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STABLE ISOTOPE EVIDENCE LINKS BREEDING GEOGRAPHY AND MIGRATION TIMING IN WOOD WARBLERS (PARULIDAE)

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ABSTRACT.—Tracking seasonal movements of songbirds is a key step in understanding the annual cycle of migrants. To better understand autumn migration of wood warblers, I analyzed stable-hydrogen isotope ratios of feathers collected from three species captured during stopover at the Bosque del Apache National Wildlife Refuge, New Mexico. To assess the form and strength of the relationship between timing of migration and breeding origins, I regressed stable-hydrogen isotope ratios of feathers against date of capture. These analyses indicated that Orange-crowned Warblers (*Vermivora celata*) and Common Yellowthroats (*Geothlypis trichas*) breeding in the southern portion of these species' ranges precede their northern conspecifics in autumn migration. By contrast, Yellow Warblers (*Dendroica petechia*) from northern breeding sites arrived before more southerly breeding conspecifics. This pattern is similar to that reported previously in Wilson's Warbler (*Wilsonia pusilla*). These findings suggest that, among wood warblers, (1) timing of autumn migration is often strongly related to breeding location and (2) interspecific variation in the direction of this relationship is large. The direction and strength of these patterns have implications for our understanding of inter- and intraspecific geographic variation in the life histories of migrants. *Received 7 March 2005, accepted 24 July 2005.*

Key words: Bosque del Apache, migration, stable-hydrogen isotope ratio, wood warbler.

Evidencia de Isótopos Estables Conecta la Geografía de Nidificación con el Momento de la Migración en Especies de Parulidae

RESUMEN.—Realizar seguimientos de los movimientos estacionales de las aves canoras es un paso clave para entender el ciclo anual de las aves migratorias. Para entender mejor la migración de otoño de las reinitas (Parulidae), analicé las proporciones de isótopos estables de hidrógeno en plumas de tres especies que fueron obtenidas de aves capturadas en Bosque del Apache National Wildlife Refuge, New Mexico. Para establecer la forma y la fuerza de la relación entre el momento en que las aves migran y sus áreas reproductivas de origen, realicé una regresión entre las proporciones de isótopos estables de hidrógeno presentes en las plumas y la fecha de captura. Estos análisis indicaron que los individuos de las especies *Vermivora celata* y *Geothlypis trichas* que se reproducen en la parte sur de las distribuciones de estas especies migran antes que los individuos coespecíficos de la parte norte. En contraste, los individuos de la especie *Dendroica petechia* provenientes de sitios de cría ubicados al norte arribaron antes que los individuos provenientes de sitios de cría ubicados al sur. Este patrón es similar al documentado previamente para *Wilsonia pusilla*. Estos hallazgos sugieren que, en las reinitas, el momento en que las aves migran está frecuentemente asociado fuertemente con las áreas de cría y que la variación interespecífica en la dirección de esta relación es

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amplia. La dirección y la fuerza de estos patrones tienen implicaciones para nuestro entendimiento de los patrones de variación geográfica inter- e intraespecífica en las historias de vida de las aves migratorias.

OUR LIMITED ABILITY to track individual birds through their annual cycle is a primary constraint on our understanding of migratory ecology and life-history variation. In the past decade, stable-hydrogen isotopes have become a primary means for quantifying the movement ecology of migratory animals (Kelly and Finch 1998, Hobson 1999). Cormie et al. (1994) were first to show that stable-hydrogen isotope ratios of plants and consumers reflected those of local precipitation. Chamberlain et al. (1997) and Hobson and Wassenaar (1997) examined stable-hydrogen isotope ratios as markers for identifying breeding locations of migratory birds. This technique is based on an underlying north-south gradient in the stable-hydrogen isotope ratio of precipitation in North America (Bowen and Revenaugh 2003, Meehan et al. 2004). Stable-hydrogen isotope ratios of bird feathers have been used as markers of breeding latitude for North American populations of numerous migratory songbirds (Wassenaar and Hobson 2000a, 2001; Hobson et al. 2001, 2004a; Meehan et al. 2001; Rubenstein et al. 2002; Clegg et al. 2003; Kelly et al. 2005).

In general, ornithologists have focused more on breeding and wintering sites than on the migratory phase of the life cycle (Moore et al. 1995). Several recent studies suggest that *en route* events are an important source of mortality (e.g. Sillett and Holmes 2002) and have effects that carry over to the breeding and wintering seasons (Smith and Moore 2005). In particular, interspecific temporal variation in migration has been an underappreciated facet of *en route* ecology. Smith et al. (2003) present a useful description of two possible population-level patterns in temporal variation in autumn migration: type I, when southern populations migrate before northern populations; and type II, when northern populations migrate before southern populations. Although these two types reflect the end-points of a conceptual continuum of possible movement patterns, there are very few data on songbird migration for use in assessing how common each type might be. Quantitative measures of the modal pattern of migration timing and its variation across taxa, time, and space

would improve our understanding of avian ecology and evolutionary biology.

The relationship between timing of migration and breeding origins can be evaluated using extrinsic and intrinsic markers of migrants captured *en route* (e.g. leg bands and stable-hydrogen isotope ratios; Rubenstein and Hobson 2004). Smith et al. (2003) used this approach to evaluate timing of Sharp-shinned Hawk (*Accipiter striatus*) migration. Among wood warblers, Kelly et al. (2002) used stable-hydrogen isotope ratios to demonstrate that during autumn, Wilson's Warblers (*Wilsonia pusilla*) from northern latitudes pass through New Mexico earlier, on average, than conspecifics that breed at lower latitudes.

My objective was to determine what patterns of migration timing exist in other Parulidae (hereafter "wood warblers"). In particular, is there a relationship between breeding location and timing of autumnal migratory passage among wood warblers? To address this question, I measured stable-hydrogen isotope ratios of feathers collected from three species of migratory wood warblers captured *en route*.

METHODS

As part of a songbird-migration banding project, technicians collected feathers from migratory wood warblers from 7 August through 30 October 1998 at the Bosque del Apache National Wildlife Refuge (NWR), New Mexico (33°48'N, 106°52'W). Technicians removed a primary feather from each bird before banding and releasing them. I focused on three species of long-distance migrant wood warblers: Orange-crowned Warbler (*Vermivora celata*), Yellow Warbler (*Dendroica petechia*), and Common Yellowthroat (*Geothlypis trichas*). I expected comparisons among these species to be instructive for several reasons. First, because the species are widely distributed, the stable-hydrogen isotope gradient between southern and northern breeding birds should be large. Second, these species were commonly captured in autumn across a broad range of dates (Yong and Finch 2002). Third, because these species are almost

exclusively passage migrants at the Bosque del Apache NWR (i.e. neither breeding nor wintering on site), captured birds were migrants rather than residents. Finally, these species represent three different genera within the wood warblers. Consequently, if there is variation in the fundamental form of the relationship of migration timing with breeding origin, we might reasonably expect to see this variation in this sample.

Analysis of stable-hydrogen isotope ratios was done via continuous-flow isotope-ratio mass spectrometry (CFIRMS) using pyrolysis combustion. Feather-sample preparation followed the methods of Kelly et al. (2002). I washed feathers in detergent and thoroughly rinsed them to remove oil, dirt, and residual detergent. Before isotopic analysis, feathers were oven-dried at 100°C to remove water. I removed 0.1–0.2 mg of the distal end of each feather and wrapped them in a silver capsule. All isotope analyses were conducted at the University of New Mexico's Stable Isotope Laboratory. Feathers were loaded into an autosampler from which they were dropped into a high-temperature reduction furnace (Finnigan TC/EA, Thermo Electron Corporation, Waltham, Massachusetts) interfaced through an open split (Finnigan MAT ConFlo II) with a mass spectrometer (Finnigan MAT Delta plus XL). The reduction furnace was used to pyrolyze feather samples at 1,450°C. Wassenaar and Hobson (2000b) have shown that ~23% of hydrogen in feathers is exchangeable with atmospheric hydrogen. I present δD values of bulk feather tissues, not corrected for the exchangeable fraction of hydrogen contained in the feathers (Wassenaar and Hobson 2000b, 2003). Values of δD that are corrected for exchangeable hydrogen are more useful than uncorrected values; however, data reported here were collected in the winter of 2002, before a method of online comparative equilibration was widely known or available. All samples were air-equilibrated for two weeks prior to sampling, so that differential exchange was not a problem. I express the ratio of stable-hydrogen isotopes (H_2/H_1) in a sample as the parts per thousand (‰) deviation from standard mean ocean water (vSMOW = 0‰). We report deviation from these standards in delta notation: $\delta D = ([\text{stable-hydrogen isotope ratio}_{\text{sample}} / \text{stable-hydrogen isotope ratio}_{\text{standard}}] - 1) \times 1,000$. δD is in parts per thousand (‰) deviation from standard mean ocean water (vSMOW) with an analytical precision of ± 2.0 ‰.

I assumed that δD values of feathers were an accurate marker of breeding latitude for two reasons: (1) because these wood warblers replace their flight and body feathers only once during the year (i.e. immediately postbreeding on the breeding grounds; Pyle 1997), these feathers carry the isotopic signature from the breeding site throughout the year. Timing of molt of primary feathers of these species is well known. All three of these species undergo a complete, definitive prebasic molt on the breeding grounds (Sogge et al. 1994, Pyle 1997, Guzy and Ritchison 1999, Lowther et al. 1999). Detailed studies have been published on the definitive prebasic molts of both Orange-crowned and Yellow warblers. Among Orange-crowned Warblers, molt begins immediately after breeding, lasts for approximately eight weeks on the breeding grounds, and progresses from primaries (P1–P9) through secondaries to rectrices (Foster 1967). In James Bay, Yellow Warblers began molt, on average, 8 days after young fledged, and remigial molt lasted 37 days in females and 43 days in males (Rimmer 1988).

(2) Flight-feather δD values have been demonstrated to be highly predictive of latitude of breeding site in a broad spectrum of migratory birds (Table 1). I could not find any study of a North American passerine that was known to undergo prebasic molt during the postbreeding–pre migratory period in which northern breeders did not have feathers with more depleted stable-hydrogen isotope ratios than southern conspecifics. Even in American Redstarts (*Setophaga ruticilla*), where Norris et al. (2004) recently showed that experimentally induced repeated nest failures can cause birds to move south of their breeding sites to complete their molt, other studies (Hobson et al. 2004b) have shown good agreement between predicted and observed values of stable-hydrogen isotope ratios. There have been a few reported cases in nonpasserine where observed feather stable isotope values did not match predicted values for a given location (e.g. Meehan et al. 2003, Wunder et al. 2005). However, given the consistent pattern evident in a broad diversity of songbirds, I assumed a continuous relationship between stable-hydrogen isotope ratios of feathers and the latitudes at which birds bred and molted their feathers.

I used least-squares regressions in which δD value of feathers was the dependent variable and migration passage date was the independent

TABLE 1. Studies showing a negative relationship between δD values of feathers and latitude of breeding sites of species in North America.

Species	Reference(s)
White-crowned Sparrow (<i>Zonotrichia leucophrys</i>)	Kelly et al. 2002
Black-throated Blue Warbler (<i>Dendroica caerulescens</i>)	Chamberlain et al. 1997, Rubenstein et al. 2002
Red-winged Blackbird (<i>Agelaius phoeniceus</i>)	Wassenaar and Hobson 2000a
American Redstart (<i>Setophaga ruticilla</i>)	Chamberlain et al. 1997, Hobson et al. 2004b
Wilson's Warbler (<i>Wilsonia pusilla</i>)	Kelly et al. 2002, Clegg et al. 2003
Swainson's Thrush (<i>Catharus ustulatus</i>)	Wassenaar and Hobson 2001, Kelly et al. 2005
Bicknell's Thrush (<i>C. bicknelli</i>)	Hobson et al. 2004a
Loggerhead Shrike (<i>Lanius ludovicianus</i>)	Hobson and Wassenaar 2001
Cooper's Hawk (<i>Accipiter cooperii</i>)	Meehan et al. 2001, 2003; Lott et al. 2003
Sharp-shinned Hawk (<i>A. striatus</i>)	Smith et al. 2003

variable. I interpret slopes that deviate significantly from zero as evidence that birds that bred at different latitudes differ in timing of migration. I evaluated significance of all statistical tests with a critical value of 0.05, and data are reported as means \pm SD unless otherwise noted.

RESULTS

Slopes of least-squares regression lines of stable-hydrogen isotope ratios plotted against capture dates were significantly different from zero in all three species of wood warbler examined (Fig. 1). In Orange-crowned Warblers and Common Yellowthroats, the slopes were significantly less than zero, indicating that birds that bred at southern latitudes migrated through New Mexico earlier than those from northern latitudes. By contrast, for Yellow Warblers, the slope was significantly greater than zero, indicating that birds that bred at northern latitudes arrived, on average, at the New Mexico banding site earlier than southern breeders.

DISCUSSION

Data presented here, combined with those of Kelly et al. (2002), allow comparison of the relationship between timing of autumn migration and latitude of breeding sites among four common western warblers from different genera. In none of these well-studied species did I find any literature that suggested that timing of migration was related to latitude of the breeding sites. On the basis of stable-hydrogen isotope data, I suggest that it is common for wood warblers to show a nonrandom pattern in timing of migration that

is systematically associated with the latitude of breeding sites. It is unclear whether the slopes documented here would be constant among stopover sites throughout the west or if they are unique to each location. Further investigation of the robustness of these patterns through time and space would be useful. In particular, time-series analyses from feathers collected at multiple stopover sites across species' migratory range over several years could contribute to our understanding of the spatiotemporal plasticity of migratory behavior.

Data presented here provide some insight into the temporal pattern of migration in these species, but they do not allow inference about the spatial relationship between breeding origins and winter sites. It would be interesting to know whether early-migrant Yellow Warblers from northern latitudes are heading to the southern end of the species' winter range (leapfrog pattern), as occurred in Wilson's Warbler (Kelly et al. 2002, Clegg et al. 2003). Alternatively, these birds may winter in northern Mexico (chain migration). Determining which one of these patterns best describes the migratory biology of these species will require isotope data from throughout the breeding and wintering range of these species. In particular, it would be useful to know whether the timing of migration of northern and southern migrants (i.e. type I vs. type II migration; *sensu* Smith et al. 2003) is generally associated with leapfrog or with chain migration.

Nonrandom temporal patterns of migration in relation to location of breeding sites have implications for both stopover ecology and our understanding of the annual cycle of

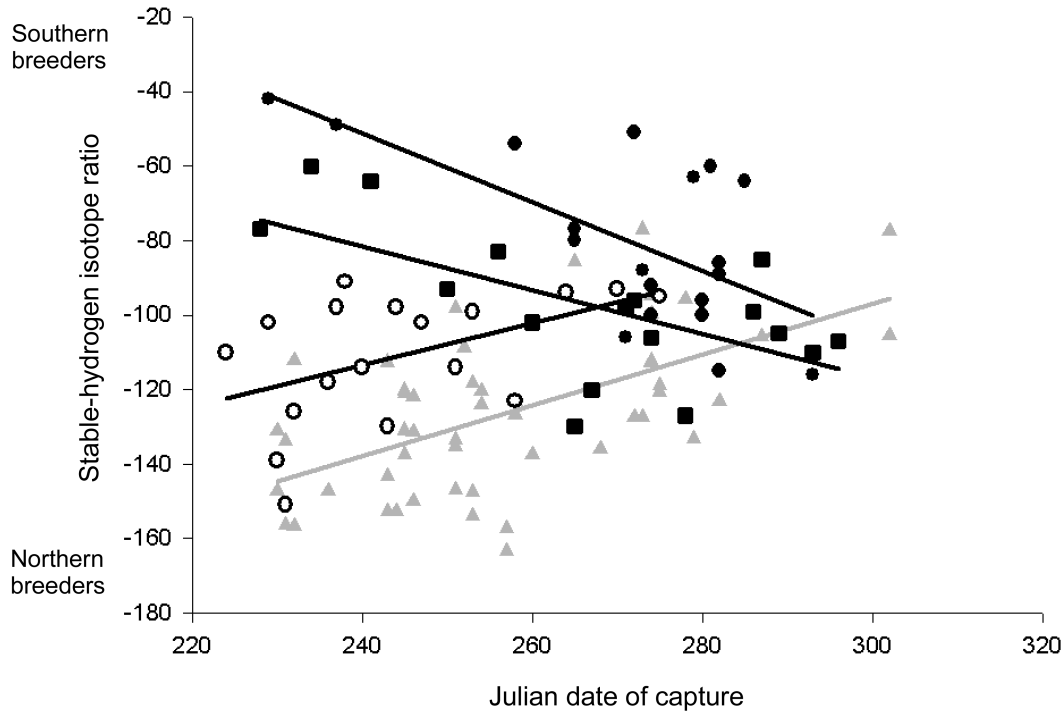


FIG. 1. Hydrogen stable-isotope ratio (δD) of feathers from individual wood warblers plotted against date of capture during autumn migration. Data are from Bosque del Apache National Wildlife Refuge in central New Mexico. Orange-crowned Warblers = filled squares, Yellow Warblers = open circles, and Common Yellowthroats = closed circles. Regression lines (black) fit to these data have slopes that deviate from zero (Yellow Warbler: $r^2 = 0.23$, $P < 0.05$, $n = 18$, $\delta D = 0.56 \times \text{date} - 248$; Orange-crowned Warbler: $r^2 = 0.38$, $P < 0.05$, $n = 17$, $\delta D = -0.59 \times \text{date} + 60$; Common Yellowthroat: $r^2 = 0.41$, $P < 0.05$, $n = 19$, $\delta D = -0.92 \times \text{date} + 170$). The gray least-squares regression line and triangles are for Wilson's Warbler from Kelly et al. 2002 ($r^2 = 0.34$, $P < 0.05$, $n = 65$, $\delta D = 0.68 \times \text{date} - 301$).

migrants. Historically, stopover-ecology studies have treated each individual as an independent random sample in analyses of fat scores, stopover durations, and habitat selection. Results reported here suggest that this assumption of independence is invalid and likely masks meaningful among-individual variation. It is more likely that birds that travel predictably different migration distances and arrive at stopover sites at predictably different dates employ predictably different stopover strategies.

More broadly, these patterns in timing of migration likely have implications for explaining variation in individual fitness and productivity of populations. The migratory phase of the annual cycle, arguably, exerts the greatest selective pressure on individuals (e.g. highest postfledging mortality rates; Sillett and

Holmes 2002). The mechanisms of this selection likely include competition, predation, seasonal changes in food supply, and weather variation (Moore et al. 1995). If inter- and intraspecific variation in timing of migration are shaped by these selective pressures, this selection should also be detectable as associated variation in physiological, behavioral, and population metrics. For example, do early autumn migrants establish the best winter territories, maintain good energetic condition, and depart early in spring? Accumulating evidence supports the idea that such carryover effects are more pervasive and consequential than has been recognized previously (e.g. Marra et al. 1998, Norris et al. 2003, Smith and Moore 2005).

At present, it is unclear whether timing of autumn migration, specifically, has either direct

consequences for individual fitness or substantial carryover effects. Assessing these effects requires linking stopover sites to breeding territories and wintering sites, along with developing better methods for assessing the spatiotemporal patterns in migratory mortality. These would be major advances in our understanding of migratory life histories. Achieving this goal will require better integration and application of intrinsic and extrinsic marker technologies for tracking movements of individual organisms.

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