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Assessing migratory connectivity for a long-distance migratory bird using multiple intrinsic markers

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Abstract. Patterns of migratory connectivity are a vital yet poorly understood component of the ecology and evolution of migratory birds. Our ability to accurately characterize patterns of migratory connectivity is often limited by the spatial resolution of the data, but recent advances in probabilistic assignment approaches have begun pairing stable isotopes with other sources of data (e.g., genetic and mark–recapture) to improve the accuracy and precision of inferences based on a single marker. Here, we combine stable isotopes and geographic variation in morphology (wing length) to probabilistically assign Wood Thrush (*Hylocichla mustilena*) captured on the wintering grounds to breeding locations. In addition, we use known-origin samples to validate our model and assess potentially important impacts of isotopic and morphological covariates (age, sex, and breeding location). Our results show that despite relatively high levels of mixing across their breeding and nonbreeding ranges, moderate levels of migratory connectivity exist along an east–west gradient. In addition, combining stable isotopes with geographic variation in wing length improved the precision of breeding assignments by 10% and 37% compared to assignments based on isotopes alone or wing length alone, respectively. These results demonstrate that geographical variation in morphological traits can greatly improve estimates of migratory connectivity when combined with other intrinsic markers (e.g., stable isotopes or genetic data). The wealth of morphological data available from museum specimens across the world represents a tremendously valuable, but largely untapped, resource that is widely applicable for quantifying patterns of migratory connectivity.

Key words: deuterium; geographical variation; hydrogen isoscapes; Hylocichla mustilena; *intrinsic markers; migratory connectivity; morphology; probabilistic assignment; stable isotopes; Wood Thrush.*

INTRODUCTION

Quantifying the migratory connectivity of animal populations is essential for understanding the evolutionary processes that shape life history and the ecological processes that affect population dynamics (Webster et al. 2002), as well as for interpreting population trends (Runge and Marra 2005, Dunn et al. 2006) and determining the principal threats driving regional population trends (Hobson 2005, Faaborg et al. 2010, Marra et al. 2011). This is in large part because events in the avian annual cycle are often inextricably linked, such that events in one season can "carry over" to subsequent seasons, having profound impacts on population dynamics (Marra et al. 1998). Despite the long-standing interest in movement ecology, establishing the linkages between populations of migratory species has remained challenging because these species generally occupy a variety of disparate locations and move across jurisdictional boundaries throughout their annual cycle (Rubenstein and Hobson 2004, Webster and Marra 2005, Faaborg et al. 2010).

To track the migratory movements of birds, scientists have utilized both extrinsic (e.g., mark–recapture, VHF and satellite telemetry, light-level archival geolocators; Combreau et al. 2011, Ryder et al. 2011) and intrinsic approaches (e.g., morphology, genetics, and stable isotopes; Rubenstein and Hobson 2004). Extrinsic approaches such as mark–recapture are often limited by low recapture rates (Webster et al. 2002), whereas direct-tracking technologies can be costly (e.g., satellite telemetry) and suffer from low resolution (e.g., geolocators). Genetic markers suffer from low resolution because many migratory species show little genetic structure across their breeding or nonbreeding ranges (Colbeck et al. 2008, Irwin et al. 2011), although these markers have proven useful when such structure exists (Chabot et al. 2012, Rundel et al. 2013). Stable isotopes, however, are a valuable tool for understanding migratory patterns because, despite low resolution, they are

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relatively inexpensive, large numbers of samples can be obtained, and the abundance of certain stable isotopes varies predictably over large geographic areas (Hobson 2005, Hobson and Wassenaar 2008, Inger and Bearhop 2008).

In particular, stable hydrogen isotopes have emerged as a key tool for estimating migratory connectivity in many bird species. The composition of stable hydrogen isotopes in rainfall varies with latitude and altitude across North America (Bowen et al. 2005), and this stable isotopic signature is incorporated into the tissues grown at a given location (e.g., feathers and claws; Hobson and Wassenaar 1997). Because most migratory songbirds molt their feathers on their breeding grounds prior to fall migration (Pyle 1997), and because feathers are metabolically inert after growth (Hobson and Wassenaar 1997), stable hydrogen isotope signatures in feathers (δ^2H_f) can be compared with known isoscapes to determine the geographic origin of birds sampled away from their breeding sites (Hobson et al. 2012). The ability to use these feather isoscapes to make probabilistic assignments to their region of origin has been one of the largest advances for quantifying the migratory connectivity of both Nearctic–Neotropical migrants (Hobson et al. 2004, Norris et al. 2006, Sarasola et al. 2008) and Palearctic–Afrotropical migrants (Pain et al. 2004, Szép et al. 2009). Despite these advances, a number of limitations and challenges associated with using stable isotopes to make geographic assignments still exist (Van Wilgenburg and Hobson 2011).

The main limitation of using hydrogen isotopes to make probabilistic assignments and assess migratory connectivity is the limited resolution of inference. First, the continental isoscape for hydrogen isotopes provides broad latitudinal clines, but has much poorer longitudinal resolution (Bowen et al. 2005), often resulting in broad geographic assignments of origin (Wunder et al. 2005). Moreover, the precipitation-based hydrological models used to estimate hydrogen isoscapes are based on long-term averages and may fail to reflect interannual variation (Hobson et al. 2012). Second, interindividual variation due to age can reduce the resolution of assignments and decrease the probability of correct assignments (Langin et al. 2007, Haché et al. 2012). Finally, given that a number of ecophysiological factors may influence the isotopic discrimination linking rainfall and tissue, researchers may require species-specific tissue base maps and assignment algorithms (Hobson 2011, Hobson et al. 2012, Hallworth et al. 2013).

Given the challenges of using stable isotopes to quantify migratory connectivity, researchers continue to seek approaches that will improve accuracy and precision of the geographic assignments based on hydrogen isotopes. One recent advance has been the development of assignment algorithms that can probabilistically determine the origin of individuals across a continuous surface (Van Wilgenburg and Hobson 2011). Unlike earlier methods that assigned individuals to large, predefined regions (Royle and Rubenstein 2004, Boulet et al. 2006, Norris et al. 2006), the use of a continuous surface provides a more accurate assessment of potential breeding origins. Furthermore, this approach allows researchers to easily estimate the uncertainty associated with assignments by quantifying the size of the geographic area identified as potential origin (Chabot et al. 2012). The ability to quantify uncertainty is an important advance because imprecise assignments are of little use for assessing migratory connectivity even if accuracy is high (Martin et al. 2007).

A second recent development toward improving assignments and establishing linkages between breeding and wintering populations involves combining stable isotopes with other sources of data. At present, most assignments based on multiple data sources have combined multiple stable isotopes (Royle and Rubenstein 2004, Hobson et al. 2009) or stable isotope data with genetic data (Clegg et al. 2003, Kelly et al. 2005, Boulet et al. 2006, Chabot et al. 2012, Rundel et al. 2013), banding data (Van Wilgenburg and Hobson 2011), or regional abundance (Royle and Rubenstein 2004, Norris et al. 2006). Combining multiple sources of data has been shown to improve both the accuracy (Royle and Rubenstein 2004, Kelly et al. 2005, Rundel et al. 2013) and precision (Van Wilgenburg and Hobson 2011, Chabot et al. 2012) of assignments, but each of these data sources has inherent limitations and not all sources are equally useful for all species. As a result, there is a continued need to identify and combine novel data sources that can help to characterize species-specific geographical variation.

One source of geographic variation that has not been combined with stable isotopes or widely used in migratory connectivity studies is morphological traits that show predictable geographical variation (Gómez-Díaz and González-Solís 2007). Many species of migratory birds show geographic variation in morphology, including body size (Conklin et al. 2011), wing length (Saracco et al. 2009), bill size (Greenberg et al. 2012), and plumage characteristics (Lehtonen et al. 2009, Paxton et al. 2010). These morphological traits represent a potentially valuable source of data for studying migratory connectivity in many species (Paxton et al. 2010), but to date there have been no attempts to combine morphological traits with other data sources to probabilistically assign individuals to breeding locations.

Here, we combine stable isotope and morphological data to probabilistically assign Wood Thrush (*Hylocichla mustilena*) captured on the wintering grounds to breeding locations. In addition, we use data from breeding Wood Thrush to validate the accuracy and precision of our model and to assess how factors such as age, sex, and breeding origin influence our assignments. Finally, we use these probabilistic assignments to assess the degree of migratory connectivity between breeding and wintering populations. Wood Thrush represent an ideal species to assess these methods because their breeding range spans a large stable isotopic gradient and wing length in this species is positively correlated with latitude (Fig. 1). In addition, Wood Thrush populations in North America have declined by >50% since the 1960s (Evans et al. 2011). Given the extent of this decline, the Wood Thrush is listed as a "Species of Conservation Concern" (U.S. Fish and Wildlife Service 2008), a "priority species" for 30 U.S. states, and is considered threatened by the Committee on Endangered Species of Canada. Accurate estimates of migratory connectivity are critical to identifying the principle threats driving regional population trends and developing effective strategies and partnerships to mitigate these threats (Marra et al. 2011).

METHODS

Data collection

Wood Thrushes were captured during the nonbreeding season (November–March) at six banding stations that were operated as part of the Monitoreo de Sobrevivencia Invernal (MoSI) program between 1999 and 2008 (DeSante et al. 2005). Study areas included Los Tuxtlas in southern Veracruz, Mexico (RBTT); Cerro San Gil (CSGI) in eastern (Izabal) Guatemala; Reserva Privada El Jaguar (JAGU), Reserva Nacional Volcán Mombacho (MOMB), and Esperanza Verde (GUAT) in Nicaragua, and at Centro Agronómico Tropical de Investigación y Enseñanza (CATI) in Costa Rica. Individuals were banded with USGS aluminum bands and aged (second-year, SY; vs. after-second-year, ASY) using plumage criteria and rectrix shape following Pyle (1997). For each individual, we collected morphological data (unflattened wing chord) and sampled feathers (e.g., two outer rectrices, one from each side). These feathers were stored in the Neotropical Migratory Bird Conservation Genetics Project of the University of California, Los Angeles, California, USA (T. B. Smith). Stable isotope analysis of all feather samples was performed at the Smithsonian Stable Isotope Mass Spectrometry Laboratory in Suitland, Maryland, USA (Appendix A).

To assess the degree of migratory connectivity between breeding and nonbreeding populations, we grouped individuals into three broad regions corresponding roughly to the northern, central, and southern portions of the nonbreeding range (Fig. 2). Because sample sizes from several MoSI stations were small (Table 1), these groupings were necessary to detect significant differences from random mixing of breeding populations.

Assignment models

To assign individuals to potential breeding locations, we first created base maps describing the variation in hydrogen isotope abundance in feathers (δ^2H_f) and wing chord (W) across the Wood Thrush breeding range. Given that second-year (SY) Wood Thrush have significantly shorter wings than adults (ASY; $F_{1,\,10079} = 455.50$, $P < 0.001$), we produced separate wing chord base maps for SY and ASY individuals. To estimate the hydrogen isoscape (Appendix C: Fig. C1), we converted a map of expected amount-weighted growing-season precipitation δ^2H values (δ^2H_p; Bowen et al. 2005) to expected feather δ^2H values (δ^2H_f) using the following correction factor: $\delta^2H_f = -175.57 + 0.95\ \delta^2H_p$, which was estimated from a large sample of ground foraging Neotropical migratory songbirds (Hobson et al. 2012). In their analysis, Hobson et al. (2012) found no support for age-based differences in hydrogen isotope discrimination and therefore we did not apply any age-specific correction to the δ^2H values.

To interpolate age-specific spatial variation in Wood Thrush wing morphology, we used unflattened wing chord measurements from 2271 individuals sampled at 64 bird-banding stations operated during the breeding season (May–August) as part of the Monitoring Avian Productivity and Survivorship (MAPS) program between 2002 and 2011 (DeSante and Kaschube 2009; Fig. 1A). We used ordinary kriging with a stable semivariogram model (Nugget = 2.92, Sill = 1.55, Lag = 0.88) to create an interpolated map of range-wide variation in wing chord (Fig. 1A). Specifically, we used mean wing chord values from MAPS sampling locations to predict wing chord across the entire breeding range. We then extracted predicated wing chord values to a 30 × 30 km grid equivalent to that which had been used for stable isotope analyses. Although wing chord varies by sex, we chose not to create sex-specific maps because we did not have information about the sex of nonbreeding birds. While including sex-specific wing chord variation in the model would improve the accuracy and precision of our assignments, assignment rates of known-origin birds were high without this information (see *Validation results*), suggesting that our methods were adequate for estimating the breeding origin of both male and female Wood Thrush. All spatial analyses were done using geostatistical analyst in ArcMap version 10.1 (ESRI 2012).

Assignments of nonbreeding individuals

We first assigned nonbreeding birds to potential breeding locations using isotope values and wing chord separately. To do this, we calculated the likelihood that each raster cell represented the breeding location for each individual using a normal probability density function:

$$f(y* \mid \mu_i, \sigma) = \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{(y* - \mu_i)^2}{2\sigma^2}}$$

where $f(y* \mid \mu_i,\sigma)$ is the likelihood that an individual with δ^2H_f or $W = y*$ originated from cell i; μ_i is the predicted δ^2H_f or W value for cell i; and σ is the standard deviation of δ^2H_f or W values within a single

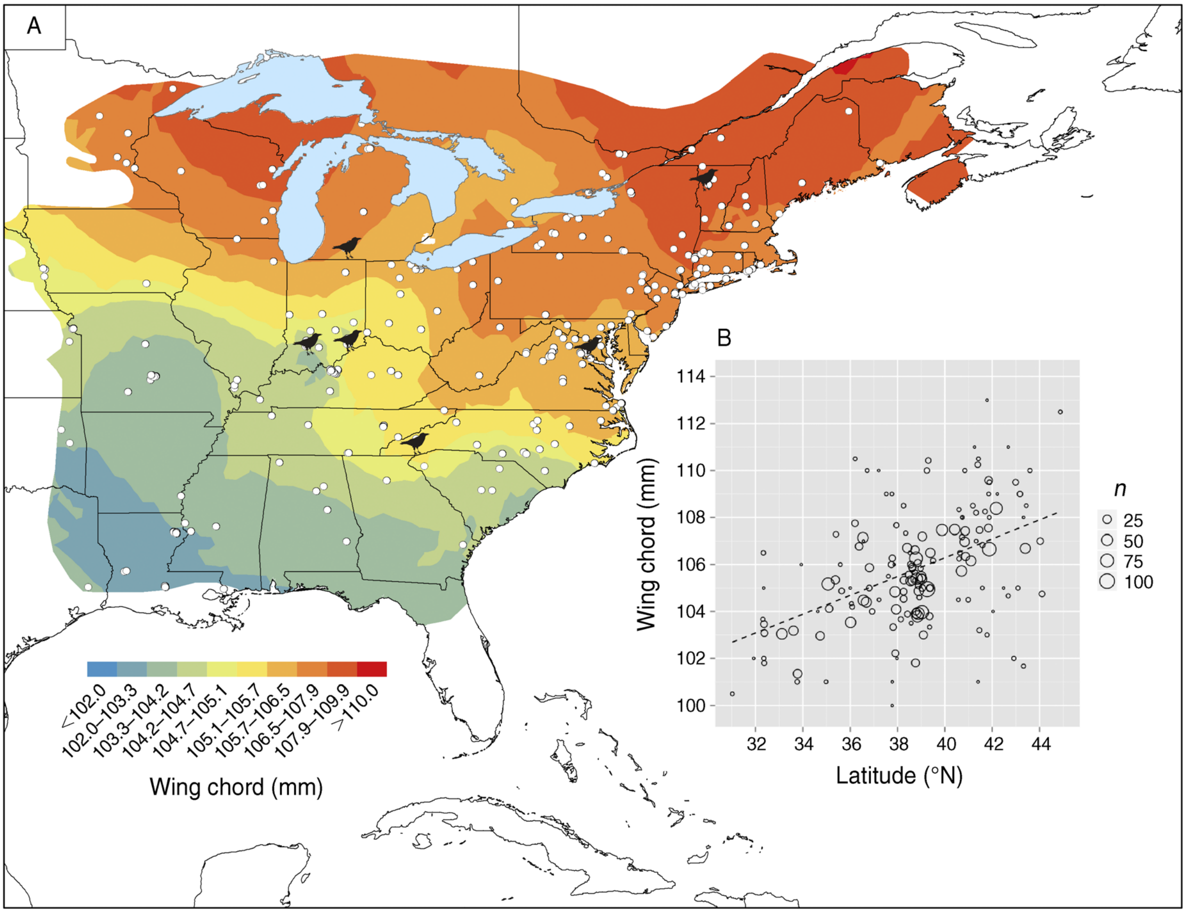

FIG. 1. Sampling locations of feathers (bird icons) and morphological data (white dots) used in validation and to probabilistically assign Wood Thrush (*Hylocichla mustelina*) sampled in nonbreeding areas to their breeding origin. (A) Ordinary kriging shows the spatial pattern of latitudinal variation in Wood Thrush morphology. (B) Wood Thrush wing chord length shows a linear increase with latitude (wing = 90.54 + 0.39 × latitude; $F_{1,4867} = 376.29$, $P < 0.001$, $r^2 = 0.07$). The key indicates that point size is proportional to the number of individuals sampled for morphological data.

breeding site. Wing chord standard deviation was calculated using data collected at the MAPS stations located across the breeding range and was estimated to be 3.3 mm. We estimated the δ^2H_f standard deviation from published values of within-site δ^2H_f variation in Wood Thrush; this SD was assumed to be 10‰ (Powell and Hobson 2006).

Next, we assigned individuals using both stable isotope values and wing chord by estimating the likelihood that each raster cell represented the breeding location of each nonbreeding individual, using a bivariate normal probability function as follows:

$$f(x*, y* \mid \mu_i, \Sigma)$$

$$= \frac{1}{2\pi\sigma_x\sigma_y\sqrt{1-\rho^2}} \exp\left(-\frac{1}{2(1-\rho^2)}\left[\frac{(x* - \mu_x)^2}{\sigma_x^2} + \frac{(y* - \mu_y)^2}{\sigma_y^2} - \frac{2\rho(x-\mu_x)(y-\mu_y)}{\sigma_x\sigma_y}\right]\right)$$

where $f(x^*, y^* \mid \mu_i, \Sigma)$ is the likelihood that an individual with $\delta^2H_f = x^*$ and $W = y^*$ originated from cell i; $\mu_i = \begin{pmatrix}\mu_x \\ \mu_y\end{pmatrix}$ is the mean δ^2H_f and W of cell i; ρ is the correlation between δ^2H_f and W; and

$$\Sigma = \begin{bmatrix} \sigma_x^2 & \rho\sigma_x\sigma_y \\ \rho\sigma_x\sigma_y & \sigma_y^2 \end{bmatrix}$$

is the variance covariance matrix for δ^2H and W, which was estimated from the predicted δ^2H and W values for each cell across the entire breeding range. All analyses were performed in the R statistical computing environment (R Development Core Team 2008) using the "mnormt" package (Azzalini 2012).

Mapping "likely" breeding origins

For each nonbreeding individual, the likelihoods calculated for the three assignment models (wing chord, isotope, and wing chord + isotope) were rescaled to highest likelihood for that assignment, resulting in

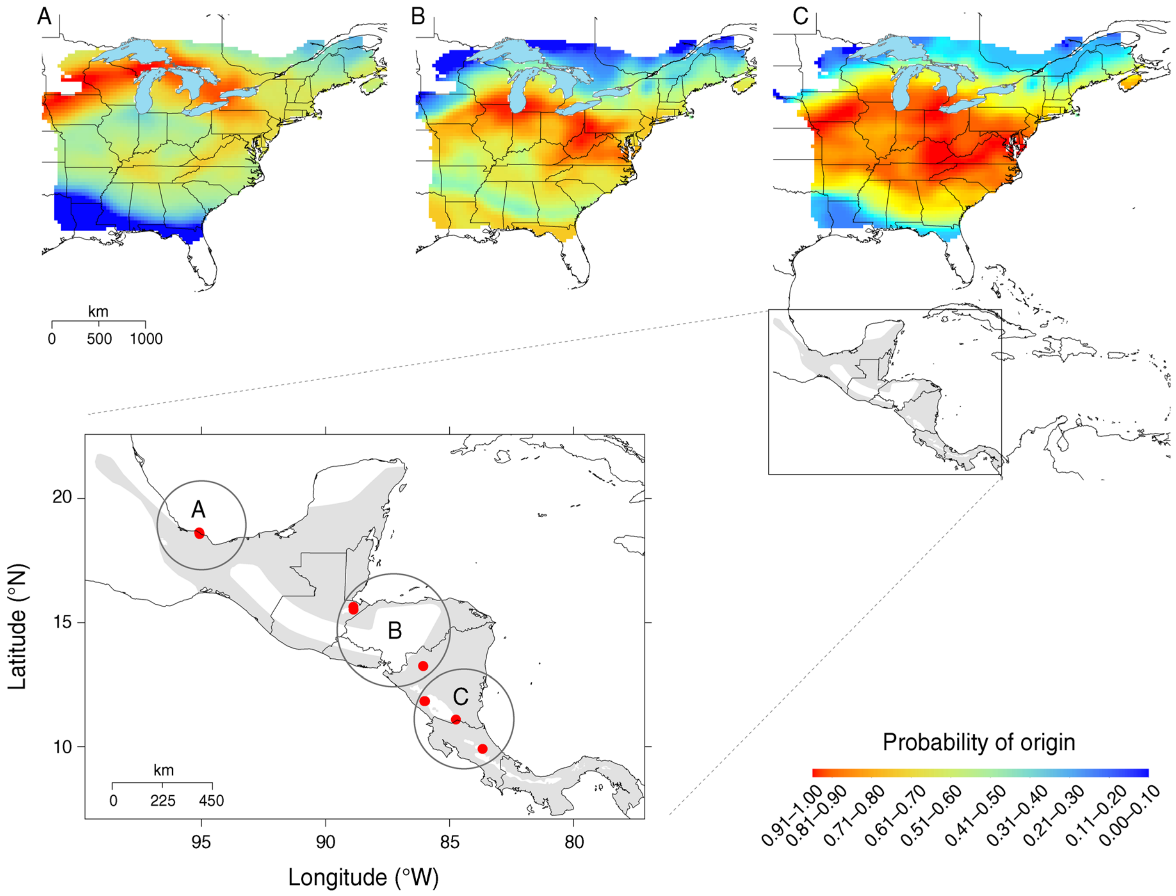

Fig. 2. The predicted probability of Wood Thrush origin using data from stable isotopes and geographic variation in wing morphology for birds sampled in the (A) northern, (B) central, and (C) southern portions of the nonbreeding range (gray shaded area in the inset). Red circles in the nonbreeding range map mark the MoSI (Monitoreo de Sobrevivencia Invernal) stations where feather samples and wing chord measurements were collected for nonbreeding Wood Thrush, i.e., the stations in Table 1.

relative likelihoods that ranged from 0 to 1. We then converted the relative likelihoods to "likely" or "unlikely" breeding locations by assigning cells containing the upper 75% of relative likelihoods a value of "1" and all other cells a value of "0" (Van Wilgenburg and Hobson 2011). This resulted in a binary map for each individual showing the most likely breeding origins based on each assignment model. More stringent thresholds (90%) would result in more cells being identified as likely, resulting in higher accuracy but lower precision, whereas less stringent thresholds (67%) have the opposite effects. We chose to use a 75% threshold to balance this trade-off, but present results using a 67% threshold for comparison.

We then produced overall "connectivity" maps for each nonbreeding region by overlaying the assignment maps of all individuals from that region and summing the number of individuals predicted to have originated within each cell using a raster calculator in ArcMap version 10. To quantify migratory connectivity between breeding and nonbreeding regions, we divided the breeding region into four quadrants (northeast, northwest, southeast, southwest; Appendix C: Fig. C1). For each individual, we calculated the mean likelihood of all raster cells within each quadrant and assigned individuals to the quadrant with the highest mean likelihood. For each nonbreeding region, we then summed these assignments to determine the percentage of individuals assigned to each breeding quadrant. We further used these assignments to test for latitudinal or longitudinal trends in patterns of migration. To test for latitudinal patterns (e.g., chain vs. leap-frog migration), we classified individuals assigned to the northeast and northwest quadrants as "northern" and individuals assigned to the southeast and southwest quadrants as "southern." To test for longitudinal patterns (e.g., migratory divide), we combined the northeast and southeast quadrants and the northwest and northeast quadrants to create "eastern" and "western" regions.

Given the null expectation of complete mixing of breeding populations on the nonbreeding grounds (i.e., no connectivity), the percentage of individuals assigned to each breeding quadrant should be equal to relative breeding abundance of each quadrant (Royle and Rubenstein 2004). Significant differences from this null expectation indicate regions that exhibit stronger connectivity than expected under complete mixing. To estimate the null expectation for our assignments, we used data from the North American Breeding Bird Survey (BBS; Robbins et al. 1986) to estimate the relative abundance of Wood Thrush breeding in each quadrant. Specifically, we used the mean count for each BBS route to compute relative numbers of Wood Thrush counted in each quadrant. Although BBS data suffer from several limitations (Sauer and Link 2011), Wood Thrush are easily detected during the breeding season and BBS surveys cover the entire breeding range. As a result, these data should provide a reasonable estimate of the expected percentages for our breeding quadrants.

Model validation

To assess the accuracy of our assignment models, we conducted a separate analysis using wing chord and isotope data collected from breeding Wood Thrush. Individuals were captured between 2009 and 2011 as part of separate projects at six locations that span the breeding range (bird symbols in Fig. 1A) and represent a mixture of age and sex classes (Table 2). To ensure that individuals were breeding at the location where they were sampled, we only included individuals captured between 1 June and 31 July. We assigned each individual using the models previously described, and individuals were assigned correctly if the raster cell containing the actual breeding location was identified as a likely origin. We estimated the uncertainty of each assignment as the total number of raster cells that were scored as likely breeding locations.

RESULTS

The assignments of nonbreeding individuals to potential breeding locations using stable isotopes and morphology suggest that Wood Thrush exhibit moderate connectivity across their breeding and nonbreeding ranges (Table 3, Fig. 2). Only region A, the westernmost nonbreeding region, had breeding assignments that differed from the null expectation of complete mixing ($\chi^2 = 58.52$, df = 3, $P < 0.001$), indicating that this region had significantly more birds assigned to the northwest quadrant than expected, based on the relative breeding abundance in the northwest. In contrast, the percentage of assignments to each quadrant did not differ from complete mixing in region B ($\chi^2 = 3.67$, df = 3, $P = 0.29$) or in region C ($\chi^2 = 1.16$, df = 3, $P = 0.76$).

When quadrants were paired (i.e., north vs. south and east vs. west), the assignments suggest that Wood Thrush exhibit a weak migratory divide, with western breeding populations more likely to winter in western nonbreeding sites and eastern breeding populations more likely to winter in eastern nonbreeding sites (Table 3). Region A contained more western individuals than expected based on complete mixing ($\chi^2 = 4.34$, df = 1, $P = 0.04$), whereas region B, the most central nonbreeding region, contained nearly equal numbers of eastern and western individuals ($\chi^2 = 0.88$, df = 1, $P = 0.35$). Region C did contain more birds from the eastern half of the breeding range (Table 3), although the proportion of eastern and western individuals did not differ from complete mixing ($\chi^2 = 0.072$, df = 1, $P = 0.79$).

No clear latitudinal migration pattern (e.g., leap-frog vs. chain) emerged from our assignments. Region A did contain more northern individuals than expected based on complete mixing ($\chi^2 = 12.38$, df = 1, $P = 0.004$), but region B ($\chi^2 = 0.13$, df = 1, $P = 0.72$) and region C ($\chi^2 = 1.066$, df = 1, $P = 0.31$) did not. Taken together, our assignments suggest that there is a generally high level of mixing of breeding populations on the nonbreeding grounds, particularly for eastern and southern breeding populations. However, western populations, particularly individuals from the northwestern portion of the breeding range, do appear to show some degree of connectivity during the nonbreeding season.

Validation results

Overall, the assignment rate for the wing chord model (97.5%; Table 4) was significantly higher than the rate of the hydrogen model (80.1%; $\chi^2 = 17.3$, df = 1, $P < 0.01$)

TABLE 1. Summary of nonbreeding sampling regions for Wood Thrush (*Hylocichla mustelina*), with station codes, geographic coordinates, and the number of ASY and SY individuals.

Region	Station	Latitude (°N)	Longitude (°W)	Sample size		
				ASY	SY	Total
A	RBTT	18.58694	95.07722	15	3	18
B	CSGI	15.63889	88.86944	9	3	12
B	JAGU	13.23250	86.05250	5	2	7
C	MOMB	11.83222	86.00833	5	0	5
C	GUAT	11.08639	84.73611	4	3	7
C	CATI	9.89865	83.86944	2	3	5

Notes: Regions and stations are shown in Fig. 2; ASY and SY are after-second-year and second-year birds.

Table 2. Summary of validation sampling locations for Wood Thrush, with geographic coordinates and the number of ASY and SY individuals of each sex captured at each Monitoring Avian Productivity and Survival (MAPS) station used to validate our assignment models.

State	Latitude (°N)	Longitude (°W)	ASY Male	ASY Female	SY Male	SY Female	Total
North Carolina	35.41114	83.12166	15	3	13	1	32
Virginia	38.70961	77.146699	13	2	11	1	27
Indiana	38.83829	86.82134	24	3	0	1	28
Michigan	42.15833	85.47387	3	3	0	0	6
Vermont	44.50697	73.15053	8	0	19	0	27

and the joint model (74.1%; $\chi^2 = 26.8$, df = 1, $P < 0.01$). The assignment rates did not differ between the hydrogen and joint models ($\chi^2 = 1.53$, df = 1, $P = 0.22$). Assignment rates using the joint model did not differ between age classes ($\chi^2 = 0.42$, df = 1, $P = 0.52$) or between males and females ($\chi^2 = 0.06$, df = 1, $P = 0.94$; Table 5). As expected, the assignment rates were lower when a 67% threshold was used to identify likely breeding locations (Appendix B: Table B1)

The differences in assignment rates were driven mainly by the low assignment rate of North Carolina samples using the hydrogen and joint models (Table 4). The North Carolina site is located within a mountainous area in the western part of the state (Fig. 1), and the high elevations result in predicted hydrogen values that are more depleted than at low-elevation sites at the same latitude (Appendix C: Fig. C1). However, Wood Thrush generally breed only at low elevations (Evans et al. 2011), resulting in hydrogen values that are enriched relative to the predicted values. Thus, many North Carolina individuals were assigned to more southerly locations, even when wing chord was included in the assignments. When the North Carolina samples were excluded, the assignment rates did not differ between the models ($\chi^2 = 1.1$, df = 1, $P = 0.58$).

Although wing chord data alone produced an accurate assignment model, combining the two markers substantially reduced the uncertainty of assignments and increased model precision (mean ± SD number of cells identified as likely: hydrogen only = 2071 ± 586 cells; wing chord only = 2943 ± 586 cells; joint assignment = 1877 ± 592 cells). On average, the joint model resulted in a 37% reduction in the area assigned as "likely" compared to the assignments based on wing chord alone (paired *t* test: $t = 18.7$, df = 119, $P < 0.01$), and a 10% reduction compared to assignments based on hydrogen alone ($t = 6.73$, df = 119, $P < 0.01$).

Discussion

Quantifying patterns of migratory connectivity is critical to understanding the ecology and evolution of migratory species as well as for creating effective management and conservation strategies. In this study, we present a novel method for quantifying migratory connectivity that combines multiple intrinsic data sources to probabilistically assign individuals to breeding locations. Our results for Wood Thrush demonstrate that, despite relatively high levels of mixing across their breeding and nonbreeding ranges, there is evidence of moderate connectivity along an east–west gradient. This pattern is consistent with previously reported east–west divides in several other species of Nearctic–Neotropical migrants (Smith et al. 2005, Boulet et al. 2006, Norris et al. 2006). Our ability to detect longitudinal migration patterns is surprising, given that both hydrogen isotopes and wing chord are considered latitudinal markers (Hobson and Wassenaar 1997). However, while both markers vary primarily along a north–south gradient, the clines of each marker run at a slight angle (Fig. 1; Appendix C: Fig. C1), and our results suggest that this amount of longitudinal information is sufficient to detect eastern vs. western migration patterns.

The longitudinal patterns of migratory connectivity described here for Wood Thrush are largely consistent with data from other sources (e.g., geolocators; Stutchbury et al. 2009, Stanley et al. 2012). Previous studies, however, were largely based on single breeding populations and as such have limited ability to assess range-wide linkages between breeding and wintering sites (McKinnon et al. 2013). The use of historical migration routes is one hypothesis that might explain east–west

Table 3. Summary of nonbreeding assignments for Wood Thrush: the percentage of individuals from each nonbreeding region assigned to each breeding quadrant.

Nonbreeding region	Northeast	Northwest	Southeast	Southwest
A	15.0 (3/20)	55.0 (11/20)	20.0 (4/20)	10.0 (2/20)
B	31.6 (6/19)	5.3 (1/19)	15.8 (3/19)	47.3 (9/19)
C	33.3 (6/18)	11.1 (2/18)	27.8 (5/18)	27.8 (5/18)

Note: In parentheses are the number of individuals assigned and the total sample size.

TABLE 4. Results of validation assignments for Wood Thrush: the percentage of individuals correctly assigned to their breeding location.

State	Hydrogen only	Wing chord only	Joint
North Carolina	40.1 (13/32)	100 (32/32)	25.0 (8/32)
Virginia	85.2 (23/27)	92.6 (25/27)	81.5 (22/27)
Indiana	96.4 (27/28)	89.2 (25/28)	96.4 (27/28)
Michigan	100 (6/6)	100 (6/6)	100 (6/6)
Vermont	100 (27/27)	96.3 (26/27)	96.3 (26/27)
Total	80.1 (97/120)	97.5 (117/120)	74.1 (89/120)

Note: In parentheses are the number of individuals correctly assigned and the total sample size.

patterns of connectivity in Wood Thrush. Populations may be genetically predisposed to use migratory routes established prior to population range expansion (Delmore et al. 2012), and these "traditional" routes may be reinforced and/or constrained by contemporary weather conditions and the associated costs of using alternatives (Able 1973, Lundberg and Alerstam 1986). Data from both Swainson's Thrush and Wood Thrush appear to support the idea that breeding longitude is a good predictor of fall migration routes and, to a lesser extent, subsequent wintering areas (Stanley et al. 2012, Cormier et al. 2013; C. Q. Stanley et al., *unpublished data*). Regardless of the exact mechanisms that maintain patterns of longitudinal migratory connectivity, these linkages probably reflect both ecological and evolutionary factors.

Accuracy and precision in probabilistic assignment models

Validation is critical to testing the accuracy and precision of assignment models; our validation tests confirm that our models correctly assigned most individuals to their breeding location regardless of age or sex. Interestingly, although the assignment rate of our joint model was similar to that for other taxa (e.g., birds, Chabot et al. [2012]; sea turtles, Stewart et al. [2013]), the assignments based on wing chord alone were often more accurate but less precise than the joint assignments. Incorrect assignments based on the joint model tended to occur when individuals had strong disagreement between the markers. For example, five individuals from the North Carolina population had unusually enriched isotope values (indicating southern origin), but unusually long wing chord (indicating northern origin). In each case, the assignments based on only one marker correctly identified the actual breeding location, yet in each case the true site was at the periphery of the area identified as the "likely" origin. When the markers were combined, the relative likelihood for the true location dropped below the critical threshold required for correct assignment, leading to incorrect assignment for these individuals using the joint model.

To improve the spatial resolution of connectivity maps, assignment models should aim to simultaneously maximize accuracy and precision because highly accurate but imprecise assignments provide limited information about the degree of migratory connectivity and the development of regional conservation priorities (Martin et al. 2007). While combined data sources in the joint model led to a slight reduction in the accuracy of assignments for some locations (e.g., North Carolina), the use of multiple markers led to a large increase in the precision of assignments. For example, our assignments based on wing chord alone had very high accuracy (97.5%), but very low precision (mean ± SD = 2943 ± 586). While precision was better when using isotopes alone (2071 ± 586 cells identified as "likely" origin), combining the markers resulted in a 37% increase in precision of wing chord alone and a 10% increase over isotopes alone. Similar increases in precision have been found in other studies that make probabilistic assignments using multiple data sources. For example, combining stable isotope data with band recoveries resulted in a 67% increase in the precision of assignments of White-throated Sparrows (*Zonotrichia albicollis*) compared to assignments based on isotopes alone (Van Wilgenburg and Hobson 2011). Similarly, Chabot et al. (2012) found that assignments of Loggerhead Shrikes (*Lanius ludovicianus*) based on both genetic data and stable isotopes led to a three- to fivefold increase in precision compared to either marker alone. Ultimately, given the balance between maximizing region-specific accuracy and range-wide

TABLE 5. Age- and sex-specific assignment rates for Wood Thrush using joint assignment: the percentage of individuals correctly assigned to their breeding location.

State	ASY correct	SY correct	Male correct	Female correct
North Carolina	16.6 (3/18)	35.7 (5/14)	28.6 (8/28)	0 (0/4)
Virginia	73.3 (11/15)	91.7 (11/12)	79.2 (19/24)	100 (3/3)
Indiana	92.5 (25/27)	100 (1/1)	91.2 (22/24)	100 (4/4)
Michigan	100 (6/6)	NA (0/0)	100 (3/3)	100 (3/3)
Vermont	100 (8/8)	94.7 (18/19)	96.3 (26/27)	NA (0/0)
Total	68.7 (46/67)	76.1 (35/46)	73.6 (78/106)	76.9 (10/13)

Note: In parentheses are the number of individuals correctly assigned and the total sample size.

precision, we argue that the increased precision associated with the joint model justifies the slight decrease in accuracy compared to the use of either marker alone.

Despite the strong performance of our model, there are a number of important caveats to consider when making probabilistic assignments with isotope and morphology data. First, the accuracy of our validation samples could have been influenced by the dispersal of individuals between breeding locations (Chabot et al. 2012). Results of our validation assignments, however, only would have been impacted by long-distance dispersal events (roughly >100 km), given the spatial resolution of our markers. Given that long-distance dispersal of this magnitude is generally rare (Tittler et al. 2009), we expect that dispersal events probably had a small impact on the accuracy of our validation assignments. Furthermore, while long-distance dispersal may have lowered the accuracy of our validation samples, dispersal between breeding sites would not influence the assignment of birds sampled during the nonbreeding season, and therefore dispersal does not impact our conclusions about migratory connectivity.

A second factor that could influence both the accuracy and precision of our assignments is site-specific individual variation in isotope signatures and wing morphometrics. Several studies have shown that δ^2H_f feather values from passerines known to have originated at the same location can vary by as much as 10–15‰ (Powell and Hobson 2006, Langin et al. 2007; C. Rushing, *unpublished data*) and wing chord can show similar within-site variation. Some of this variation may be due to age or sex differences in isotope discrimination or body size. For example, there is some evidence that hydrogen isotope discrimination varies between age classes, leading several studies to apply age-specific correction factors (Haché et al. 2012, Studds et al. 2012). However, based on the results of Hobson et al. (2012), we chose not to apply any age corrections to our base map. The fact that assignment rates were similar for both ASY and SY individuals confirms that our models were robust to any age-specific isotope discriminations. Although our models were able to correct for age, we were unable to account for sex-specific variation because thrushes on the wintering grounds cannot be accurately sexed using plumage characters alone. Including sex-specific wing chord predictions in our model would almost certainly improve the accuracy and precision of our assignments. Regardless, even after controlling for age and sex, residual within-site variation (Langin et al. 2007) will still remain a key source of error for both accuracy and precision. As probabilistic assignment approaches advance, the incorporation of multiple isotope markers, particularly those that vary longitudinally (Sellick et al. 2009), and the use of informative priors in Bayesian models (Royle and Rubenstein 2004, Van Wilgenburg and Hobson 2011, Hallworth et al. 2013), will undoubtedly help to improve model performance.

Using morphological variation to inform migratory connectivity

Evolutionary biologists and taxonomists alike have long been interested in characterizing and explaining geographic variation in avian morphology across species' ranges including along latitudinal or altitudinal gradients (Mayr 1956, Hamilton 1961, Browning 1994, Arizaga et al. 2006, Nudds and Oswald 2007, McKay 2008, Rising et al. 2009, Paxton et al. 2010, Greenberg et al. 2012). Moreover, a substantial body of work has characterized how natural selection (Greenberg et al. 1998, Lehtonen et al. 2009) and sexual selection (Møller 1995, Dunn et al. 2008, Potti and Canal 2011) have shaped phenotypic variation. Although the ecological and evolutionary forces behind these patterns remain controversial (Watt et al. 2010), these investigations have produced a wealth of data that can provide valuable information for geographic assignments (Conklin et al. 2011). Here, we have demonstrated that geographic variation in morphology has the potential to greatly improve estimates of migratory connectivity when combined with other markers, particularly in cases where gradients of morphological variation complement gradients of other markers (e.g., isotopes or genetic data).

Morphological data offer several distinct advantages for quantifying migratory connectivity. First, geographic variation of many traits has already been described for many species, providing researchers with readily accessible information for conducting assignments (McKay 2008). Second, in cases where geographic variation has not been adequately quantified, base maps can be created using data from museum collections (Pyke and Ehrlich 2010). Third, morphological data are often easier and less expensive to collect than other forms of data, making it feasible to sample a large number of individuals. Furthermore, many relevant traits (e.g., body size, wing length) are measured as part of standard sampling protocols, making it possible to conduct assignments using existing data sets. Given the widespread morphological variation observed in many species, the wealth of existing data, and the advantages just outlined, morphological traits represent a tremendously valuable, but largely untapped, resource for quantifying patterns of migratory connectivity.

Although the enigmatic declines of migratory songbirds have been well publicized, closer examination reveals that most species show substantial variation in regional population trends, with some areas showing sharp declines while others have remained stable or even increased (Faaborg et al. 2010). Without accurate information about migratory connectivity, it is impossible to determine where and when populations face limiting factors or to develop effective management strategies to mitigate regional threats (Martin et al.

2007, Marra et al. 2011). Here, we demonstrate that combining intrinsic data sources is a useful approach for increasing the spatial precision of range-wide migratory connectivity estimates. Further development of these methods, for example by combining intrinsic markers with novel extrinsic markers (e.g., geolocators), promises to advance our understanding of the basic ecology and evolution of long-distance migrant birds, and will allow strategic habitat conservation to protect declining populations.

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SUPPLEMENTAL MATERIAL

Appendix A

Description of stable isotope analysis methods (*Ecological Archives* A024-027-A1).

Appendix B

Comparison of assignment rates under 67% and 75% thresholds for identifying "likely" vs. "unlikely" breeding locations (*Ecological Archives* A024-027-A2).

Appendix C

The δ^2H isoscape, feather sampling locations (bird icons) and the quadrants used in validation and to quantifying range wide migratory connectivity for Wood Thrush (*Ecological Archives* A024-027-A3).