



Breeding latitude and timing of spring migration in songbirds crossing the Gulf of Mexico

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Each spring, millions of songbirds migrate across the Gulf of Mexico on their way to breeding sites in North America. Data from radar and migration monitoring stations have revealed broad patterns in the spatial and temporal course of trans-Gulf migration. Unfortunately, we have limited information on where these birds have previously spent the winter and where they are migrating to breed. Here we measure stable-hydrogen isotopes in feathers (δD_f) to infer the breeding latitude of five species of songbirds – hooded warblers *Wilsonia citrina*, American redstarts *Setophaga ruticilla*, black-and-white warblers *Mniotilta varia*, ovenbirds *Seiurus aurocapilla*, and northern waterthrushes *S. noveboracensis* – that were captured at a stopover site along the coast of southwestern Louisiana in spring 2004. Values of δD_f across all species ranged from -163 to -35‰ ($n = 212$), and within most species the range was consistent with the latitudinal extent of known breeding sites in central and eastern North America. Individuals that arrived first along the northern Gulf coast had δD_f values indicative of southerly breeding sites in hooded warblers, American redstarts, black-and-white warblers, and ovenbirds, but no relationship was found between passage timing and δD_f for northern waterthrushes. Our findings suggest that spring passage is often timed to coincide with the emergence of suitable conditions on breeding areas, with southern breeding birds migrating first.

The timing of arrival at breeding areas has important fitness consequences for migratory birds (Perrins 1970, Kokko 1999). Individuals arriving early benefit from a longer breeding season and face reduced competition for territories and mates (Price et al. 1988, Verboven and Visser 1998, Moore et al. 2005). However, they also risk exposure to harsher spring conditions (weather, food availability) as they move north (Newton 2007). Such tradeoffs have contributed to the selection of arrival schedules in migratory birds, which may vary among species in relation to life history characteristics (Rubolini et al. 2002), among populations in relation to breeding latitude and elevation (Sanz 1997), and within populations in relation to sex (Francis and Cooke 1986, Yong et al. 1998, Swanson et al. 1999).

Migrants *en route* to breeding areas often deviate from a straight-line trajectory to take advantage of prevailing wind patterns or to avoid ecological barriers (e.g. water bodies, mountain ranges, deserts; Alerstam 2001). The Gulf of Mexico is a formidable barrier for many Neotropical migrants that breed in eastern North America. Three broad routes have been described in relation to this geographic feature: (1) a circum-Gulf route through eastern Mexico, (2) a trans-Gulf route from the Yucatan Peninsula and the

surrounding area to the northern Gulf Coast, and (3) a circum-Gulf route through the West Indies and Florida (Stevenson 1957). Despite the risk of encountering unfavorable weather (Lowery 1946), the trans-Gulf route is common among eastern breeders because it is the shortest route for birds over-wintering in Central and South America and wind patterns are generally favorable in spring (Gauthreaux 1999, Stutchbury et al. 2009).

Radar technology has been used to study large-scale patterns in the spatial and temporal distribution of birds crossing the Gulf of Mexico in spring (Gauthreaux 1971, Gauthreaux et al. 2006), but this technique is limited in that it cannot identify species. Migration monitoring stations document terrestrial passage patterns at smaller scales and several are positioned along the northern Gulf coast. Data collected at these stations provide massive amounts of information on the *en route* ecology of migrants (see Moore 1999 for review), including passage timing (Moore et al. 1990, Marra et al. 2005), energetic condition (Kuenzi et al. 1991, Yong and Moore 1994), stopover duration and rates of fat deposition (Moore and Kerlinger 1987, Moore and Yong 1991), and habitat use (Moore et al. 1990). Yet these studies cannot attribute specific

breeding locations to individual birds because only a very small percentage are ever recaptured at breeding sites (<1% for songbirds, Webster et al. 2002).

With the advent of stable isotopes, we can now infer breeding destinations by measuring intrinsic geographic markers in feathers grown on the breeding grounds after the previous breeding season (e.g. Wassenaar and Hobson 2001, Mazerolle et al. 2005, Kelly 2006). Stable-hydrogen isotopes (δD) vary predictably with latitude and elevation across continental landmasses (Bowen et al. 2005). Since birds incorporate local isotopic signatures into their tissues when they eat and drink (Hobson et al. 1999), δD values in feathers (δD_f) are usually indicative of the region of molt (Hobson and Wassenaar 1997, Kelly et al. 2002, Langin et al. 2007; but see Powell and Hobson 2006). This approach has been used to infer the breeding origin of songbirds captured during the migratory phase of the annual cycle (e.g. Kelly et al. 2002, Mazerolle et al. 2005, Paxton et al. 2007), yet none have focused on the trans-Gulf flyway in spring.

Here we apply stable-isotope techniques to examine the breeding latitude of songbirds captured in southwestern Louisiana during active migration, after completing a flight across the Gulf of Mexico. Our focal species are five of the most frequently captured migratory birds along the Louisiana coast: hooded warblers *Wilsonia citrina*, American redstarts *Setophaga ruticilla*, black-and-white warblers *Mniotilta varia*, ovenbirds *Seiurus aurocapilla*, and northern waterthrushes *S. noveboracensis*. All are small (8–25 g), medium- to long-distance migratory birds that are widely distributed throughout their respective breeding areas in North America and wintering areas in Central America, the Caribbean, and northern South America (Table 1; Evans Ogden and Stutchbury 1994, Van Horn and Donovan 1994, Eaton 1995, Kricher 1995, Sherry and Holmes 1997). Like most passerines, these species undergo a complete post-breeding molt prior to their departure for fall migration and carry those feathers with them for the duration of the annual cycle (Pyle 1997). They also have high site fidelity on breeding areas, so adults generally return to the territory they held the previous year (Morse 1989). We therefore measured the hydrogen isotopic composition of tail feathers to infer the latitude of the breeding destination. We predicted that birds breeding in the southern United States would arrive at

stopover sites in Louisiana earlier than birds breeding further north because of corresponding delays in temperature and plant phenology with movement north across latitudes (Zhang et al. 2004).

Materials and methods

Field methods

Birds were captured at a migration monitoring station near the town of Johnson's Bayou in southwestern Louisiana (29° 45'N, 93° 37'W). The station is located within a narrow strip of forested wetland along the coastline (called a chenier) and is a key stopover where birds can rest and replenish body stores after completing their northward flight across the Gulf of Mexico (Moore and Kerlinger 1987, Barrow et al. 2000). Radar technology during spring migration has shown that most peaks in migrant density along the northern Gulf coast occur just west of this site, at 95° W (data from 2001–2004; Gauthreaux et al. 2006). It is therefore an ideal location for sampling birds from the main flyway across the Gulf of Mexico. It is also an excellent site because none of the study species breed in the area, so all of the individuals captured at the station are actively migrating.

From 24 March to 7 May 2004, 30 mist-nets (12 × 2.6 m, 30 mm mesh) were opened each day from an hour after sunrise to sunset (except during inclement weather), resulting in a seasonal total of 9,053 net h. Our focal species started arriving in late March, with the most southerly breeder, the hooded warbler, arriving considerably earlier than the other species (see Table 1 for long-term averages). From 29 March to 7 May, we collected tail feathers (R4) from a portion of the hooded warblers (n = 55), American redstarts (n = 21), black-and-white warblers (n = 32), ovenbirds (n = 60), and northern waterthrushes (n = 44) captured at the site. The samples were representative of most of the range of passage dates for each species (see Table 1); in all cases the first arrival was sampled, but for four species some individuals were captured within 2–3 days after the final date of feather sampling (n = 3 hooded warblers (2% of individuals), 15 black-and-white warblers (17%), 6 ovenbirds (6%), 8 northern waterthrushes (11%)). Birds were individually marked with an aluminum USFWS band and sex was determined (when possible) using Pyle (1997).

Stable-isotope analysis

Feathers were analyzed for δD_f at the Queen's Facility for Isotope Research in Kingston, Ontario, Canada. To remove surface oil and debris, the feathers were immersed in a 2:1 chloroform:methanol solution for 24 h, drained and air-dried under a fume hood for 72 h. A small sample (0.1–0.2 mg) from the tip of each tail feather was loaded into a silver capsule and exposed in an oven (at 100° C) for 24 h to remove condensation on the feather surface. None of the samples included the rachis, which has been shown to differ in isotopic composition from feather barbs (Wassenaar and Hobson 2006). After removing the capsules from the oven they were immediately crushed, and the samples analyzed for δD_f using a reduction furnace (Finnigan TC/EA at 1,450° C) coupled to an isotope ratio mass spectrometer

Table 1. The range in latitudes each species occupies during stationary periods of the annual cycle (data from Mills 2006), as well as their passage timing (mean \pm SD, with range in parentheses) along the northern Gulf coast (data from 1987–2004; F. R. Moore, unpubl. data). A Julian date of 100 corresponds to 10 April in non-leap years, and 9 April in leap-years (as was the case during this study).

	Latitudinal range:		Spring passage: Julian date
	Breeding	Wintering	
Hooded warbler	29° – 43°N	9° – 23°N	103 \pm 10 (80–135)
American redstart	31° – 65°N	17°S – 25°N	119 \pm 9 (91–134)
Black-and-white warbler	30° – 65°N	8°S – 33°N	110 \pm 13 (80–136)
Ovenbird	34° – 56°N	8° – 30°N	115 \pm 10 (87–134)
Northern waterthrush	45° – 60°N	3°S – 28°N	114 \pm 9 (86–134)

(Finnigan MAT Delta Plus XL). Stable-hydrogen isotope values (in ‰) are reported relative to Vienna standard mean ocean water (V-SMOW) according to the formula: $\delta D = [(^2H/^1H_{\text{sample}} \div ^2H/^1H_{\text{standard}}) - 1] \times 1000$. Duplicate samples from the same feather differed from one another by $3 \pm 2\text{‰}$ (mean \pm SD, $n=24$; all species combined). Mineral standards were analyzed every six samples and their δD values were consistent with previous measurements in our laboratory.

Data analysis

We used a randomization procedure for comparing δD_f values among species. Unlike traditional statistical tests, this approach generates a distribution for the test statistic that is based on resampling of the actual data, and then computes a P-value that reflects the probability that individuals were randomly distributed across groups with respect to the response variable. To do this, we used a procedure within the program PERM that was specifically designed for comparing isotope data among groups (in this case, the groups were species; Duchesne et al. 2006), and ran 1,000 permutations (resampling events) for each of 10 iterations. For each pair-wise comparison, we used the average P-value across iterations and applied a sequential Bonferroni correction (Holm 1979) to control for type 1 error.

Next, we wanted to determine the extent to which the birds we sampled were representative of the latitudinal

extent of their species' breeding range. To do this, we defined five 30‰-wide isotope zones and assigned birds to a zone based on the isotopic composition of their tail feathers: zone 1 $< -155\text{‰}$, zone 2 = -155 to -125‰ , zone 3 = -125 to -95‰ , zone 4 = -95 to -65‰ , and zone 5 $\geq -65\text{‰}$. The geographic extent of each zone can be seen in Fig. 1, based on the isotopic basemap produced by Meehan et al. (2004) and a feather-precipitation discrimination factor of -25‰ (Wassenaar and Hobson 2001). This approach was used because, although the hydrogen isotopic composition of songbird feathers is strongly correlated with latitude in North America (Hobson and Wassenaar 1997, Kelly et al. 2002), δD_f is not always a precise estimate of an individual's molting latitude (Wunder et al. 2005, Powell and Hobson 2006, Langin et al. 2007).

In addition to assigning birds to an isotope zone, we also calculated the proportion of each species' breeding range that was located in each zone. We restricted our analysis to breeding areas east of the continental divide (see Fig. 1), as trans-Gulf migrants are thought to consist primarily of breeders in the central and eastern portions of North America (Morse 1989). We also excluded breeding areas for the northern waterthrush in Alaska, some of which were north of the continental divide. We downloaded range maps from NatureServe (Ridgely et al. 2005), continental divide data from the US Geological Survey and Natural Resources Canada, and, using the isotopic basemap cited above, made our calculations in ArcGIS (v. 9.2). Ideally we

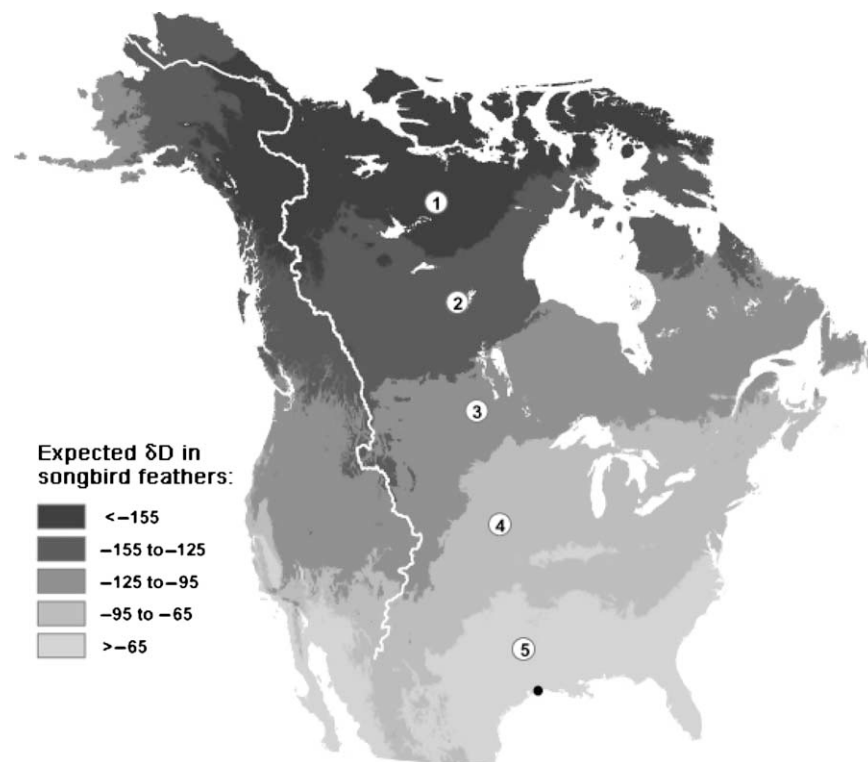


Figure 1. Geographic delineations for the hydrogen-isotope zones defined for this study (numbered 1–5). The data represent expected δD values (in ‰) for feathers grown in those regions and are based on spatial variation in growing-season precipitation (from Meehan et al. 2004), offset by the discrimination factor describing the difference between δD in precipitation and songbird feathers (-25‰ , Wassenaar and Hobson 2001). The white line is the location of the continental divide through Canada and the US, which was used to exclude breeding areas in western North America when calculating the proportion of the breeding range that overlaps each isotope zone. The solid dot is the location of the study site near Johnson's Bayou, Louisiana. This map was created using an equal-area projection.

would have incorporated abundance estimates into our calculations, but unfortunately the breeding ranges of four focal species (all but the hooded warbler) extend north of the geographic extent of routes run by the North American Breeding Bird Survey.

Finally, passage timing was related to the hydrogen isotopic composition of songbird feathers using nonparametric procedures in JMP IN 5.1 (SAS 2006). This approach was taken because the passage data were not normally distributed and could not be improved through transformations.

Results

The hydrogen isotopic composition of feathers from songbirds passing through Louisiana varied significantly among species. Hooded warblers had higher δD_f values ($-59 \pm 11\text{‰}$ (mean \pm SD), $n = 55$) – indicating that they grew their feathers at lower latitudes – compared to American redstarts ($-75 \pm 31\text{‰}$, $n = 21$), black-and-white warblers ($-80 \pm 14\text{‰}$, $n = 32$), ovenbirds ($-75 \pm 16\text{‰}$, $n = 60$), and northern waterthrushes ($-127 \pm 21\text{‰}$, $n = 44$; permutation tests in PERM, $P < 0.001$ for all pairwise comparisons). Northern waterthrushes also had lower δD_f values than all of the other species (all $P < 0.001$). None of the other pairwise comparisons were significant.

Within most species, the range in δD_f values corresponded to the range expected based on the location of known breeding areas in central and eastern North America (see Fig. 2). However, the most northerly-breeding populations of American redstarts, black-and-white warblers, and ovenbirds were not represented in the birds sampled. It is possible that those populations pass through the Gulf coast after 7 May, or fail to stopover in coastal habitats. Regardless, the wide range in δD_f values – both within and among species – indicates the birds originated from breeding populations across a wide latitudinal gradient in central and eastern North America.

With regard to migratory timing, individuals from southern breeding populations had earlier spring passage dates than those from further north for hooded warblers (Spearman rank, $r_s = -0.72$, $P < 0.001$, $n = 55$), American redstarts ($r_s = -0.67$, $P = 0.001$, $n = 21$), and black-and-white warblers ($r_s = -0.72$, $P < 0.001$, $n = 32$), but not for ovenbirds ($r_s = -0.18$, $P = 0.16$, $n = 60$) or northern waterthrushes ($r_s = 0.26$, $P = 0.09$, $n = 44$; Fig. 3). These relationships remained the same when sample sizes were sufficient to analyze males and females separately (results available upon request). Similar results were also obtained for most species when conducting categorical analyses with the isotope data, except that in this case ovenbirds assigned to the most southerly isotope zone had earlier passage dates than those assigned to more northerly zones (Kruskal-Wallis test, $K = 7.0$, $P = 0.03$).

Discussion

It has long been known that southern populations of many migratory birds arrive on breeding areas earlier than northern populations, and that the first spring arrivals at

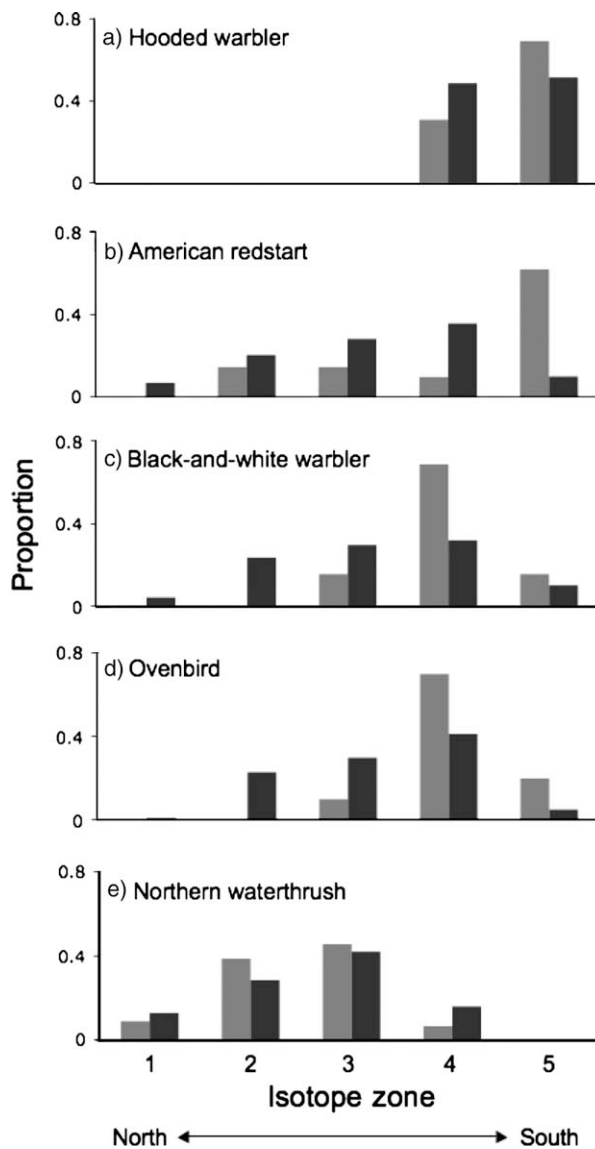


Figure 2. The proportion of birds assigned to each isotope zone (light bars) for: (a) hooded warblers ($n = 55$), (b) American redstarts ($n = 21$), (c) black-and-white warblers ($n = 32$), (d) ovenbirds ($n = 60$), and (e) northern waterthrushes ($n = 44$) captured along the coast of southwestern Louisiana in the spring of 2004, as well as the proportion of the species' breeding ranges in each isotope zone (dark bars). Birds were assigned to isotope zones based on the hydrogen isotopic composition of their tail feathers (see Fig. 1).

a given latitude usually stop to breed there (Cooke 1888). At a stopover located south of all potential breeding sites, we tested the relationship between passage timing and breeding latitude by measuring the hydrogen isotopic composition of tail feathers from five species of songbirds captured along the southwestern coast of Louisiana. For most species the range of δD_f values was consistent with the known latitudinal range of breeding sites in central and eastern North America and, as predicted, hooded warblers, American redstarts, black-and-white warblers, and (to some degree) ovenbirds from southerly breeding populations arrived along the northern Gulf coast earlier than those

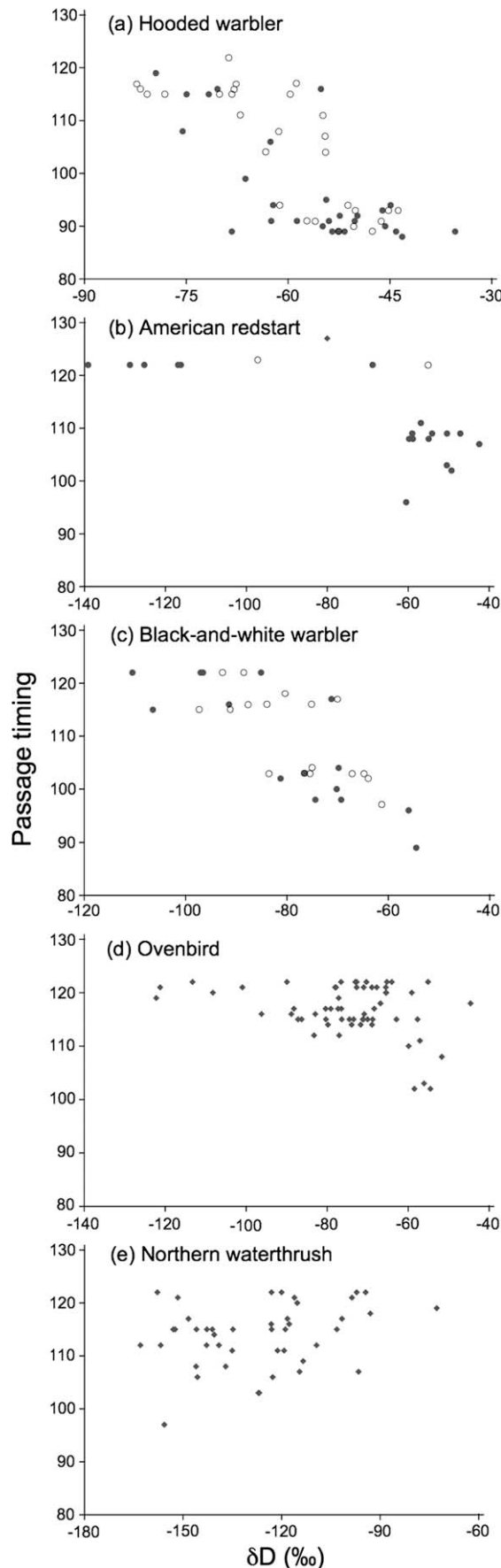


Figure 3 (Continued)

from more northerly breeding populations (Fig. 3). Interestingly, δD_f was not related to passage timing in northern waterthrushes.

Our study assumes that δD_f is a reliable indicator of molting latitude. However, that may not be the case for birds breeding in western North America (e.g. Wunder et al. 2005) where hydrogen-isotope patterns are complicated by rain-shadow effects (Bowen et al. 2005). We cannot exclude the possibility that some of the birds we sampled originated from western populations. But in a recent study, Boulet et al. (2006) used not only hydrogen isotopes, but also genetic markers, to examine the breeding origin of yellow warblers *Dendroica petechia* migrating through southwestern Louisiana in spring. Individuals were found to originate from populations across a wide range of latitudes (δD_f ranged from -118 to -59‰ , $n = 31$), but all had mitochondrial haplotypes indicative of eastern populations ($n = 40$). This is consistent with the view that most trans-Gulf migrants breed in central and eastern North America (Morse 1989).

Of all the studies that have measured δD_f in songbird feathers collected during spring migration, only one has detected a significant relationship between the timing of spring passage and the latitude of the breeding destination (Wilson's warblers *Wilsonia pusilla*; Paxton et al. 2007). The authors argued that their result was consistent with leap-frog migration in that species, as southerly breeding populations of Wilson's warblers had been previously shown to winter the furthest north (Kelly et al. 2002). This argument assumes that departure timing is uniform across wintering sites and that southerly breeders arrive at temperate stopovers earlier because they have a shorter distance to travel. We have no information on the wintering origin of the individuals sampled in this study, and migratory connectivity has only been studied in one of our focal species. Nevertheless, in that one focal species – the American redstart – breeding and wintering populations do not exhibit a system of leap-frog migration (Norris et al. 2006), and even when individuals are overwintering at the same site, they depart earlier on spring migration if they are bound for more southerly breeding areas (Studds et al. 2008). For the other species, it remains possible that populations differ in the timing of passage through Louisiana because of corresponding differences in migration distance, yet we believe factors on breeding areas provide a more plausible explanation. Populations of these species are exposed to latitudinal differences in temperature and plant phenology across their respective breeding areas in spring (Zhang et al. 2004). For hooded warblers, American redstarts, black-and-white warblers, and possibly ovenbirds, we suggest that arrival along the northern Gulf coast may be timed to coincide with the emergence of suitable phenolo-

Figure 3. Spring passage timing (Julian date) in relation to δD_f for (a) hooded warblers ($r_s = -0.72$, $P < 0.001$, $n = 55$), (b) American redstarts ($r_s = -0.67$, $P = 0.001$, $n = 21$), (c) black-and-white warblers ($r_s = -0.72$, $P < 0.001$, $n = 32$), (d) ovenbirds ($r_s = -0.18$, $P = 0.16$, $n = 60$), and (e) northern waterthrushes ($r_s = 0.26$, $P = 0.09$, $n = 44$) migrating through southwestern Louisiana in 2004 (solid circle = male, open circle = female, triangle = unknown sex). A Julian date of 100 is the 9th of April (as 2004 was a leap year).

gical conditions on breeding areas occupied the previous year.

In contrast, we did not find a relationship between passage timing and δD_f in the northern waterthrush, despite the fact that southern populations are known to arrive on breeding areas earlier than northern populations (Eaton 1995). This result may be due to inter-specific differences in breeding latitude. Northern waterthrushes breed the furthest north, so at the point of stopover along the Gulf coast they would have the longest distance to travel and therefore the most opportunity to adjust their rate of migration in order to time their arrival at breeding destinations appropriately. An alternate explanation is that δD_f may not reflect breeding latitude in some (or all) northern waterthrush populations. Individuals may molt a distance from their breeding site (e.g. Cherry 1985, Wassenaar and Hobson 2001), or there may not be a tight link between δD in the species' food items and δD in the growing-season precipitation. Northern waterthrushes feed primarily on aquatic food items (Eaton 1995), which may have a different hydrogen isotopic signature than surrounding terrestrial food webs because of water inputs from elsewhere (stream flow) or the evaporation of standing water (Hobson 2005). As a result, it may not be appropriate to calculate expected δD_f values for this species using the isotopic composition of growing-season precipitation. Feathers collected from breeding populations would be useful for teasing apart these competing hypotheses.

Given the differences in migratory timing among breeding populations, feather collections at migratory stopover sites may be useful to study the phenological consequences of climate change. Long-term data sets in northern regions have detected earlier passage dates in warmer years (Marra et al. 2005, Mills 2005, Tøttrup et al. 2006). Rather than earlier departure from wintering sites, these patterns are thought to be driven by changes in the rate of migration through temperate latitudes, which have experienced larger changes in temperature. Patterns of spring passage along the Gulf coast are unlikely to advance with the changing climate because it is the first temperate stopover for trans-Gulf migrants. Even so, passage data from stopovers along the Gulf coast can be compared with data from more northerly sites to detect changes in the rate of migration (e.g. Marra et al. 2005). Measuring δD_f in feathers of those migrants would enable comparisons among birds breeding at similar latitudes, not just birds of the same species. That said, this technique would have limited utility in regions that lack a strong and consistent latitudinal trend in δD (e.g. Europe; Bowen et al. 2005).

Our findings not only document temporal patterns of spring passage, but they also reveal the wide range in breeding destinations for songbirds captured along the Gulf coast. This serves to highlight the significance of the trans-Gulf flyway, as well as the importance of coastal cheniers as stopovers in southwestern Louisiana (see also Moore and Kerlinger 1987). Habitat is crucial for migrants throughout their inter-continental journey (Moore 2000). However, it is even more crucial at the end of over-water flights, particularly when migrants encounter unfavorable weather and need to rest and replenish depleted fuel stores (Gauthreaux 1971, Moore and Kerlinger 1987, Newton 2006). Results presented here demonstrate that songbirds

breeding across central and eastern North America use coastal cheniers as stopovers during spring migration.

In some cases, birds were disproportionately representative of one breeding region (i.e. isotope zone) over another. For instance, over half of the American redstarts were assigned to the southern isotope zone, even though it only encompasses 10% of the species' breeding range (Fig. 2). This cannot be due to abundance because redstarts occur at low densities in the southern portion of their breeding range (data from the North American Breeding Bird Survey; see Norris et al. 2006). Instead, redstarts from those breeding populations may be overwintering in locations for which it advantageous to make a trans-Gulf crossing (Central America and western South America). Norris et al. (2006) measured δD_f in redstart populations across the species' wintering range and only found southern breeders overwintering in Trinidad and Tobago; however, the western portion of South America was not sampled so southern breeders may also overwinter there.

Hydrogen-isotope analysis is a useful tool for revealing the breeding origin of birds captured during the migratory phase of the annual cycle. Here we show that songbirds breeding across much of central and eastern North America use the trans-Gulf flyway in spring. Individuals that arrive first along the northern Gulf coast appear to be destined for the most southerly breeding sites, although that is not the case for all species. Knowledge of connectivity among breeding and wintering populations can be useful when examining the breeding origin of birds at stopover sites (e.g. Kelly et al. 2002, Boulet et al. 2006). Of our focal species, such data were only available for the American redstart. Future studies should not only examine δD_f in feathers collected at additional stopover sites, but also the degree of connectivity among stationary populations. The northern waterthrush would be of particular interest because arrival timing along the northern Gulf coast does not appear to correspond with phenological patterns at breeding destinations.

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