower Colorado River and Arivaca Creek (not shown). The δD_x values between -140‰ and -159‰ (found only within the Yukon Territory) were not included in histograms, because they represent $<2\%$ of the total warblers sampled for all sites combined.

Wassenaar 1997). These data also indicate that there is a high degree of breeding-site philopatry for warblers, at least at the broad geographic scale measured with stable hydrogen isotopes, because feathers were collected only from adults that had not yet molted and, therefore, the δD value represented their breeding location the previous year. At smaller geographic scales, Chase et al. (1997) found relatively low levels of philopatry. Taken together, these data indicate that birds return to the same region, but not necessarily the same site in succeeding years.

Consistent with continental patterns observed in δD of growing-season precipitation (Ingraham 1998), δD values of feathers collected across the breeding grounds had a significant negative relationship with both latitude and elevation, confirming that more depleted values of δD occur at higher latitudes and elevations. Although latitude has the largest contribution to the pattern of δD values, elevation has the potential to confound the precision of determining breeding locations based on δD , just as it does for carbon isotopes (Graves et al. 2002). Although models that incorporate elevation as a component in

the map of δD values for growing-season precipitation have reduced this error (Meehan et al. 2004), elevation in mountainous western North America makes determining geographic origins more complicated. For example, some of the scatter of δD values over the migratory season observed here could have been attributable to the confounding effect of elevation (Fig. 3).

Timing of migration with respect to breeding location.—Comparison across multiple migration stations in California and Arizona suggests that there is structure in the timing of the warbler's spring migration with respect to breeding locations. Warblers that bred the previous year at more southern locations migrated through the Southwest earlier than warblers that bred the previous year at more northern locations. Previous work on the warbler's wintering distribution showed that the latitudinal sequence of δD on the wintering grounds is opposite that of the breeding grounds (i.e., warblers breeding at southern latitudes winter at more northern latitudes; Kelly et al. 2002, Clegg et al. 2003). The combination of our data with those from the wintering grounds indicates a leap-frog migration for warblers during the spring migration. In this proposed scenario, warblers wintering at more northern latitudes migrate through first to breed at more southern latitudes and are leap-frogged by warblers migrating from more southern wintering latitudes to breeding locations at more northern locations. Furthermore, this pattern was consistent from one year to the next. These findings are consistent with previous work that documented a similar pattern in the timing of migration in warblers passing through a single site in New Mexico in the fall (Kelly et al. 2002), but contrast with those authors' findings during spring migration.

The easternmost collection site in this study, San Pedro, showed a similar but statistically weaker relationship between timing of migration and δD values compared with the other sites. This weaker relationship may be attributable to the narrower range of δD values exhibited by warblers passing through this location, combined with an overall shorter period during which warblers migrated through the San Pedro riparian corridor. These same factors may explain why a previous study in New Mexico by Kelly et al. (2002) failed to find a similar timing pattern for migrating warblers in the spring of one year. Although the range of δD values

reported for the site in New Mexico is similar to those collected at the San Pedro site (Kelly et al. 2002), direct comparison of δD values is not possible because of differences in the methods used to correct for nonexchangeable hydrogen.

The differential timing of migration found here for different sex and age classes is consistent with other migration studies for many Neotropical migrants, including Wilson's Warbler (Gauthreaux 1982, Francis and Cooke 1986, Otahal 1995, Yong et al. 1998, Woodrey 2000). The arrival date of males was consistently earlier than that of females at all sites, potentially because of differing selection pressures on breeding strategies between sexes (Gauthreaux 1982). Although the temporal pattern was significant for males and females, the differential timing between the sexes corresponded to a shift in the patterns of δD and accounted for some of the variation observed in the overall temporal pattern at each site. Likewise, the truncated period of migration for SY age classes also contributed to this variation.

Documentation of leap-frog migration for warblers during both spring (present study) and fall (Kelly et al. 2002) is important for two reasons. First, extrinsic and intrinsic factors controlling migration differ between spring and fall and, therefore, could potentially lead to different migration patterns. Seasonal differences in weather and prevailing winds can cause continent-wide differences in migration pathways for Neotropical migrants in the United States. This creates an overall clockwise migration pattern, with migration pathways biased more westward in the spring and eastward in the fall (Bellrose and Graber 1963, Gauthreaux 1980, Moore et al. 1995). Evidence for these patterns has been found in both eastern and western migration systems in the United States (Phillips 1975, Crawford and Stevenson 1984, Rappole and Ramos 1994, Finch and Yong 2000). In addition, the differing constraints that fall and spring migration place on birds of different sexes and ages increases the potential for alternate migration patterns in these two seasons (Gauthreaux 1982, Yong et al. 1998). Even with these considerable differences between spring and fall migration, the present study confirmed that leap-frog migration occurs during both seasons in warblers. Second, leap-frog migration has broader implications for the ecology and evolution of warblers. Differences in the distances traveled during migration by different

breeding populations have the potential to act as a selective force shaping physiological and morphological traits, length of stay at migratory stopover sites, breeding, and wintering ecology. Understanding the migration strategy of warblers provides the basis to begin testing alternative models for the evolution of leap-frog migration (Greenberg 1980; Lundberg and Alerstam 1986; Holmgren and Lundberg 1993; Bell 1996, 1997) and potential differences in breeding, wintering, and migration strategies exhibited among western populations of warblers.

Differences in δD among the migration stations.—Differences in δD values among our sampled migration stations indicate that different breeding populations of warblers are using different migratory pathways across the migratory front from west to east. Warblers from western migration stations (e.g., Big Sur and Colorado River Delta) were dominated by δD values consistent with breeding locations within coastal and Pacific slope regions, whereas eastern migration stations (e.g., San Pedro) had larger proportions of warblers with δD values consistent with breeding locations in the western Canadian provinces and Alaska. Interior sites, such as the Lower Colorado River and Arivaca Creek, had warblers with a wide range of δD values, consistent with breeding locations within the interior of the warblers' breeding range. Overall, this pattern indicates that warblers from different breeding areas use different migratory pathways and suggests that habitat alteration at specific areas across the west–east expanse of the migratory route could differentially affect warblers at different breeding areas.

Detailed examination of the west–east pattern indicates that it is not a continuous gradient of change across the southwestern migration route; differences in mean δD values between some stations are greater than expected on the basis of their distance from each other. For instance, the Colorado River Delta is 160 km southwest of the Lower Colorado River site, yet the latter was more similar in its range of δD values to Arivaca Creek, a site 440 km to the east. Likewise, the range of δD values at Arivaca Creek was more similar to that at the Lower Colorado River site than to that of the San Pedro site 200 km to the east (Fig. 1). These differences suggest that the broad west–east pattern is modified by other factors, such as topography and habitat features, which together shape migratory routes

across the southwestern United States. For example, the Colorado River Delta and the Lower Colorado River locations are separated by the Sand Hills and Chocolate Mountains, a range with a main axis oriented northwest to southeast. Similarly, the San Pedro site lies within the Sierra Madre mountain range, which extends from Mexico into the United States and is at a much higher elevation than Arivaca Creek, which lies at a lower elevation at the foothills of this mountain range. Dry, desert mountain ranges like these may serve as migratory corridor boundaries.

All evidence suggests that the warblers sampled here are the two western subspecies *W. p. pileolata* and *W. p. chryseola*, and not the eastern subspecies *W. p. pusilla*. Although the three subspecies cannot be accurately distinguished by morphological characteristics during migration, documentation of a distinct migration route in the east indicates separate migration pathways between western and the most eastern populations of warblers (Ammon and Gilbert 1999). The migration pathways to more central breeding areas are less clear. Thus, we have included breeding locations as far west as the Canadian Province of Saskatchewan. We would expect the San Pedro migration station to be the most likely site to have eastern subspecies, yet the δD_x values of most of the warblers migrating through the San Pedro were consistent with values found only within Alaska and western Canadian Provinces (-101‰ to -140‰). The δD values of the eastern breeding range, which are primarily between -60‰ and -100‰ , are more consistent with observed δD_x values of warblers migrating through the westernmost migration stations in the present study, where we would least expect eastern migrants.

Conservation implications.—Riparian habitat is one of the most heavily disturbed habitat types in the southwestern United States. It comprises <1% of the landscape yet supports the largest abundance and diversity of birds (Johnson et al. 1977, Knopf et al. 1988, Finch and Ruggiero 1993). It is critical stopover habitat for Neotropical migrants (Stevens et al. 1977, Rich et al. 2004). The present study suggests that loss of appropriate habitat at any one point across the west–east migratory route could differentially affect specific breeding populations of warblers. Our study provides another important piece of information for the management of Neotropical

migratory birds, especially in light of rapid changes the landscape of the southwestern United States is presently undergoing.

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LITERATURE CITED

- AMMON, E. M., AND W. M. GILBERT. 1999. Wilson's Warbler (*Wilsonia pusilla*). In *The Birds of North America*, no. 478 (A. Poole and F. Gill, Eds.). Birds of North America, Philadelphia.
- ASKINS, R. A., J. F. LYNCH, AND R. GREENBERG. 1990. Population declines in migratory birds in eastern North America. Pages 1–57 in *Current Ornithology*, vol. 7 (D. M. Power, Ed.). Plenum Press, New York.
- BELL, C. P. 1996. Seasonality and time allocation as causes of leap-frog migration in the Yellow Wagtail *Motacilla flava*. *Journal of Avian Biology* 27:334–342.
- BELL, C. P. 1997. Leap-frog migration in the Fox Sparrow: Minimizing the cost of spring migration. *Condor* 99:470–477.
- BELLROSE, F. C., AND R. R. GRABER. 1963. A radar study of the flight directions of nocturnal migrants. Pages 362–389 in *Proceedings XIII International Ornithological Congress* (C. G. Sibley, Ed.). American Ornithologists' Union, Washington, D.C.
- BLEM, C. R. 1980. The energetics of migration. Pages 175–224 in *Animal Migration, Orientation, and Navigation* (S. A. Gauthreaux, Jr., Ed.). Academic Press, New York.
- CHAMBERLAIN, C. P., J. D. BLUM, R. T. HOLMES, X. FENG, T. W. SHERRY, AND G. R. GRAVES. 1997. The use of isotope tracers for identifying populations of migratory birds. *Oecologia* 109:132–141.
- CHASE, M. K., N. NUR, AND G. R. GEUPEL. 1997. Survival, productivity, and abundance in a Wilson's Warbler population. *Auk* 114: 354–366.
- CLEGG, S. M., J. F. KELLY, M. KIMURA, AND T. B. SMITH. 2003. Combining genetic markers and stable isotopes to reveal population connectivity and migration patterns in a Neotropical migrant, Wilson's Warbler (*Wilsonia pusilla*). *Molecular Ecology* 12: 819–830.
- COX, G. W. 1985. The evolution of avian migration systems between temperate and tropical regions of the New World. *American Naturalist* 126:451–474.
- CRAWFORD, R. L., AND H. M. STEVENSON. 1984. Patterns of spring and fall migration in northwest Florida. *Journal of Field Ornithology* 55:196–203.
- DESANTE, D. F., AND T. L. GEORGE. 1994. Population trends in the landbirds of western North America. Pages 173–190 in *A Century of Avifaunal Change in Western North America* (J. R. Jehl, Jr., and N. K. Johnson, Eds.). Studies in Avian Biology, no. 15.
- FINCH, D. M., AND L. F. RUGGIERO. 1993. Wildlife habitats and biological diversity in the Rocky Mountains and northern Great Plains. *Natural Areas Journal* 13:191–203.
- FINCH, D. M., AND W. YONG. 2000. Landbird migration in riparian habitats of the middle Rio Grande: A case study. Pages 88–98 in *Stopover Ecology of Nearctic–Neotropical Landbird Migrants: Habitat Relations and Conservation Implications* (F. R. Moore, Ed.). Studies in Avian Biology, no. 20.
- FRANCIS, C. M., AND F. COOKE. 1986. Differential timing of spring migration in wood warblers (Parulinae). *Auk* 103:548–556.
- GAUTHREAUX, S. A., JR. 1979. Priorities in bird migration studies. *Auk* 96:813–815.
- GAUTHREAUX, S. A., JR. 1980. The influence of global climatological factors on the evolution of bird migratory pathways. Pages 517–525 in *Acta XVII Congressus Internationalis Ornithologici* (R. Nöhring, Ed.). Deutsche Ornithologen-Gesellschaft, Berlin.

- GAUTHREAUX, S. A., JR. 1982. Age-dependent orientation in migratory birds. Pages 68–74 in *Avian Navigation* (F. Papi and H. G. Wallraff, Eds.). Springer-Verlag, Berlin.
- 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 USA* 99:8096–8100.
- GREENBERG, R. 1980. Demographic aspects of long-distance migration. Pages 493–504 in *Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation* (A. Keast and E. S. Morton, Eds.). Smithsonian Institution Press, Washington, D.C.
- HAGAN, J. M., III, AND D. W. JOHNSTON, Eds. 1992. *Ecology and Conservation of Neotropical Migrant Landbirds*. Smithsonian Institution Press, Washington, D.C.
- HOBSON, K. A. 2003. Making migratory connections with stable isotopes. Pages 379–392 in *Avian Migration* (P. Berthold, E. Gwinner, and E. Sonnenschein, Eds.). Springer-Verlag, Berlin.
- 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.
- HOLMGREN, N., AND S. LUNDBERG. 1993. Despotism behaviour and the evolution of migration patterns in birds. *Ornis Scandinavica* 24: 103–109.
- INGRAHAM, N. L. 1998. Isotopic variation in precipitation. Pages 87–118 in *Isotope Tracers in Catchment Hydrology* (C. Kendall and J. J. McDonnell, Eds.). Elsevier Science, Amsterdam, The Netherlands.
- JOHNSON, R. R., L. T. HAIGHT, AND J. M. SIMPSON. 1977. Endangered species vs. endangered habitats: A concept. Pages 68–79 in *Importance, Preservation, and Management of Riparian Habitat* (R. R. Johnson and D. A. Jones, Eds.). U.S. Department of Agriculture, Forest Service, General Technical Report RM-43.
- KELLY, J. F., V. ATUDOREI, Z. M. SHARP, AND D. M. FINCH. 2002. Insights into Wilson's Warbler migration from analyses of hydrogen stable-isotope ratios. *Oecologia* 130:216–221.
- KELLY, J. F., AND R. L. HUTTO. 2005. An east–west comparison of migration in North American wood warblers. *Condor* 107:197–211.
- KETTERSON, E. D., AND V. NOLAN, JR. 1982. The role of migration and winter mortality in the life history of a temperate-zone migrant, the Dark-Eyed Junco, as determined from demographic analyses of winter populations. *Auk* 99:243–259.
- KNOPE, F. L., R. R. JOHNSON, T. RICH, F. B. SAMSON, AND R. C. SZARO. 1988. Conservation of riparian ecosystems in the United States. *Wilson Bulletin* 100:272–284.
- LUNDBERG, S., AND T. ALERSTAM. 1986. Bird migration patterns: Conditions for stable geographical population segregation. *Journal of Theoretical Biology* 123:403–414.
- MARRA, P. P., K. A. HOBSON, AND R. T. HOLMES. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science* 282:1884–1886.
- MAZEROLLE, D. F., K. A. HOBSON, AND L. I. WASSENAAR. 2005. Stable isotope and band-encounter analyses delineate migratory patterns and catchment areas of White-throated Sparrows at a migration monitoring station. *Oecologia* 144:541–549.
- MEEHAN, T. D., J. T. GIEMAKOWSKI, AND P. M. CRYAN. 2004. GIS-based model of stable hydrogen isotope ratios in North American growing-season precipitation for use in animal movement studies. *Isotopes in Environmental and Health Studies* 40: 291–300.
- 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.
- MIZUTANI, H., M. FUKUDA, Y. KABAYA, AND E. WADA. 1990. Carbon isotope ratio of feathers reveals feeding behavior of cormorants. *Auk* 107:400–403.
- MOORE, F. R., S. A. GAUTHREAUX, JR., P. KERLINGER, AND T. R. SIMONS. 1995. Habitat requirements during migration: Important link in conservation. Pages 121–144 in *Ecology and Management of Neotropical Migratory Birds: A Synthesis and Review of Critical*

- Issues (T. E. Martin and D. M. Finch, Eds.). Oxford University Press, New York.
- MOORE, F. R., AND T. R. SIMONS. 1992. Habitat suitability and stopover ecology of Neotropical landbird migrants. Pages 345–355 *in Ecology and Conservation of Neotropical Migrant Landbirds* (J. M. Hagan III and D. W. Johnston, Eds.). Smithsonian Institution Press, Washington, D.C.
- OTAHAL, C. D. 1995. Sexual differences in Wilson's Warbler migration. *Journal of Field Ornithology* 66:60–69.
- PHILLIPS, A. R. 1975. The migrations of Allen's and other hummingbirds. *Condor* 77:196–205.
- PYLE, P. 1997. *Identification Guide to North American Birds, Part I: Columbidae to Phocidae*. Slate Creek Press, Bolinas, California.
- RAPPOLE, J. H., AND M. A. RAMOS. 1994. Factors affecting migratory bird routes over the Gulf of Mexico. *Bird Conservation International* 4:251–262.
- RICH, T. D., C. J. BEARDMORE, H. BERLANGA, P. J. BLANCHER, M. S. W. BRADSTREET, G. S. BUTCHER, D. W. DEMAREST, E. H. DUNN, W. C. HUNTER, E. E. INIGO-ELIAS, AND OTHERS. 2004. *Partners in Flight North American Landbird Conservation Plan*. Cornell Lab of Ornithology, Ithaca, New York.
- RIDGLEY, R. S., T. F. ALLNUT, T. BROOKS, D. K. McNICOL, D. W. MEHMAN, B. E. YOUNG, AND J. R. ZOOK. 2003. *Digital Distribution Maps of the Birds of the Western Hemisphere*, version 1.0. [Online.] Available at www.natureserve.org.
- ROBBINS, C. S., J. R. SAUER, R. S. GREENBERG, AND S. DROEGE. 1989. Population declines in North American birds that migrate to the Neotropics. *Proceedings of the National Academy of Sciences USA* 86:7658–7662.
- ROSENBERG, K. V., R. D. OHMART, W. C. HUNTER, AND B. W. ANDERSON. 1991. *Birds of the Lower Colorado River Valley*. University of Arizona Press, Tucson.
- 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. 1995. Summer versus winter limitation of populations: What are the issues and what is the evidence? Pages 85–120 *in Ecology and Management of Neotropical Migratory Birds: A Synthesis and Review of Critical Issues* (T. E. Martin and D. M. Finch, Eds.). Oxford University Press, New York.
- SILLETT, T. S., AND R. T. HOLMES. 2002. Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology* 71:296–308.
- SIMONS, T. R., S. M. PEARSON, AND F. R. MOORE. 2000. Application of spatial models to the stopover ecology of trans-gulf migrants. Pages 4–14 *in Stopover Ecology of Nearctic–Neotropical Landbird Migrants: Habitat Relations and Conservation Implications* (F. R. Moore, Ed.). *Studies in Avian Biology*, no. 20.
- STEVENS, L. E., B. T. BROWN, J. M. SIMPSON, AND R. R. JOHNSON. 1977. The importance of riparian habitat to migrating birds. Pages 156–164 *in Importance, Preservation, and Management of Riparian Habitat* (R. R. Johnson and D. A. Jones, Eds.). U.S. Department of Agriculture, Forest Service, General Technical Report RM-43.
- 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 Environmental and Health Studies* 39:1–7.
- WEBSTER, M. S., P. P. MARRA, S. M. HAIG, S. BENSCH, AND R. T. HOLMES. 2002. Links between worlds: Unraveling migratory connectivity. *Trends in Ecology and Evolution* 17:76–83.
- WOODREY, M. S. 2000. Age-dependent aspects of stopover biology of passerine migrants. Pages 43–52 *in Stopover Ecology of Nearctic–Neotropical Landbird Migrants: Habitat Relations and Conservation Implications* (F. R. Moore, Ed.). *Studies in Avian Biology*, no. 20.
- YONG, W., D. M. FINCH, F. R. MOORE, AND J. F. KELLY. 1998. Stopover ecology and habitat use of migratory Wilson's Warblers. *Auk* 115:829–842.

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