GEOGRAPHIC ORIGINS AND TIMING OF FALL MIGRATION OF THE VEERY IN NORTHERN COLOMBIA

Ana M. González-Prieto[1], Keith A. Hobson[2,4], Nicholas J. Bayly[3], and Camila Gómez[3]

[1]*Department of Biology, University of Saskatchewan, 112 Science Place, Saskatoon, Saskatchewan, S7N 5E2, Canada*
[2]*Environment Canada, 11 Innovation Boulevard, Saskatoon, Saskatchewan S7N 3H5, Canada*
[3]*SELVA: Research for Conservation in the Neotropics, Bogotá, Colombia*

Abstract. Establishing migratory connectivity between migratory birds' breeding, wintering, and stopover sites is an important component of their effective conservation and management. For neotropical migrants, geographic origins and migration patterns have been poorly documented. During fall migration of 2009, we identified geographic origins of the Veery (*Catharus fuscescens*) at stopover sites in the Sierra Nevada de Santa Marta, northern Colombia, by analyzing stable hydrogen isotopes (δD) in feathers and from values expected from a long-term isoscape for North America of δD in feathers. We evaluated the importance of the Sierra Nevada de Santa Marta to the Veery on the basis of the birds' geographic origins and assessed the relationship between timing of migration and geographic origins and age. We estimated that 100 of the 197 individuals captured originated from the southwest and/or the northeast regions of their breeding range, but applying abundance in the breeding range as an informed prior probability further delimited the potential origin of 183 individuals and increased support for origins from the northeast. Feather δD and timing of arrival at the stopover sites were negatively correlated, suggesting a chain migration. Provided that there is no molt migration, adults originated primarily from the southernmost portion of the breeding range and arrived at the stopover site before hatch-year birds. Our study reveals the power of measurements of endogenous markers to clarify origins of birds captured during migration and suggests that Veeries converge on northern Colombia potentially from across the species' breeding range.

Key words: arrival time, deuterium, feathers, migratory connectivity, stable isotopes, stopover site.

Orígenes Geográficos y Momento de la Migración de Otoño de *Catharus fuscescens* en el Norte de Colombia

Resumen. Establecer la conectividad migratoria entre los sitios de cría, de invernada y de escala de aves migratorias es un componente importante para su conservación y manejo efectivo. Para las aves migratorias neotropicales, el origen geográfico y los patrones de migración han sido pobremente documentados. Durante la migración de otoño de 2009, identificamos los orígenes geográficos de individuos de *Catharus fuscescens* en sitios de escala en la Sierra Nevada de Santa Marta, en el norte de Colombia, mediante el análisis de isótopos estables de hidrógeno (δD) en las plumas y a partir de los valores esperados de un mapa de curvas de distribución de isótopos de largo plazo para América del Norte de δD en plumas. Evaluamos la importancia de la Sierra Nevada de Santa Marta para los individuos de *C. fuscescens* sobre la base del origen geográfico de las aves y evaluamos la relación entre el momento de la migración y el origen geográfico y la edad. Estimamos que 100 de los 197 individuos capturados se originaron en el suroeste y/o en las regiones del nordeste de su área de reproducción, pero la aplicación de la abundancia en el área de reproducción como una probabilidad previa delimitó aún más el potencial origen de los 183 individuos y aumentó el apoyo a los orígenes del noreste. El δD de las plumas y el tiempo de llegada a los lugares de escala se correlacionaron negativamente, lo que sugiere una migración en cadena. Siempre y cuando no haya muda durante la migración, los adultos se originaron principalmente en la porción sur del área de reproducción y llegaron al lugar de escala antes que las aves eclosionadas en el corriente año. Nuestro estudio revela el poder de las mediciones de los marcadores endógenos para aclarar los orígenes de las aves capturadas durante la migración y sugiere que los individuos de *C. fuscescens* convergen en el norte de Colombia, probablemente desde todo el rango de distribución reproductivo de la especie.

INTRODUCTION

Effective conservation of migratory birds relies on our ability to understand interactions between different stages of their annual cycle, such as breeding, wintering, and migration (Marra et al. 1998, Webster et al. 2002). Unfortunately, for most species

of neotropical migrants that breed in North America and winter in Central or South America, little is known about the connections between the breeding range, stopover sites, and the winter range. Over the last three decades, long-term data sets have revealed population declines of many landbirds that migrate

to the neotropics (Askins et al. 1990, Sauer et al. 2008), especially those that spend the nonbreeding season in South America (Sauer et al. 2008). Conservation of these species depends on our ability to conserve habitats used by populations at all stages of their annual cycle (Moore et al. 1990, DeGraaf and Rappole 1995, Morris et al. 1996). While most attention has been directed at sites of breeding and wintering, if critical stopover habitat is degraded or transformed, the cost of migration increases and migratory success may be threatened (Yong and Moore 1997). Therefore, the identification of movements of migratory birds and the detection of key stopover sites used is an important component of the conservation of migratory populations in general (Webster and Marra 2004, Mazerolle and Hobson 2005).

Various approaches to determining the origins of birds, including conventional exogenous mark–recapture methods (banding, transmitters, geolocators), have been used successfully to infer movements of migratory wildlife (reviewed by Hobson and Norris 2008). However, these approaches are less useful for small-bodied birds, and all exogenous marking techniques are biased to the extent of the initial marked population. Additionally, all devices attached to birds are capable of altering the bird's behavior (Barron et al. 2010). Intrinsic markers such as naturally occurring ratios of stable isotopes in animals have received considerable attention because of their usefulness for identifying animals' origins without the need for individuals to be marked and recaptured (Hobson and Wassenaar 1997, Hobson 1999, 2005, Mazerolle and Hobson 2005). Of considerable use has been the association of patterns in amount-weighted average values of deuterium in precipitation during the growing season (δD_p) and δD values of feathers (δD_f) at specific locations across a continent (Hobson 2008). For example, in North America, the pattern of δD_p follows a strong gradient with latitude; values are relatively positive in the southeast and negative in the northwest (Sheppard et al. 1969, Taylor 1974), and this pattern is reflected in feathers grown by birds across that gradient (Hobson and Wassenaar 1997). This approach to tracing the breeding origins of migrants that replace feathers following breeding or those hatch-year birds that retain feathers grown at their natal sites in North America after or during their movements south has become a popular means of investigating migratory connectivity (Wassenaar and Hobson 2000, Hobson and Wassenaar 2001, Kelly et al. 2002, Norris et al. 2004, Pain et al. 2004, Mazerolle and Hobson 2005, Boulet et al. 2006, Paxton et al. 2007, Perez and Hobson 2007). Given that most species of migrant songbirds grow feathers on or close to their breeding grounds before migration (Pyle 1997), δD_f values represent an intrinsic marker of geographic location at the time of feather growth (Hobson and Clark 1992, Chamberlain et al. 1997, Hobson and Wassenaar 1997).

Here, we used δD_f values as markers of the geographic origin of Veeries (*Catharus fuscescens*) moving through two migration-stopover sites in the Sierra Nevada de Santa Marta on the Caribbean coast of Colombia. The Veery is a neotropical migrant that takes a long transoceanic route across the Gulf of Mexico (Bevier et al. 2005, Yong and Moore 1994) and presumably the Caribbean Sea during spring and fall migration. Its winter range

is restricted to south-central and southeastern Brazil (Remsen 2001), where it appears to be dependent on undisturbed forest (Stotz et al. 1992); less is known about the habitat selected by the species in other areas of South America during migration. Across North America, the Veery's population has decreased significantly in the last three decades (Sauer et al. 2008), likely, in part, because of habitat loss and fragmentation in the breeding and winter ranges (Willis and Oniki 1993, Bevier et al. 2005). The Caribbean coast of Colombia, much like the coast of the Gulf of Mexico in North America (Moore and Kerlinger 1987, Moore et al. 1990), is expected to provide important opportunities for birds to refuel after a long flight over water. This coastline is dominated by xerophytic habitats or heavily transformed tropical dry forests, with the exception of the lowland and montane tropical moist forests associated with the Darién and the Sierra Nevada de Santa Marta (Instituto Geográfico Agustín Codazzi et al. 2011). Rising over 5000 m above sea level, the Sierra Nevada de Santa Marta may therefore act as an island of high-quality stopover habitat for migratory birds. If this is the case, then individuals from across a species' breeding range might be expected to converge on the Sierra Nevada de Santa Marta, rather than each population following a separate route and entering South America at different points along the coast where habitat is less suitable. Stable-isotope analysis of Veery feathers from the Sierra Nevada de Santa Marta could therefore provide the first evidence as to whether individuals from across the wide geographical range of the Veery converge on the same region for stopover. If such convergence and subsequent concentration occurs, it would have important implications for stopover-site conservation on the northern coast of Colombia. The Veery, unlike other migrants that arrive in the region, does not overwinter in the Sierra Nevada de Santa Marta and is therefore an ideal species for the study of stopover-site use.

We also investigated if there were significant differences in the origin of hatch-year (HY) and after-hatch-year (AHY) birds, and whether the timing of arrival at the stopover site was related to the birds' latitudinal origin. Inter- and intraspecific spatiotemporal patterns of migration could allow us to predict stopover patterns and might explain variations in individual fitness and productivity of populations (Kelly 2006). For example, the timing of fall migration might have consequences for winter habitat selection, body condition, departure time in spring, and productivity during the subsequent breeding season (e.g., Marra et al. 1998, Norris et al. 2004). While we focus on the Veery, our approach is relevant to tracing the migratory connectivity of a broad range of neotropical migrants at stopover sites in the neotropics.

METHODS

STUDY SITE

Veeries were captured during fall migration between 23 September and 31 October 2009 at Reserva Quebrada Valencia (11º 14′ 10.48″ N, 73º 47′ 57.15″ W) and Hacienda La Victoria (11º 07′ 24.82″ N, 74º 05′ 17.63″ W), Sierra Nevada de Santa Marta, Colombia (Fig. 1). Reserva Quebrada Valencia

is a nature preserve that protects a significant relict of lowland humid forest, which is one of the most endangered ecosystems in the region (FPSNSM 1998). Hacienda La Victoria is a private farm containing shaded coffee plantations and a block of premontane forest associated with watershed protection.

TISSUE SAMPLING

All birds were caught by passive mist netting and banded with a single U.S. Fish and Wildlife Service aluminum band. We aged the birds were aged according to Pyle (1997), those hatched in 2009 as HY, those hatched before 2009 as AHY. We took standard measurements and collected the first primary flight feather. The first primary is grown first following breeding (Pyle 1997) and so best represents the geographic location where molt was initiated. Feathers were stored in labeled, sealed paper envelopes until analyzed.

STABLE-ISOTOPE ANALYSIS

All feathers were soaked for 4 hr in a 2:1 chloroform:methanol solution, rinsed, and dried in a fume hood for 48 hr. Material (0.33–0.37 mg) from the distal end of the vane was removed and weighed into silver capsules. Samples were analyzed by continuous-flow isotope-ratio mass spectrometry. Because of uncontrolled isotopic exchange between non-carbon-bound hydrogen in feathers and ambient water vapor (Chamberlain

FIGURE 1.   Site of study of Veery migration through Colombia, fall 2009, and species' year-round distribution.

et al. 1997), we used a comparative equilibrium approach with calibrated keratin standards to correct for this effect. We used three in-house keratin standards, chicken feather, cow hoof, and bowhead whale baleen. Therefore, the isotopic values represent only the nonexchangeable hydrogen in feathers (Wassenaar and Hobson 2003, 2006). Ratios of stable hydrogen isotopes ($^2H/^1H$) are reported in delta (δ) notation, in units per mil (‰) relative to the Vienna standard mean ocean water.

ESTABLISHING ORIGINS

We assigned origins of Veeries captured at the stopover site with an approach similar to that of Van Wilgenburg and Hobson (2011). We used digital range maps (Ridgely et al. 2007) to extract the breeding range from a GIS-based model of expected δD_p from Bowen et al. (2005) with the "extract values by mask" operation in ArcGIS Spatial Analyst. We transformed the δD_p for the species' range into a δD_f model (isoscape) by using the equation for passerines, $\delta D_f = -26.08 + 0.88 \, \delta D_p$, based on Clark et al. (2006). We assessed the likelihood that each cell within the transformed isoscape represented a potential origin for each bird sampled by

$$f(y^* \mid \mu_c, \sigma_c) = \left(\frac{1}{\sqrt{2\pi}, \sigma_c} \right) \exp\left[-\frac{1}{\sqrt{2\pi}, \sigma_c^2} (y^* - \mu_c)^2 \right]$$

(Equation 1)

where $f(y^* \mid \mu_c, \sigma_c)$ is the probability that any given cell (pixel) on the map represents a potential origin for an individual (origin y^*), given an expected mean (μ_c) δD_f based on the predicted value within the calibrated isoscape and the expected standard deviation (σ) of δD_f between individuals growing their feathers at the same locality. We estimated a value of $\sigma = 12.6‰$ as the standard deviation of the residuals from the regression equation reported above. In order to estimate "probability of origin," we used the normalized likelihoods calculated from Equation 1 as follows:

$$\pi_b = \frac{f(y^* \mid \mu_c, \sigma_c)}{\sum_{b-1}^{B} f(y^* \mid \mu_c, \sigma_c)}$$

(Equation 2)

Applying Equation 2, we obtained a set of spatially explicit probability densities for each individual. To assign all individuals to the base map, we reclassified the spatially explicit probability densities into likely versus unlikely origins by specifying odds ratios. On the basis of 2:1 odds that a given assigned bird had really originated from that cell within that range, we identified the set of cells that defined the upper 67% of estimated "probabilities of origin" (using Equation 2) and coded those as "1," all others as "0". Each bird was assigned to multiple potential origins within the isoscape at the same time. The results of the assignment for each individual were summed and mapped on the δD_f isoscape, to obtain the likely origin of the population.
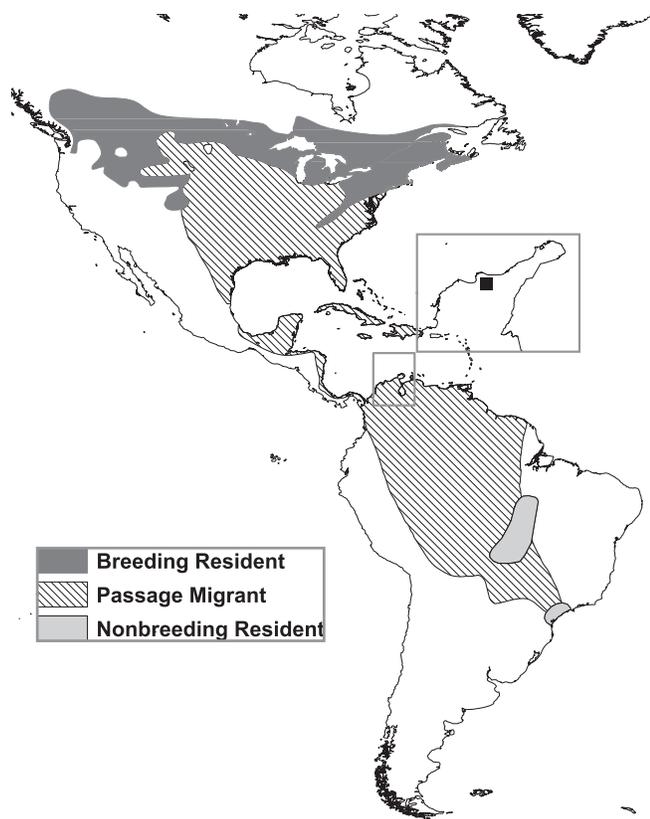
Using a Bayesian approach (Royle and Rubenstein 2004), we also assigned individuals to their potential origins by incorporating breeding-ground abundance as a prior probability. We used interpolated abundance surfaces from the North American Breeding Bird Survey (BBS) to create prior probability surfaces. We converted abundance maps to probability surfaces by normalizing the entire range surface to sum to 1. We then assessed the likelihood that each cell within the isoscape represented the origin of a given bird by assessing the posterior probability of origin given the prior probability as follows:

$$f_x = \frac{f(y^* \mid \mu_c, \sigma_c) f_p}{\sum_i f(y^* \mid \mu_c, \sigma_c) f_p}$$

(Equation 3)

where $f(y^* \mid \mu_c, \sigma_c)$ is estimated as per Equation 1 and f_p represents the spatially explicit prior probability of origin. As for the assignments based only on δD_f, we selected cells within the posterior probability surface on the basis of the odds that these cells could represent the "true" origins of an individual. We used a 19:1 odds ratio, selected the cells within the isoscape representing the upper 95% of the estimated "probabilities of origin," and classified those as "1" and all others as "0." To obtain the likely origin of the population, we summed and mapped the results of the assignment for each individual on the δD_f isoscape. All GIS analyses were done with ArcGIS, version 9.3 (ESRI, Redlands, CA).

STATISTICAL ANALYSIS

Prior to analysis, we examined δD_f values of birds sampled at the stopover sites for normality with the Shapiro–Wilk normality test. We applied a Welch's t-test to evaluate the differences between δD_f values of birds from Quebrada Valencia and Hacienda La Victoria. Dates of arrival at the stopover sites were transformed so that day 1 was equal to 23 September 2009. To examine the relationship between the latitudinal origin of birds passing through the stopover site, arrival date at the stopover site, and age, we fitted a general linear model (analysis of covariance model) with δD_f values as the response variable and arrival date and age as explanatory variables.

We compared the latitudinal origin of HY and AHY birds with a Welch's t-test. To determine if the arrival time at the stopover site was driven by age, we fitted a general linear model with arrival time as the response variable and age as explanatory variable. All statistical analyses were run in R packages. Significance for statistical tests was accepted at $P < 0.05$.

RESULTS

CAPTURES

We captured and sampled 197 birds, 154 (78%) from Quebrada Valencia and 43 (22%) from La Victoria. Values of δD_f were normally distributed (Shapiro–Wilk normality test, $W = 0.99$, $P = 0.4$). There was no significant difference in the mean δD_f values of birds from Quebrada Valencia (−84.8 ± 2.1‰)

and birds from La Victoria (−84.1 ± 1.3‰; $t_{76} = −0.29$, $P = 0.77$), so we mapped birds captured at both locations together.

ORIGINS

Isotopic values of Veery feathers sampled in Colombia were consistent with those expected from within the species' breeding range in North America (Fig. 2A, B). As shown in Fig. 2A, 100 of the 197 sampled birds were likely to have originated from within the southwestern and northeastern regions of the breeding range. In the western portion of the breeding range, most of the birds had δD_f values consistent with those expected from southwestern British Columbia east to Washington, northeastern Oregon, southern Wyoming, northeastern Utah and north-central New Mexico. In the east, birds had δD_f values consistent with those expected from the northern limit of the distribution, particularly from Minnesota east to southern Ontario, Quebec, New Brunswick, Maine, Vermont, and northern New York.

When we applied abundance in the breeding range as a prior probability (Fig. 2B) the potential origin of 183 of the sampled individuals was limited to five main areas where the Veery is numerous in the breeding season: the central part of the border between British Columbia and Washington, northeastern Minnesota and southwestern Ontario, southeastern Ontario and southwestern Quebec, and northern New Brunswick and Maine.

LATITUDINAL ORIGIN, TIMING OF MIGRATION, AND AGE

We found a relationship of δD_f with arrival time at the stopover site and age (arrival date: $F_{1,195} = 17$, $P < 0.001$; age: $F_{1,194} = 14.3$, $P < 0.001$). Latitudinal origin was negatively correlated with arrival day; birds originating from southern latitudes arrived at the stopover site before birds from northern latitudes (Table 1; Fig. 3). The same pattern applied within each age class; however, the negative relationship between latitudinal origin and arrival day was not significant for AHY birds (HY: $F_{1,120} = 5.48$, $P = 0.02$, $n = 122$; AHY: $F_{1,73} = 2.07$, $P = 0.15$, $n = 75$). Hatch-year and AHY birds differed in the presumed area in which they had molted (HY: −88.6 ± 1.3‰, $n = 122$; AHY: −78.3 ± 1.8‰, $n = 75$; $t_{148.36} = 4.72$, $P < 0.001$). Arrival day was driven by age (age: $F_{1,195} = 21.12$, $P < 0.001$, $n = 197$); AHY birds arrived at the stopover site before HY birds (Fig. 4). HY birds showed a migration peak between 12 and 17 October (day 20 and 25), while AHY birds peaked earlier, between 7 and 12 October (day 15 and 20).

DISCUSSION

The most likely geographic origins of Veeries stopping in northern Colombia, as determined by stable-isotope analysis, were the southern edge of the breeding range in the west and the northern edge of the breeding range in the east (Fig. 2). When we used information on the species' abundance from
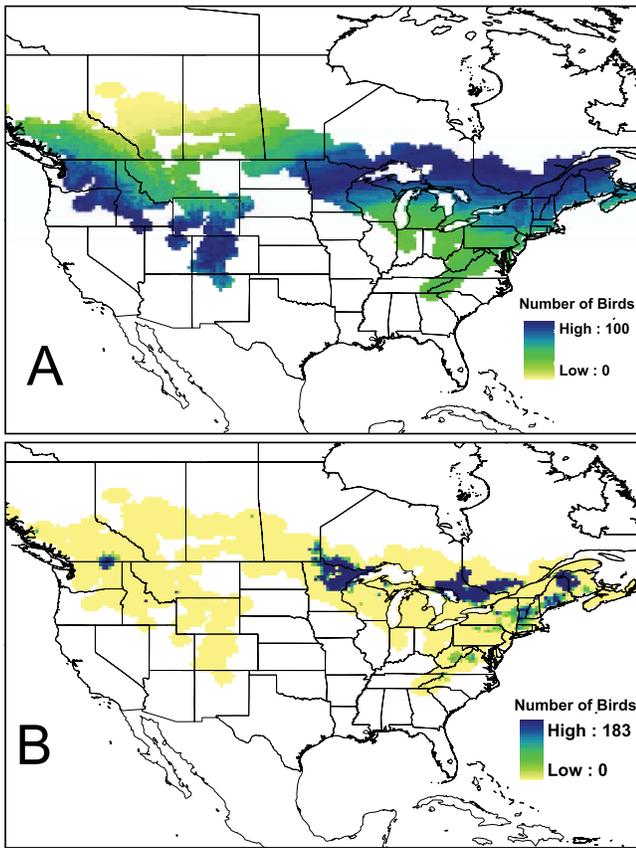
FIGURE 2.   Assigned geographic origins of 197 Veeries captured at two stopover sites on the northern coast of Colombia during fall 2009. (A) Origins inferred from stable-isotope (δD) analysis of feathers (δD$_f$) and the long-term continental pattern of δD$_p$, the amount-weighted average deuterium in precipitation during the growing season (Bowen et al. 2005), by GIS and Bayesian assignment approaches (Van Wilgenburg and Hobson 2011). The value of 100 represents the areas within the map consistent with the likely origin of 100 of the sampled birds. (B) Origin inferred from δD$_f$ and application of informed prior based on abundance in the breeding range from the North American Breeding Bird Survey (BBS). The value of 183 represents the areas within the map being consistent with the likely origin of 183 of the sampled birds.

TABLE 1.   Values of δD and arrival date by age class of migrating Veeries stopping on the north coast of Colombia during fall 2009. Day 1 = 23 September 2009.

| Sample	n	Mean	Range	SD	SE
δD HY (‰)	122	−88.6	−120.91 to −55.2	14.1	1.3
δD AHY (‰)	75	−78.3	−116.9 to −44.7	15.2	1.8
Arrival day HY	122	23.5	11 to 39	6.9	0.6
Arrival day AHY	75	18.8	1 to 34	6.8	0.8
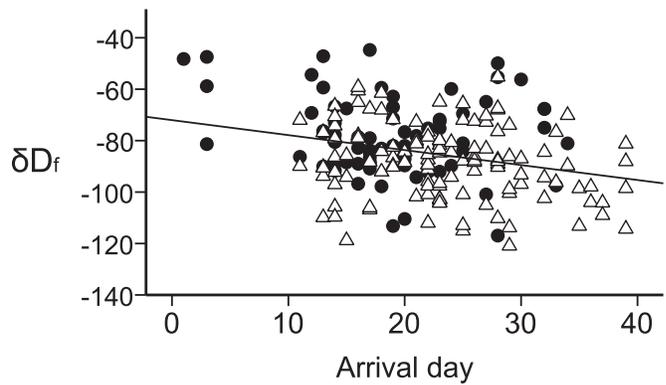
FIGURE 3.   Relationship between δD$_f$ and arrival day of Verries stopping during fall migration in Colombia. Day 1 = 23 September 2009. HY birds (n = 122), triangles; AHY birds (n = 75), circles.
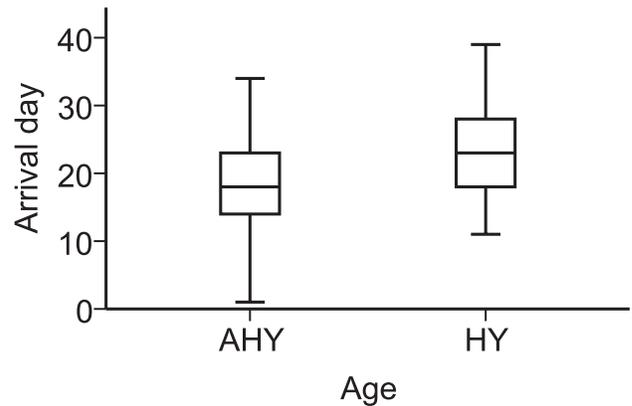

FIGURE 4.   Median arrival date of AHY (n = 75) and HY (n = 122) Veeries at stopover sites on the northern coast of Colombia during fall migration 2009. Day 1 = 23 September 2009. Upper and lower boundaries of boxes show the 25th and 75th percentiles, respectively.

the Breeding Bird Survey (Sauer et al. 2007) to generate prior probabilities of origin, the likely geographic origins were, as expected, further restricted to the areas with the highest relative abundance. On the basis of these criteria, birds moving through northern Colombia during fall migration comprised individuals from a broad cross-section of the breeding range, with a bias toward populations from the northeast (Fig. 2). However, despite the utility of relative-abundance data to better inform assignment of individuals to origin (Royle and Rubestein 2004), the approach assumes that the probability of capture of a bird from a given region within its breeding range is directly proportional to the relative abundance of the species in that region relative to the whole breeding range. In the case of the Veery, we do not know if birds from across the

breeding range use the same migration routes, so the assumption of equal probability of capture may not be valid.

Interpretation of the depiction of potential origins of migratory birds by the stable-isotope approach requires some caution (Hobson 2008). Primarily, the probability of origin as depicted here represents the isotopic solution space of

origins and not necessarily the actual origin of the sample. The nature of the deuterium isoscape for North America is such that the gradient is stronger latitudinally than longitudinally. For this reason, a solution space often occupies broad bands of longitude, as we have seen for the Veery. Therefore, we have little power to differentiate between birds originating from the southwest and northeast components of their range. Isotopic approaches that enable greater clarification of longitudinal origins would be a valuable contribution to our knowledge of use of migratory routes and stopover sites in species whose breeding range spreads over a wide range of longitudes (Boulet et al. 2006, Chamberlain et al. 1997). Additionally, multi-year studies would allow us to detect the flexibility of the migratory routes and whether individuals are originating from the same breeding areas in different years.

Assessing how breeding populations are spatially linked through the annual cycle is a key factor to the development of conservation strategies for migratory populations (Norris et al. 2006, Martin et al. 2007). Recent models predict that when breeding populations mix in their winter range, events like habitat loss in the winter range will influence population size over a wide area of the breeding range (Marra et al. 2006). The predicted origins of Veeries in the Sierra Nevada de Santa Marta suggest that individuals from across the breeding range are converging on the region. This supports the idea that the Sierra Nevada de Santa Marta may be an island of high-quality habitat on the Caribbean coast of Colombia and that the conservation of stopover habitats along the species' migratory route are necessary for the conservation of breeding populations. Remsen (2001) localized the Veery's winter range to a restricted area of southern Brazil, so populations mix during migration and also likely on their wintering grounds. The Sierra Nevada de Santa Marta has already lost over 70% of its original forest cover (FPSNSM 1998), and defining the importance of the region to other migratory species could support the case for greater protective measures. However, as stated above, the same isotopic solution space can occupy broad longitudinal bands, and consequently we cannot define the likely longitudinal origin of individuals in our sample. It remains plausible that the majority of individuals were from the northeast of the range, as suggested by Fig. 2, but we encourage examination of other stopover sites in Colombia and their relative value to the Veery and other species.

Stotz et al. (1992) proposed an elliptical migration route for the Veery in South America, with a fall migration route through western Amazonia and the spring migration route farther east. Our findings support this hypothesis, as a fall route via western Amazonia would take birds through northern Colombia. Furthermore, the Veery has been reported on the north coast of Colombia only as a fall transient (Hilty and Brown 1986). Our study sites likely represent two of the first points of landfall for birds crossing the Caribbean Sea in the fall, before they continue south to winter in Brazil (Remsen 2001).

With respect to the origin of Veeries in relation to age, AHY birds appeared to derive from more southerly locations than did HY birds. This pattern may be explained if productivity was higher in the northern or central regions of the breeding range. Alternatively, if AHY birds disperse southward away from the breeding grounds before undergoing their complete molt, this pattern could also arise. While Pyle (1997) suggested that the Veery molts flight feathers exclusively on the breeding grounds, other thrushes, such as Swainson's (*Catharus ustulatus*), have been reported molting during their southward migration (Cherry 1985, Winker et al. 1992). Wassenaar and Hobson (2001) also reported isotopic evidence for molt migration in Swainson's Thrush. Alternatively, HY birds, if subjected to metabolic demands or microclimates different from those of adults during molt, might have slightly different δD_f values even they originated from the same general location (Hobson 2008). These possibilities remain to be tested in this species.

The Veery also demonstrated a pattern in which birds from southern latitudes arrived at stopover sites before those from northern latitudes, suggesting a chain migration pattern. We observed this pattern within both age classes, though it was statistically significant only for HY birds. Chain migration has also been reported by Kelly (2006), who found that during fall migration Orange-crowned Warblers (*Oreothlypis celata*) and Common Yellowthroats (*Geothlypis trichas*) breeding in the southern portion of their ranges arrived in New Mexico before birds from more northerly latitudes. However, inferences about the spatial relationship between breeding origins and the winter destination could not be made because the winter destination of the individuals was not known. Kelly et al. (2002) found that in fall Wilson's Warblers (*Wilsonia pusilla*) migrate in the "leapfrog" pattern, individuals from northern latitudes migrating earlier and farther south than those from more southern latitudes. Hobson et al. (2007) did not find a relationship between the timing of fall passage through a stopover site in Mexico and the latitudinal origin of Swainson's Thrushes, Wood Thrushes (*Hylocichla mustelina*), or Gray Catbirds (*Dumetella carolinensis*).

With respect to the timing of migration, AHY birds arrived at the stopover sites about 10 days before HY birds. AHY birds had passed through by 27 October, whereas HY completed their passage after 31 October. HY birds have been found to be less proficient foragers than AHY birds (Wunderle 1991, Shealer and Burger 1995), so they may need additional time to store adequate energy, adjust to new habitats (Morris et al. 1996, Yong et al. 1998), and consequently depart and arrive at stopover or wintering sites later than AHY birds. Additionally, a higher speed of migration of adult birds during fall migration (Ellegren 1993) might contribute to the difference between HY and AHY birds in arrival time at our stopover sites. Murray (1966) suggested that adult and juvenile Veeries captured at a stopover site in New Jersey were migrating at the same time; in the case of the Veery it cannot be ruled out that

AHY birds begin migrating before HY birds and therefore arrive at stopover sites first.

Contrary to our results, Benson et al. (2006) reported juvenile Wilson's Warblers migrating before adults at four stopover sites in Alaska. Andres et al. (2005) and Benson and Winker (2001) found mixed results in time of passage by age class of neotropical migrants moving through Alaska, though HY birds migrated significantly earlier than older birds in more than 70% of the species. These results might be driven by the proximity of the stopover sites to the breeding grounds and by delays in departure of adults of species that undergo a complete molt before fall migration (Carlisle et al. 2005, Benson et al. 2006). Benson et al. (2006) suggested that when age-related differences during migration are evaluated, the location of the research site with respect to the breeding grounds could confound the results. Variability in the results of these studies suggests that long-term monitoring at multiple stopover sites along the migration pathways is necessary for age-related migration patterns to be determined accurately. Our results are based on one year of observations, and we acknowledge that comparison of multiple years is necessary for the constancy and flexibility of the pattern we observed to be assessed (Kelly 2006).

Other studies have found HY birds to make up over 80% of the Veeries present at coastal stopover sites during fall migration (Murray 1966, Ralph 1981, Morris et al. 1996). This "coastal effect" (Ralph 1981) is also seen in several species in inland areas (Dean et al. 2004). Lack of experience in orientation might cause young birds to use coastal areas for migration and stopover, while more experienced adult birds avoid them (Stewart et al. 1974, Taylor et al. 1994, Morris et al. 1996, Woodrey and Moore 1997); therefore, a high incidence of HY birds at a stopover site may indicate it is on the periphery of the migration route (Ralph 1981). In our study, HY birds represented 62% of the Veeries captured. These findings suggest little separation between the age classes and that these stopover sites in northern Colombia may be of equal importance to HY and AHY birds and lie on the species' main migration route. However, given the southerly location of the study region, the observed age ratio may be the result of higher mortality of HY birds along the migration route.

ACKNOWLEDGMENTS

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