

Golden-winged Warbler Migratory Connectivity Derived from Stable Isotopes*

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Abstract. Establishing migratory connectivity between breeding and nonbreeding sites of populations of migratory birds is crucial to their effective management, but the use of conventional tracking tags is not an option for most small passerines. For declining species like Golden-winged Warblers (*Vermivora chrysoptera*), it is especially important to determine the relative impact of factors on breeding and nonbreeding areas and those experienced *en route* to address means of mitigating or reversing such declines. We used measurements of naturally occurring hydrogen isotopes ($\delta^2\text{H}$) in feathers of Golden-winged Warblers sampled in Honduras ($n = 68$), Nicaragua ($n = 19$), Costa Rica ($n = 65$), Colombia ($n = 16$), and Venezuela ($n = 3$) and used the isotopic data to assign probable breeding or natal origins of individuals to a North American feather

$\delta^2\text{H}$ isoscape. We found considerable structure in migratory connectivity, with Honduran birds generally deriving from more southern portions of the breeding distribution and those in Nicaragua and Costa Rica from more northern regions. Birds in Venezuela and Colombia were generally from the Appalachians and more southern portions of their breeding distribution, suggesting the existence of a migratory divide between Appalachian and Great Lakes breeding-distribution segments in North America. Our results have important implications for the design of ongoing sampling of this species on the nonbreeding areas and the interpretation of population trajectories of birds from various regions of their breeding distribution.

Key Words: breeding ground, deuterium, migration, nonbreeding ground.

Effective conservation of migratory birds requires an understanding of geographical connections between breeding and nonbreeding populations, and migratory stopover

sites used *en route* (Webster and Marra 2005). Information on migratory connectivity serves to highlight critical habitats used by a species during most of the annual cycle and to integrate

* Hobson, K. A., S. L. Van Wilgenburg, A. M. Roth, R. E. Bennett, N. J. Bayly, L. Chavarría-Durieux, G. J. Colorado, P. Elizondo, C. G. Rengifo, and J. D. Ritterson. 2016. Golden-winged Warbler migratory connectivity derived from stable isotopes. Pp. 193–203 in H. M. Streby, D. E. Andersen, and D. A. Buehler (editors). *Golden-winged Warbler ecology, conservation, and habitat management*. Studies in Avian Biology (no. 49), CRC Press, Boca Raton, FL.

conservation efforts across hemispheres and political boundaries (Faaborg et al. 2010). For Neotropical–Nearctic migrants, habitat requirements and biogeography of populations are better understood at the breeding grounds, although it remains generally unclear which breeding areas produce the most recruits into the adult breeding population (Hobson et al. 2006, 2009). In contrast, the distribution and habitat needs of migratory birds at nonbreeding sites in Mexico, the Caribbean, and Central and South America remain poorly known, despite considerable loss of forest and other vital cover types in those areas (FAO and JRC 2012). Establishing key migratory connections between breeding and nonbreeding populations and identifying which areas make the greatest contributions to continental breeding populations are two vital goals in migratory bird conservation. However, these goals have remained largely elusive due to the practical difficulties in tracking movements of small songbirds (Hobson and Norris 2008).

The development of the use of intrinsic markers, such as ratios of naturally occurring stable isotopes in tissues, has greatly advanced understanding of animal migration (Hobson and Wassenaar 2008). In particular, the use of stable-hydrogen isotope measurements ($\delta^2\text{H}$) of tissues such as feathers or claws that are metabolically inert following formation allows a probabilistic assignment of individuals and populations to origins due to the occurrence of strong isotopic gradients of hydrogen isotope ratios in food webs at a continental scale (Hobson and Wassenaar 2008). The establishment of calibration algorithms linking $\delta^2\text{H}$ values in feathers ($\delta^2\text{H}_f$) with amount-weighted $\delta^2\text{H}$ in growing-season precipitation ($\delta^2\text{H}_p$) allows for the creation of $\delta^2\text{H}_f$ isoscapes that can be used to infer potential origins where feathers were grown. Most, but not all Neotropical migrant songbirds breeding in North America grow their feathers on or close to their breeding grounds before migration (Rohwer et al. 2005). That, together with the fact that the $\delta^2\text{H}_f$ isoscape for North America is well established compared to those of nonbreeding areas results in the isotope approach being particularly well suited to inferring breeding or natal origins of Neotropical migrants sampled at their nonbreeding locations (Hobson and Wassenaar 1997, Hobson et al. 2004, Rubenstein and Hobson 2004, Boulet et al. 2006, Norris et al. 2006).

Golden-winged Warblers (*Vermivora chrysoptera*) breed primarily in the northcentral region of the United States (Figure 12.1) with populations centered in the Appalachian Mountains from southern New York to northwestern Georgia and in the Great Lakes from Quebec to Minnesota extending northwest into Manitoba (Chapter 1, this volume). Golden-winged Warblers generally molt at their breeding grounds prior to migration (Pyle et al. 1997, Confer et al. 2011), and spend the nonbreeding season primarily in Central America and northern South America, from central Guatemala and northern Honduras south to northwestern Venezuela and western Colombia (Confer et al. 2011; Chapter 1, this volume). Most conservation efforts and concern for Golden-winged Warblers have focused on breeding ecology (Buehler et al. 2007, Thogmartin 2010), where population size has declined at an annual rate of about 2.5%–3% (Sauer et al. 2008) and where the species hybridizes with congeneric Blue-winged Warblers (*Vermivora cyanoptera*; Vallender et al. 2007, 2009). No bands have been recovered from the nonbreeding grounds and virtually nothing is known about migratory connectivity in Golden-winged Warblers. The small body mass of ~9 g has resulted in geolocators only recently becoming small enough to be tested on Golden-winged Warblers (H. M. Streby, pers. comm.) making the species a candidate for stable-isotope investigation. The stable-isotope approach is not biased with respect to origin because only one capture is required. Information on origin can be derived for all birds sampled and the approach does not influence the prior migratory behavior of the bird up to the point of sampling (Hobson 2005, Hobson and Wassenaar 2008). Last, with extensive geographic sampling, estimates of the most productive breeding regions can be delineated by examining estimated origins of hatch-year or second-year (SY) birds. Here, we present results of our investigation into migratory connectivity in Golden-winged Warblers by analyzing $\delta^2\text{H}$ in feathers ($\delta^2\text{H}_f$) from individuals captured at sites used during the nonbreeding period. We augmented our study with a species-specific feather isoscape based on a calibration between feathers and precipitation derived from after-second year (ASY) birds that have the highest probability of being associated with a set of known breeding locations in North America. Our objectives were to examine the evidence for spatial structure in

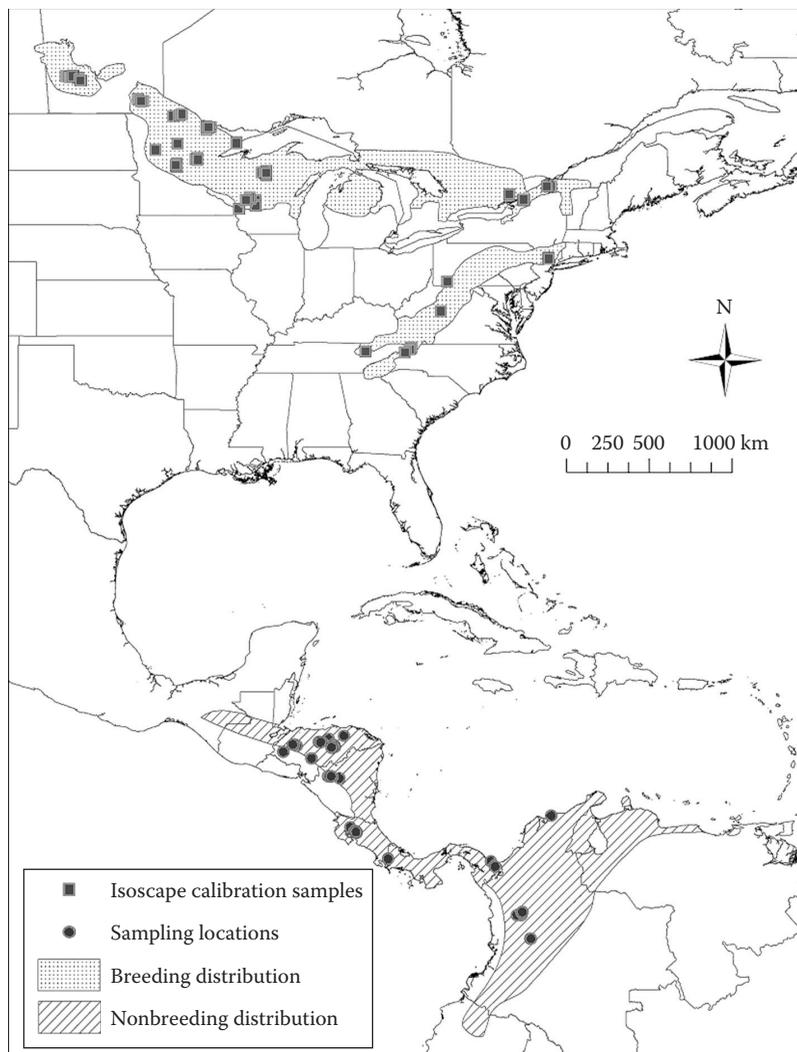


Figure 12.1. Distribution of feather collection sites (circles) within the Golden-winged Warbler nonbreeding distribution (hatched shading) and locations used to calibrate a model of expected $\delta^2\text{H}$ in Golden-winged Warbler feathers grown on the breeding distribution (stippling).

migratory connectivity versus panmixis, and establish a protocol for Golden-winged Warblers that could be used for future sampling at nonbreeding sites. Scant information is currently available and we had no *a priori* predictions concerning patterns of migratory connectivity.

METHODS

Field Methods

We obtained feather samples from Golden-winged Warblers captured at 74 locations across much of their nonbreeding distribution, grouped

at 22 distinct localities (Figure 12.1). We captured one to eight individuals per site in Honduras ($n = 68$), Nicaragua ($n = 19$), Costa Rica ($n = 65$), Colombia ($n = 16$), and Venezuela ($n = 3$) between 2003 and 2012 (Figure 12.1). We collected 171 samples at nonbreeding sites: 139 from males, 16 from females, and 16 from individuals of unknown sex. We captured birds using mist nets and call playback of male type I and type II songs during the period when most individuals are territorial, with the exception of Colombia where birds were likely captured during migration (Chandler 2011). At capture, we banded birds

with a U.S. Geological Survey aluminum leg band for individual identification. Before release, we pulled either the innermost primary of the wing (P1; $n = 92$) or a rectrix feather from the tail ($n = 61$) for subsequent stable-isotope analyses. Our sampling protocol assumes that both primaries and rectrices were grown at the same location, and preliminary mixed modeling treating individuals as repeated measures of $\delta^2\text{H}_f$ from 147 Golden-winged Warblers suggested no systematic differences in $\delta^2\text{H}_f$ between feather type grown at the same location.

Stable-Isotope Analysis

We cleaned feathers of surface oils using a 2:1 chloroform:methanol solvent rinse and then prepared them for $\delta^2\text{H}$ analysis at the Stable Isotope Laboratory of Environment Canada, Saskatoon, Canada. We determined the $\delta^2\text{H}$ value of the nonexchangeable hydrogen of feathers using the method described by Wassenaar and Hobson (2003) using two calibrated keratin hydrogen-isotope reference materials. We performed hydrogen isotopic measurements on H_2 gas derived from high-temperature (1350°C) flash pyrolysis of $350 \pm 10 \mu\text{g}$ feather (distal vane) subsamples in a Eurovector elemental analyzer (Milan, Italy) coupled with an VG Isoprime mass spectrometer (Manchester, UK) using continuous-flow isotope-ratio mass spectrometry. Measurements of the two keratin laboratory reference materials (CBS, KHS) corrected for linear instrumental drift were both accurate and precise with typical within-run mean $\delta^2\text{H} \pm \text{SD}$ values of $-197\text{‰} \pm 0.79\text{‰}$ ($n = 5$) and $-54.1\text{‰} \pm 0.33\text{‰}$ ($n = 5$), respectively. We report all results for nonexchangeable H expressed in the typical delta notation, in units per mil (‰), and normalized on the Vienna Standard Mean Ocean Water-Standard Light Antarctic Precipitation standard scale.

Data Analysis

We tested for spatial segregation of breeding populations on their nonbreeding grounds using general linear models in which we considered four *a priori* candidate models. Specifically, we used linear models to examine if birds from different breeding locations (as inferred from $\delta^2\text{H}_f$) segregated on the nonbreeding range. Our candidate models included an intercept-only model and models

including main effects for nonbreeding latitude and longitude. We used Akaike's Information Criterion with second-order bias correction (AICc) and model weights to select among competing models (Burnham and Anderson 2002). Data for linear modeling were limited to Central America where we had dense sampling and GPS-derived latitude and longitudes for all sample locations. We further examined support for parameters from our top models by examination of parameter estimates and their confidence intervals. If the 85% confidence intervals for a parameter from a model within the "top models" overlapped zero, we excluded these models from further inference as the parameters were considered noninformative (Anderson 2008, Arnold 2010).

Geographic Assignments to Origin

We depicted the putative breeding-ground origins of Golden-winged Warblers sampled at their nonbreeding locations in a probabilistic approach using a likelihood-based assignment technique (Hobson et al. 2009, Wunder 2010, Van Wilgenburg and Hobson 2011). The technique entailed the creation of a feather $\delta^2\text{H}$ isoscape using an amount-weighted precipitation-to-feather calibration algorithm ($\delta^2\text{H}_f = -45.7 + 0.74 * \delta^2\text{H}_p$) derived from work using 93 known (between-year recaptures) or presumed origin (from unbanded ASY) Golden-winged Warblers distributed across the breeding range (Figure 12.1). We used the regression parameters of our algorithm to convert $\delta^2\text{H}_p$ estimates provided by Bowen et al. (2005) into a $\delta^2\text{H}_f$ isoscape.

We estimated the likelihood that a cell (pixel) within the $\delta^2\text{H}_f$ isoscape (resolution of 0.33°) represented a potential origin for a sample by using a normal probability density function to estimate the likelihood function based on the observed $\delta^2\text{H}_f$ (Hobson et al. 2009, Wunder 2010, Van Wilgenburg and Hobson 2011). We depicted the likely origins of sampled Golden-winged Warblers by assigning individuals to the $\delta^2\text{H}_f$ isoscape one at a time. Following Hobson et al. (2009), we accomplished assignment by determining the odds that an assigned origin was correct relative to the odds that it was incorrect. We recoded the set of raster cells that defined the upper 67% of estimated "probabilities of origin" for each individual and coded those as 1, and all others as 0, resulting in one binary map

per assigned individual, which was consistent with 2:1 odds of being correct versus incorrect (Hobson et al. 2009, Van Wilgenburg et al. 2012). We then summed the results of individual assignments over all individuals by addition of the predicted surfaces (Hobson et al. 2009, Van Wilgenburg and Hobson 2011). We made geographic assignments to origin using functions within the R statistical computing environment (R Core Team 2012) using scripts employing the raster package (Hijmans and Van Etten 2012).

RESULTS

Golden-winged Warblers differed in their inferred breeding-ground origins depending on their capture location (Figure 12.2). Birds tended to be more enriched in ^2H the farther south they were captured on the nonbreeding grounds (Figure 12.2). However, for birds captured in Central America, our linear models suggested a more complex pattern of connectivity with the

top two models of variation in $\delta^2\text{H}_f$ receiving $\sim 98\%$ of the summed model weights (Table 12.1). The latitude-only model received $<2\%$ of model weight of the models in our candidate set (see w_i ; Table 12.1), and so we did not consider this model to be competitive. The second-most parsimonious model ($\Delta\text{AICc} = 1.94$) included parameters for both latitude and longitude (Table 12.1); however, the 85% confidence interval for the latitude parameter estimate overlapped zero ($\beta = -0.4$, 85% CI = -1.7 to 0.9‰), and thus was a noninformative parameter and we did not consider it further. As a result, we limited all inference to the top model, which only included a longitude covariate (Table 12.1). The parameter estimate for nonbreeding longitude from our top model ($\beta = -4.3$, 85% CI = -5.8 to -2.9‰) suggested that birds captured at our westernmost site within Central America (88.633°W) were $\sim 24.5\text{‰}$ more enriched in ^2H on average than birds from the easternmost site (85.333°W ; Figure 12.3).

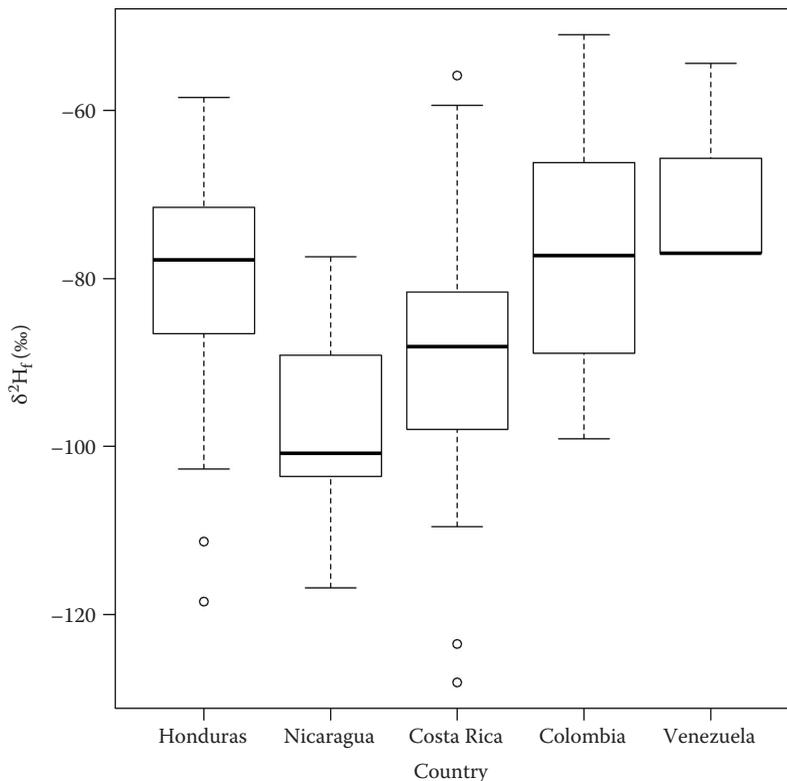


Figure 12.2. Variation in $\delta^2\text{H}_f$ within Golden-winged Warblers sampled in Honduras ($n = 68$), Nicaragua ($n = 19$), Costa Rica ($n = 65$), Colombia ($n = 16$), and Venezuela ($n = 3$) between 2003 and 2012. Dark solid line represents the median, the box indicates the interquartile range, whiskers are 1.5 times the interquartile range, and dots indicate extreme values.

TABLE 12.1

Selection among linear models exploring spatial (latitude and longitude) variation on the nonbreeding grounds in δ^2H_f from breeding-ground-grown feathers of Golden-winged Warblers captured in Costa Rica ($n = 65$), Honduras ($n = 68$), and Nicaragua ($n = 19$).

Model	K	$-2 \ln L$	$\Delta AICc$	w_i
Longitude	3	1214.02	0.00	0.71
Longitude + latitude	4	1213.84	1.94	0.27
Latitude	3	1221.04	7.03	0.02
Null	2	1231.72	15.62	0.00

K denotes the number of estimated parameters, $-2 \ln L$ denotes deviance (i.e., -2 times log-likelihood), $\Delta AICc$ denotes difference in Akaike's Information Criterion adjusted for sample size relative to the most parsimonious model, and w_i is the Akaike weight.

Golden-winged Warblers sampled in Honduras included individuals assigned locations from across the species' breeding distribution, but the majority of birds was consistent with the more southerly portions of their breeding distribution

(Figures 12.3 and 12.4). We assigned most Golden-winged Warblers sampled in Honduras to breeding-ground origins consistent with a region including Wisconsin through Michigan in the west and south along the Appalachian Mountains to the extreme southern edge of their breeding distribution. Consistent with the results of our linear modeling (Figure 12.3), the proportion of Golden-winged Warblers consistent with origins in the northern portion of the breeding distribution was greater in eastern Honduras than western Honduras (Figure 12.4a,b). Up to 70% of the birds captured in eastern Honduras (east of $87^\circ W$) were consistent with breeding origins south of $45^\circ N$ (Figure 12.4a). Between 3% and 40% of the birds sampled in eastern Honduras were consistent with regions north of $45^\circ N$ (Figure 12.4a). In contrast, up to 93% of the birds sampled in Honduras west of $87^\circ W$ were assigned to breeding origins south of $45^\circ N$. Only $\sim 6\%$ – 26% of the sample was isotopically consistent with areas north of $45^\circ N$, including the southern Manitoba

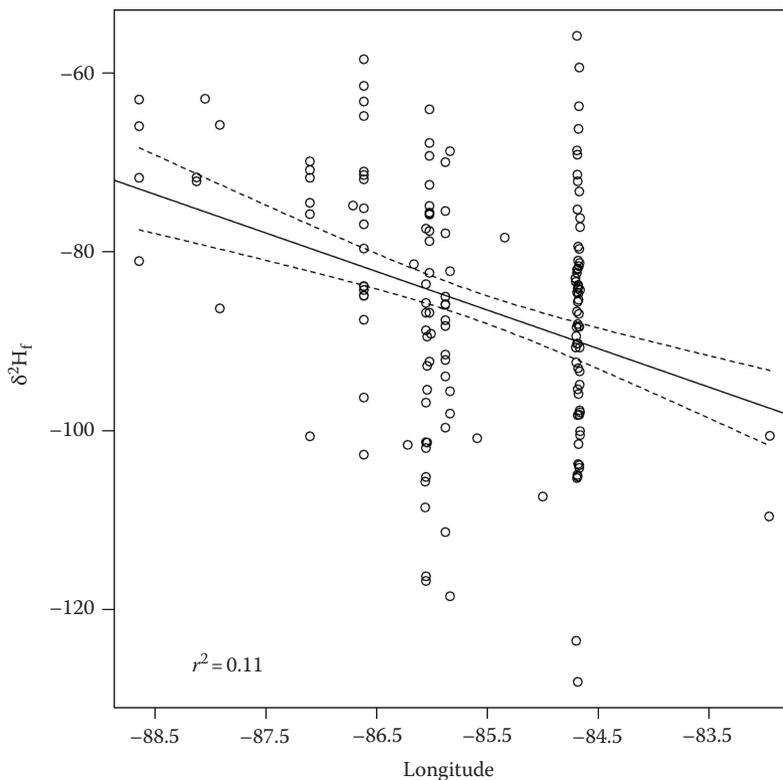


Figure 12.3. Relationship between δ^2H_f and longitude for Golden-winged Warblers sampled in Costa Rica ($n = 65$), Honduras ($n = 68$), and Nicaragua ($n = 19$). Solid line is least squares fit, with dashed lines representing 85% confidence intervals.

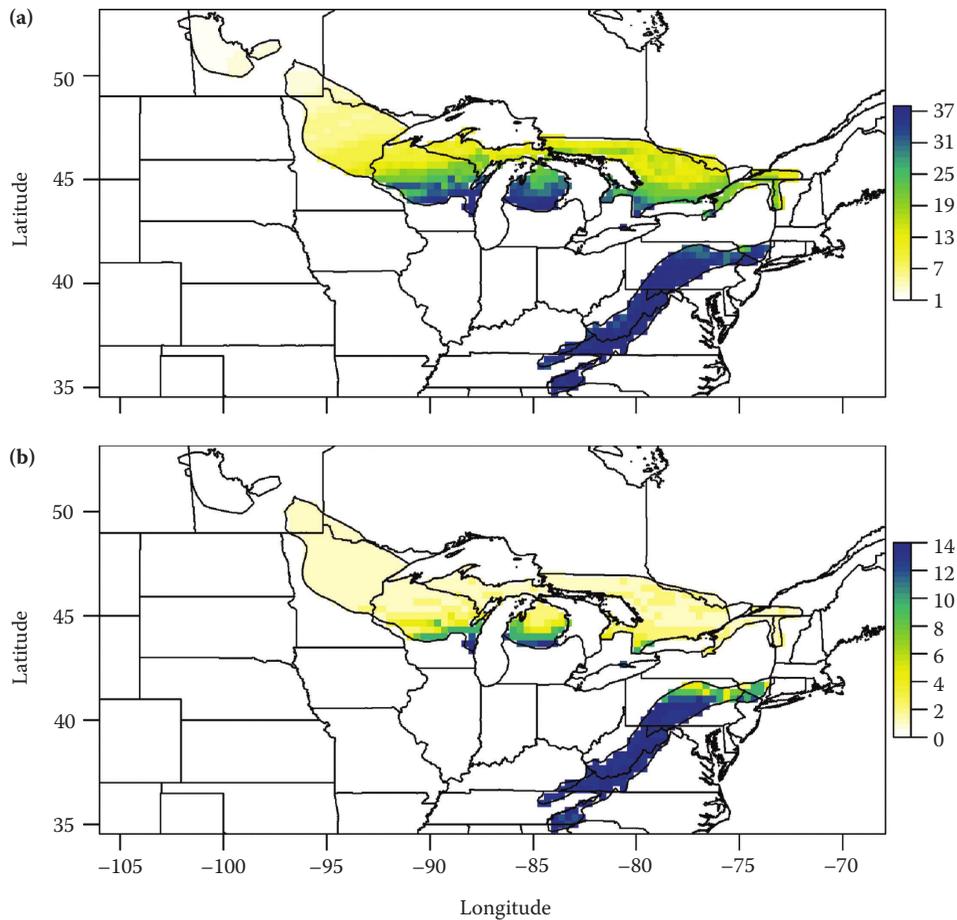


Figure 12.4. Geographic distribution of assigned origins for 68 Golden-winged Warblers sampled in (a) eastern Honduras (east of 87°W, $n = 53$) and (b) western Honduras (west of 87°W, $n = 15$) inferred from $\delta^2\text{H}_r$. Assignments were based on likelihood-based comparison of observed $\delta^2\text{H}_r$ against predicted $\delta^2\text{H}_r$ from a species-specific calibration of the isoscape of Bowen et al. (2005); see “Methods” section for details. Numbers on legend indicate the number of individuals in the sample that were isotopically consistent with similarly colored portions of the map at our selected (2:1) odds ratio.

breeding population, whereas none of the sample was consistent with the north-westernmost breeding population (Figure 12.4b).

In contrast to birds captured in Honduras (Figure 12.4), birds captured in Nicaragua and Costa Rica were assigned origins that were generally farther north (Figure 12.5a,b). Most of the Golden-winged Warblers sampled in Nicaragua were consistent with origins in a region from New York state through Ontario and the Great Lakes region and into Minnesota and southern Manitoba in the northwest (Figure 12.5a). High variation in feather isotope ratios ($\delta^2\text{H}_r$) among individuals captured in Costa Rica (Figure 12.2) implied origins from throughout the breeding distribution (Figure 12.5b); however, the majority of Costa

Rican samples were assigned to midlatitudes of the species breeding distribution, from Minnesota in the west to Cape Cod and Pennsylvania in the east (Figure 12.5b). Several individuals captured in Costa Rica were also consistent with origins in the Appalachian Mountains and the northwestern extreme of the species breeding distribution (Figure 12.5b).

Golden-winged Warblers captured in South America were largely consistent with origins in the southern extremes of the breeding distribution (Figure 12.5c,d). A majority of samples from Colombia derived from origins in the Appalachian Mountains or portions of the breeding distribution abutting the southern end of Lake Michigan, whereas ≤ 5 birds ($\leq 31\%$) were assigned to upper

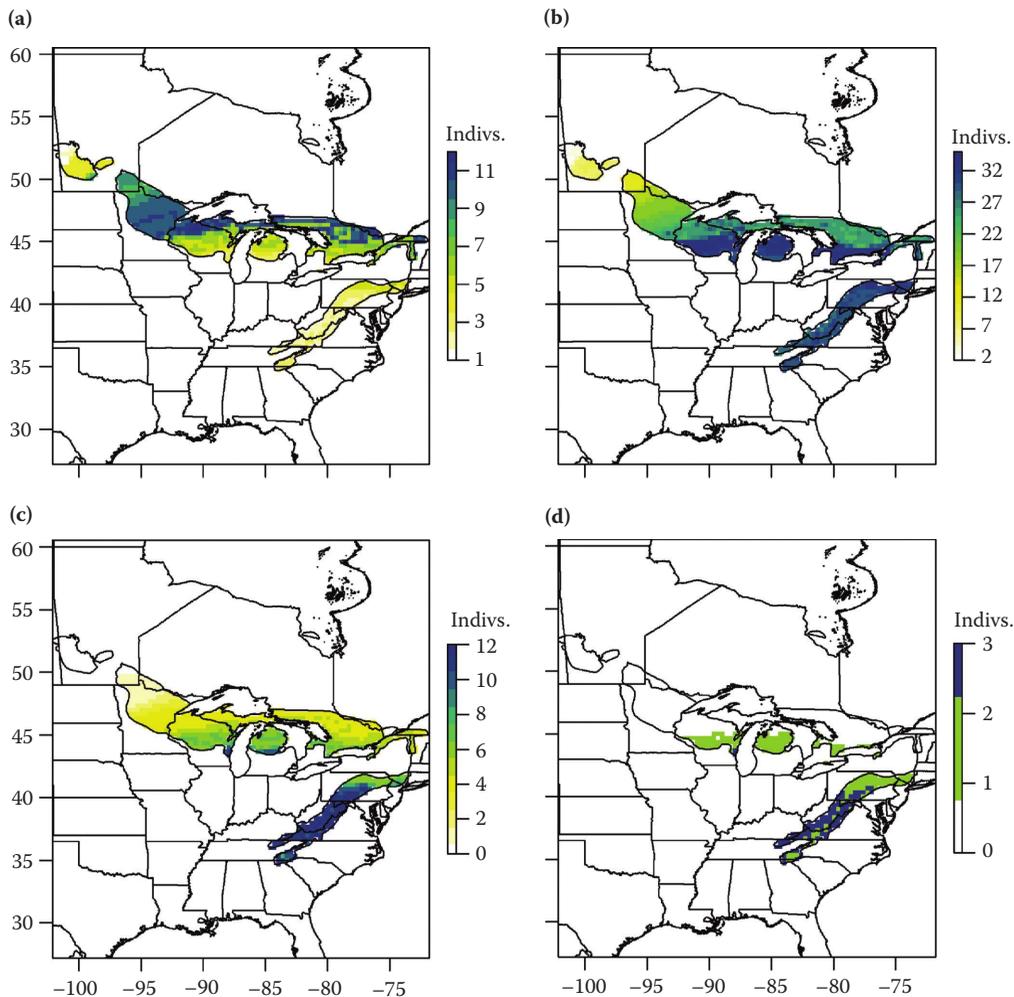


Figure 12.5. Geographic distribution of assigned origins for Golden-winged Warblers sampled in (a) Nicaragua ($n = 19$), (b) Costa Rica ($n = 65$), (c) Colombia ($n = 16$), and (d) Venezuela ($n = 3$) inferred from $\delta^2\text{H}_f$. Assignments were based on likelihood-based comparison of observed $\delta^2\text{H}_f$ against predicted $\delta^2\text{H}_f$ from a species-specific calibration of the isoscape of Bowen et al. (2005); see "Methods" section for details. Numbers on legend indicate the number of individuals in the sample that were isotopically consistent with similarly colored portions of the map at our selected (2:1) odds ratio.

New York State and regions north of the Great Lakes (Figure 12.5c). All three birds captured in Venezuela were consistent with the southernmost portion of the breeding distribution along the Appalachian Mountains; however, southern portions of the disjunct northern distribution could also represent potential origins for these individual birds (Figure 12.5d).

DISCUSSION

Despite modest sample sizes from some locations in Central America, our study provides

evidence for structure in the migratory connectivity between breeding sites in North America and nonbreeding sites in Central and South America for Golden-winged Warblers. Samples of birds from the southernmost portion of the nonbreeding distribution in Colombia and Venezuela were among the highest $\delta^2\text{H}_f$ values representing origins in the southernmost regions of the breeding distribution, whereas those from Central America were generally lower, suggesting more northerly origins. Within Central America, we further discovered that a greater proportion of birds in more easterly locations originated from more northerly

breeding locations compared to those in western Central America, which derived from more southern origins.

Although our results are not definitive, we suggest a potential migratory connectivity scenario operating in Golden-winged Warblers involving three migratory pathways. Some birds from southern breeding populations may cross the Caribbean Sea, make landfall in northern Central America, and fly overland to Honduras. Samples collected in Venezuela and Colombia were associated with the most southern breeding origins consistent with the southern Appalachian Mountains. The most parsimonious migratory routes for birds migrating to South America would appear to be via trans-Gulf of Mexico migration or following a trans-Caribbean Sea path through the eastern Caribbean Islands to arrive on nonbreeding areas via eastern Venezuela. Fall migration records from eBird (2012) include sparse observations along the Caribbean Island chain, which provide partial support for the eastern Caribbean as a potential migratory route to South America. In contrast, birds from more northern and northwestern breeding areas may migrate across the Gulf of Mexico and settle directly in eastern Honduras, Nicaragua, and Costa Rica. As eBird migration records for Golden-winged Warbler are sparse in Mexico north of Veracruz, we predict that circum-Gulf of Mexico migration is relatively rare in Golden-winged Warblers.

The putative migratory structure we have described largely corresponds to breeding latitude, which also corresponds to populations experiencing differential population trends because southern breeding populations are known to be experiencing the steepest rates of decline (Buehler et al. 2007). In addition to the loss of breeding habitat in the Appalachian Mountains, the compounding stresses of long migration and scarcity of fueling sites could negatively affect populations of birds from more southerly breeding origins that migrate to Colombia and Venezuela. Bayly et al. (2012, 2013) have convincingly shown the importance of migratory refueling sites in forested remnants of coastal Colombia for trans-Caribbean Sea migrants, and these habitats are declining in extent due to ongoing deforestation. Possibly, southern-breeding Golden-winged Warblers have declined most precipitously due to factors operating at both ends of the migratory route.

Our study has demonstrated the strength of using $\delta^2\text{H}_f$ analyses coupled with a detailed species-specific $\delta^2\text{H}_f$ breeding-ground isoscape for describing the origins of Neotropical migrants captured at sites used during the boreal winter. Stable isotopes have clear advantages over conventional mark-recapture techniques that have generally failed to describe migratory connectivity for migratory songbirds. Our results should also guide future research on Golden-winged Warblers at sites used during both the breeding and nonbreeding seasons. For example, renewed sampling efforts in Venezuela and Colombia would improve estimates of the proportion of those populations that migrate there from the southeastern portion of their breeding distribution. Further isotopic sampling in Central America may improve understanding of how different populations settle along a latitudinal gradient. For example, the northern edges of the nonbreeding distribution in Guatemala and Belize have yet to be sampled.

Linking regional population trends on the breeding grounds with differential migratory routes or ultimate nonbreeding destinations is an important goal for the conservation of Golden-winged Warblers. Rubenstein et al. (2002) used stable-isotope methods to show that declining, southern breeding populations of Black-throated Blue Warblers (*Setophaga caerulescens*) spent the nonbreeding season in the eastern Antilles, unlike more stable northern breeding populations. That result provided evidence that habitat loss on the nonbreeding grounds may be an important driver of regional differences in breeding population trends. Similarly, and again using stable-isotope approaches, strong migratory connectivity has been demonstrated for Wilson's Warblers (*Cardellina pusilla*; Kelly et al. 2002) and American Redstarts (*Setophaga ruticilla*; Norris et al. 2006), which may allow population-specific conservation. As geolocators become small enough to be used on Golden-winged Warblers without adversely affecting their migratory behavior, we suggest that these tags be deployed to test the hypotheses we have generated here based on stable-isotope data. Last, with more sampling across sites used during the nonbreeding period, it may be possible to identify those regions of the breeding distribution contributing most to the recruitment of young birds (Hobson et al. 2009).

ACKNOWLEDGMENTS

We are extremely grateful to M. I. Moreno, A. Paez, G. Suarez, and J. Sanabria for collecting samples on the wintering grounds. We thank U.S. Forest Service International Programs and The Nature Conservancy for financial support and Universidad Nacional de Colombia for collaboration. We are also grateful to the following individuals who contributed breeding ground samples for isoscape calibration: K. Aldinger, J. Chernek, J. Confer, D. Flaspohler, M. Fowlds, M.-F. Julien, J. Larkin, K. Percy, C. Smalling, H. Streby, and R. Vallender. We are thankful for assistance supplied by the Honduran Ornithological Association, Mancomunidad MAPANCE, J. Wilson, T. Daulton, D. King, J. Guevara, F. Elizondo Camacho, A. el Socorro, The Nature Conservancy, Universidad Nacional de Colombia, CORANTIOQUIA, and the San Vito Bird Club for their assistance. B. M. Alvarez, M. Allen, A. Crosby, and C. Gryba prepared feathers for stable-isotope analysis. Funding was provided by grants from the U.S. Fish and Wildlife Service Region 3, the Inter-Departmental Recovery Fund, the MTU Ecosystem Science Center, U.S. Forest Service International Programs, Neotropical Migratory Bird Conservation Act, the National Science Foundation, and an operating grant to KAH from Environment Canada.

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