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ESTIMATING ORIGINS OF THREE SPECIES OF NEOTROPICAL MIGRANT SONGBIRDS AT A GULF COAST STOPOVER SITE: COMBINING STABLE ISOTOPE AND GIS TOOLS

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Abstract. Measurement of stable-hydrogen isotopes (δD) in feathers of migrating birds can provide information on where feathers were grown in North America, at least to an approximate band of latitude. This approach has greatly increased our ability to investigate aspects of avian migration and stopover ecology, since origins of unmarked individuals at migration stopover sites can be estimated for the first time. However, few studies have explored the power of combining isotope measurements with geographic information system (GIS) methods. We measured δD values in feathers of hatching-year (HY) Swainson’s Thrushes (Catharus ustulatus; n = 60), Wood Thrushes (Hylocichla mustelina; n = 113), and Gray Catbirds (Dumetella carolinensis; n = 158) at Ft. Morgan Peninsula, Alabama (30°10′N, 88°00′W), a migration stopover site along the Gulf coast. By applying an elevation-corrected hydrogen isotope basemap for birds in North America, we derived a GIS surface depicting expected feather δD values across the continent. We then used GIS to constrain the possible origins of the sampled populations by considering only values falling within the North American breeding ranges of the species. We depicted likely origins of migrating birds by the 50% and 75% tolerance limits of the data. Our GIS analysis indicated that our captured populations represented much-reduced regions of possible origin based on the North American breeding distributions. Gradients in abundance data from the North American Breeding Bird Survey (BBS) allowed us to further narrow possible origins within isotopic boundaries for Wood Thrushes and Gray Catbirds. This exercise provided a means by which priority regions and habitats could be assessed at large continental scales based on actual productivity. We suggest the combination of isotopic and GIS tools provides a powerful means to derive conservation priorities and to investigate key factors involved in the ecology of avian migration and stopover.

Key words: deuterium, geographic information systems, migratory connectivity, stable isotopes, stopover.

Estimación del Origen de Aves Canoras Migratorias Neotropicales de Tres Especies en un Sitio de Parada en la Costa del Golfo: Una Combinación de Herramientas de Isótopos Estables y SIG

Resumen. La medición de isótopos estables de hidrógeno (δD) en las plumas de las aves migratorias puede proveer información importante acerca del lugar geográfico en Norteamérica donde crecieron las plumas, o por lo menos aproximar la localización dentro de una banda latitudinal específica. Esta técnica ha aumentado considerablemente nuestra capacidad de investigar aspectos de la migración y la ecología de las paradas migratorias de las aves, debido a que por primera vez es posible determinar el origen de individuos no marcados en sitios de paradas migratorias. Sin embargo, pocos estudios han explorado el poder de combinar medidas de isótopos con métodos de sistemas de información geográfica (SIG). En este estudio, medimos los valores de δD en plumas de individuos de las especies Catharus ustulatus (n = 60), Hylocichla mustelina (n = 113) y Dumetella carolinensis (n = 158) en su afio de eclosión en la península de Ft. Morgan, Alabama (30°10′N, 88°00′W), un sitio de paradas migratorias en la costa del Golfo. Mediante la aplicación de un mapa base de isótopos de hidrógeno corregido por la elevación para las aves de Norteamérica y utilizando un SIG, derivamos una superficie que representa los valores de δD esperados para plumas en todo el continente. Luego utilizamos el SIG para restringir los posibles orígenes de la población muestreada,
considerando sólo los valores que cayeran dentro de los rangos de distribución reproductiva de las especies en Norteamérica. Representamos los posibles orígenes de las aves migratorias mediante los límites de tolerancia de los datos del 50% y del 75%. Nuestro análisis de SIG indicó que las poblaciones capturadas representaban distribuciones mucho más reducidas con base en las distribuciones reproductivas de las aves de Norteamérica. Datos de gradientes de abundancia provenientes de la base de datos de conteos de aves reproductivas de Norteamérica nos permitieron aproximar aún más los posibles orígenes dentro de los límites sugeridos por los isótopos para H. mustelina y D. carolinensis. Este ejercicio representó un medio para determinar regiones y hábitats prioritarios para la conservación a una escala continental con base en la productividad real de las regiones. Sugerimos que el uso combinado de técnicas de isótopos y SIG representa un medio poderoso para determinar prioridades para la conservación, y para investigar factores clave sobre la ecología de la migración y las paradas migratorias.

INTRODUCTION

Birds captured during migration at stopover sites can be used to investigate a number of questions, ranging from the establishment of population trends in the case of long-term monitoring stations (Dunn et al. 1997, 2006, Ballard et al. 2003) to those dealing with the evolution of migration and stopover ecology (Moore et al. 2005). Although such capture affords the opportunity to individually mark birds with leg bands, few birds are ever recovered, and most birds intercepted are unmarked and of unknown origin (Brewer et al. 2000, Hobson 2003). Knowledge of the breeding or natal origin of individuals during fall or spring migration and in winter would allow the examination of several questions relating to how the timing of migration, duration of stopover, and body condition may be linked to distance traveled or anticipated distance left to travel. In addition, establishing the geographic region of origin of the population being sampled would allow better-informed insight into factors ultimately responsible for changes in populations of birds using that site (Wassenaar and Hobson 2001, Webster et al. 2002, Webster and Marra 2005, Dunn et al. 2006). Although conventional mark-recapture methods are biased and hence poorly suited to examining such questions, analysis of stable hydrogen isotopes in feathers provides a tool for identifying the breeding origins of migrants (Hobson and Wassenaar 1997, Hobson 2003).

In North America, the ratio of deuterium to hydrogen (D/H, typically expressed as δD) in rainfall varies in a predictable, broad-scale geographic pattern (Bowen et al. 2005), and growing-season rainfall values based on multi-decadal datasets from the International Atomic Energy Agency are reflected in local food webs and animal tissues (Cormie et al. 1994, Wassenaar and Hobson 1998, Gröcke et al. 2006). That precipitation signal is also translated through diet into the δD values of feathers grown by birds living in the area, both by juveniles growing their first set of feathers and by adults replacing molted feathers (Chamberlain et al. 1997, Hobson and Wassenaar 1997). Stable-hydrogen isotope signatures in passerine feathers are typically 25% depleted in the heavy isotope compared to mean annual growing season δD in precipitation (Wassenaar and Hobson 2000a, but see Bowen et al. 2005), and have been used successfully to determine latitudinal zones of natal or breeding origin for several passerines and nonpasserines (Wassenaar and Hobson 2000a, 2001, Hobson and Wassenaar 2001, Meehan et al. 2001, Kelly et al. 2002, Rubenstein et al. 2002, Smith et al. 2003, Hobson et al. 2004). However, more recent investigations suggest that raptors may show a different relationship between feather δD values and mean annual precipitation values (Hobson 2005, Smith and Dufty 2005, Lott and Smith 2006), and this simple relationship observed for passerines may be more complex in certain areas of the continent or depend on the species involved (Bowen et al. 2005, Wunder et al. 2005, Lott and Smith 2006, Powell and Hobson 2006).

In this study we used δD measurements of feathers to investigate the breeding grounds or natal origins of Swainson’s Thrushes (Catharus ustulatus), Wood Thrushes (Hylocichla mustelina), and Gray Catbirds (Dumetella carolinensis) migrating through stopover sites along the Gulf coast at Ft. Morgan Peninsula, Alabama. Our objectives were to delineate areas of origin of birds moving through this coastal region and to investigate possible correlates of migration phenology. In addition, we demonstrate how combining geographical information systems
(GIS) technology with elevation-corrected digital isotopic basemaps (Meehan et al. 2004) and North American Breeding Bird Survey (BBS) data can be used to better quantify and visually depict possible origins of migrating populations.

METHODS

STOPOVER SITE

The Fort Morgan, Alabama (30°10’N, 88°00’W) stopover site was located approximately 15 km west of Gulf Shores, Alabama, within Bon Secour National Wildlife Refuge. This site was dominated by scattered slash pine (Pinus elliottii) interspersed among hummocks of sand live oak (Quercus geminata) and yaupon (Ilex vomitoria).

SAMPLE

Primarily hatching-year (HY) birds were captured during our study and analyses were restricted to this age class. Subcutaneous fat, unflattened wing chord, and mass (to the nearest 0.1 g) were recorded. Visible subcutaneous fat and muscle mass were quantified according to scales developed by Helms and Drury (1960) and Bairlein (1985), respectively. All measurements were made by trained individuals who were periodically tested to ensure validity and repeatability of measures. Each bird was aged and sexed according to characteristics outlined in Pyle (1997), then fitted with a U.S. Fish and Wildlife Service aluminum leg band.

Swainson’s Thrushes were captured in 2002 only, from 11 September to 22 October. We captured 59 HY Wood Thrushes from 27 September to 27 October 2000 and 36 HY birds from 22 September to 21 October 2001. We also sampled 15 adult Wood Thrushes during the 2000 (n = 4), 2001 (n = 9), and 2002 (n = 2) seasons. Gray Catbirds were captured and sampled from 27 September to 27 October 2000 (n = 73) and from 24 September to 18 October 2002 (n = 85).

STABLE ISOTOPE ANALYSES

Feathers were cleaned in a 2:1 chloroform:methanol solvent rinse and prepared for stable-hydrogen isotope analysis at the National Water Research Institute in Saskatoon, Canada. Stable-hydrogen isotope analyses of feathers are complicated due to the problem of uncontrolled isotopic exchange between samples and ambient water vapor (Wassenaar and Hobson 2000b). Elsewhere we describe in detail how we used keratin standards as a means of correcting for this effect so that the values reported here are equivalent to nonexchangeable feather hydrogen (Wassenaar and Hobson 2003). Briefly, the process involves the simultaneous measurement of unknowns with several replicates of three different keratin standards whose nonexchangeable δD values are known and which span the range of expected feather values. Algorithms generated from each run that relate δD values of unknowns to their expected nonexchangeable values are then used on a run-by-run basis.

Stable-hydrogen isotope measurements of feathers and keratin standards were performed on H_2 derived from high-temperature flash pyrolysis of feathers and continuous-flow isotope-ratio mass spectrometry (CF-IRMS). Pure H_2 was used as the sample analysis gas and the isotopic reference gas. A Eurovector 3000™ (Milan, Italy) high temperature elemental analyzer (EA) with autosampler was used to automatically pyrolyse feather samples to a single pulse of H_2 gas (and N_2 and CO gas). The resolved H_2 sample pulse was then introduced to the isotope ratio mass spectrometer (Micromass Isoprime™ [Manchester, England] with electrostatic analyzer) via an open split capillary. All δD results are expressed in the typical delta notation, in units of per mil (‰), and normalized on the Vienna Standard Mean Ocean Water – Standard Light Antarctic Precipitation (VSMOW–SLAP) standard scale. Repeated analysis of hydrogen isotope intercomparison material IAEA-CH-7 (−100‰), routinely included as a check, yielded an external repeatability of better than ±1.5‰. This method eliminates variation due to isotope exchange with ambient water vapor, but because not all laboratories follow this recommended standardization technique, our δD values may not be comparable to those reported by others. Based on within-run measurements of intercomparison material and consideration of within-feather variance (Wassenaar and Hobson 2006), we estimate our laboratory error to be ±3‰.

STATISTICAL ANALYSES AND GIS METHODS

Prior to analyses, δD values were examined graphically and tested for normality of feather
δD values using Kolmogorov-Smirnov tests. Swainson’s Thrush δD values were not normally distributed (P < 0.05), however graphical examination of the histogram suggested this was only due to a lack of samples from the northernmost origins; therefore, all subsequent analyses were conducted assuming a normal distribution. Wood Thrush and Gray Catbird data showed no evidence of departure from a normal distribution (P > 0.2). We used a general linear model (GLM) with feather δD as the dependent variable, year and day as factors, and, where available, fat score, muscle mass, wing length, and body mass as covariates. Individual patterns of the response of feather δD with day and body measures were investigated using linear regression.

Origins of thrushes and catbirds were mapped separately using a georeferenced, altitude-corrected dataset of expected growing-season average δD in precipitation (Meehan et al. 2004). This dataset is available online (<http://biology.unm.edu/wolf/precipitationD.htm>) as a raster grid file that can be imported into GIS software. To reflect isotopic discrimination from precipitation to feather δD values, we used a Spatial Analyst mathematical operation to create a new expected feather δD surface by adding -25%o (as found previously for passerines; Hobson and Wassenaar 1997, Wassenaar and Hobson 2001) to the value of each cell using ArcGIS 9.0 (ESRI, Redlands, California). All subsequent queries were done using the expected feather δD layer. Sensitivity to the assumed fractionation value of -25%o was examined by creating two separate layers of expected feather values, one using a discrimination of -22%o and the other assuming a discrimination value of -28%o.

We delineated origins of migrants by portraying the statistical tolerance limits (TLs; Walpole and Meyers 1993) for δD data from feather samples. In contrast to confidence intervals, which express the confidence around the estimation of a parameter such as the mean, tolerance limits represent the limits within which a specified proportion of the population will fall at an expressed level of confidence. Tolerance limits are calculated as follows:

\[
T_{\text{Lower}} = \bar{y} - k_2s; \quad T_{\text{Upper}} = \bar{y} + k_2s,
\]

where \(s\) is the standard deviation in the sample, and \(k_2\) is a factor determined so that the intervals cover at least a proportion \(p\) of the population with confidence, \(\gamma\). The calculation of \(k_2\) is as follows:

\[
k_2 = \sqrt{\frac{(N - 1)(1 + 1/N)Z^2_{\gamma, N - 1}}{2(1 - p)/2}}.
\]

\(Z_{\gamma, N - 1}\) is the critical value of the chi-square distribution with degrees of freedom, \(N - 1\), that is exceeded with probability \(\gamma\). \(Z^2_{(1 - p)/2}\) is the critical value of the normal distribution that is exceeded with probability \(1 - p)/2\) for the desired confidence level. We computed TLs to encompass 50% and 75% of the population, at a 95% confidence level. This should be interpreted as having 95% confidence that 50% and 75% of the population, respectively, come from within the calculated limits. We selected tolerance limits as opposed to confidence intervals because they are much more conservative and represent the origins of proportions of the population instead of just the sample.

Tolerance limits were mapped using the feather δD basemap. For each collection location, locations on the raster basemap falling within the 50% and 75% TLs were selected as potential origins using Spatial Analyst to reclassify all cells. Cells outside the 75% tolerance limits were classified as containing no data and cells falling within the calculated tolerance limits were assigned values of 50% or 75%. The resulting raster image was then converted to vector format for further manipulation. Sensitivity analysis was conducted by portraying the calculated 75% tolerance limits on the raster layers created assuming -22%o and -28%o discrimination values as described above. The selected cells from both these layers were combined into a single layer (hereafter sensitivity layer). The 50% and 75% TLs from the -25% discrimination-based layer were then draped over the sensitivity layer to portray the area of origin and how much it would shift north (-22%o) or south (-28%o) under different fractionation values. Potential origins were further limited by using the ArcGIS Geoprocessing Wizard to restrict the expected origins to only those areas falling within the well-established breeding range of each species using a georeferenced species distribution map.

<table>
<thead>
<tr>
<th>Species</th>
<th>Year</th>
<th>Age</th>
<th>n</th>
<th>δD 95% CI (%)</th>
<th>δD median (%)</th>
<th>δD range (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Swainson’s Thrush</td>
<td>2002</td>
<td>HY</td>
<td>56</td>
<td>-139.8 to -126.6</td>
<td>-140.2</td>
<td>-169.0 to -72.7</td>
</tr>
<tr>
<td>(Catharus ustulatus)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wood Thrush</td>
<td>2000</td>
<td>HY</td>
<td>58</td>
<td>-62.6 to -54.7</td>
<td>-58.7</td>
<td>-94.9 to -31.2</td>
</tr>
<tr>
<td>(Hylocichla mustelina)</td>
<td>2001</td>
<td>HY</td>
<td>36</td>
<td>-58.6 to -52.5</td>
<td>-55.8</td>
<td>-78.1 to -39.1</td>
</tr>
<tr>
<td></td>
<td>2000–2002</td>
<td>AHY</td>
<td>14</td>
<td>-59.0 to -40.7</td>
<td>-45.9</td>
<td>-77.2 to -27.4</td>
</tr>
<tr>
<td>Gray Catbird</td>
<td>2000</td>
<td>HY</td>
<td>73</td>
<td>-77.5 to -71.9</td>
<td>-75.3</td>
<td>-99.5 to -40.9</td>
</tr>
<tr>
<td>(Dumetella carolinensis)</td>
<td>2002</td>
<td>HY</td>
<td>83</td>
<td>-66.0 to -61.3</td>
<td>-63.4</td>
<td>-94.8 to -37.2</td>
</tr>
</tbody>
</table>

To further interpret the likely origins of Wood Thrushes and Gray Catbirds captured at our study locations, we generated an abundance surface for each species. Abundance surfaces were created using interpolations of the North American Breeding Bird Survey available online (<http://www.mbr-pwrc.usgs.gov/bbs/geographic_information/geographic_information_products_.htm>). The surfaces were clipped to the same area corresponding to the calculated tolerance intervals for both Wood Thrush and Gray Catbird. This was done to highlight any spatial trends in population abundance within zones of likely origin based on δD signatures. We did not perform this exercise for the Swainson’s Thrush because the BBS does not adequately cover its breeding range. However, we further limited the likely origins of Swainson’s Thrushes by overlaying a digital depiction of the Pacific drainage basin from the drainage basins of North America (Graham et al. 1999). Populations of Swainson’s Thrush sampled along the Gulf coast are unlikely to originate west of the continental divide, as populations breeding west of the divide mostly migrate along the west coast (Evans Mack and Yong 2000).

RESULTS

SWAINSON’S THRUSH

We found no effects on feather δD values of day, or the covariates fat, muscle mass, wing length, and body mass ($F_{19,55} = 1.1, P = 0.37$; Table 1, 2). As expected, our single-year HY sample showed the most depleted feather δD values, corresponding to the more northerly distribution of this species compared to the other two species examined. The most probable area of origin for HY Swainson’s Thrushes covered the southern portions of western boreal forest and the Hudson Bay lowlands of Manitoba, Saskatchewan, and Alberta, the lowlands of Alaska, interior British Columbia, and the interior of the northwestern United States (Table 3, Fig. 1). However, since the western populations derived from the Pacific drainage basin most likely do not migrate through the Gulf coast site, interior British Columbia was likely not part of the solution (Fig. 1). Assumed discrimination values had little effect on the area and position of the estimated geographic origins of the population. Sensitivity analysis suggested the probable origins of the population were relatively robust to the assumed discrimination value, with changes of ±3% resulting in minimal (~±100 km) changes to the estimated zones of origin (Fig. 1).

WOOD THRUSH

For HY birds, our GLM model showed no overall significant effects on feather δD values of year, day, or the covariates fat, muscle mass, wing length, and body mass ($F_{32,94} = 1.0, P = 0.432$; Table 1, 2). For the smaller group of AHY birds, we also found no significant effects on feather δD values of any of the variables measured. In addition, we found no differences in feather δD values among both year groups of HY and the AHY group ($F_{2,109} = 2.6, P = 0.08$). However, for consistency, our GIS depiction of origins was restricted only to the combined HY groups.

GIS analysis suggested the probable area of origin of 75% of the HY population of Wood Thrushes migrating through the Gulf Coast stopover sites was a narrow belt through the southeastern region of the U.S. (Table 3, Fig. 2). Furthermore, abundance data from the North American Breeding Bird Survey suggest that within this zone of probable origin,

<table>
<thead>
<tr>
<th>Species</th>
<th>Factor</th>
<th>Year</th>
<th>n</th>
<th>Mean ± SD</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Swainson’s Thrush</td>
<td>Fat score</td>
<td>2002</td>
<td>56</td>
<td>2.7 ± 1.5</td>
<td>0.0 to 5.0</td>
</tr>
<tr>
<td></td>
<td>Muscle score</td>
<td>2002</td>
<td>56</td>
<td>1.8 ± 0.7</td>
<td>0.5 to 3.0</td>
</tr>
<tr>
<td></td>
<td>Wing length (mm)</td>
<td>2002</td>
<td>56</td>
<td>95.8 ± 2.9</td>
<td>90.0 to 101.5</td>
</tr>
<tr>
<td></td>
<td>Mass (g)</td>
<td>2002</td>
<td>56</td>
<td>33.4 ± 9.5</td>
<td>21.6 to 44.8</td>
</tr>
<tr>
<td>Wood Thrush</td>
<td>Fat score</td>
<td>2000</td>
<td>58</td>
<td>2.1 ± 1.2</td>
<td>0.0 to 5.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2001</td>
<td>36</td>
<td>1.9 ± 1.1</td>
<td>0.0 to 5.0</td>
</tr>
<tr>
<td></td>
<td>Muscle score</td>
<td>2000</td>
<td>58</td>
<td>2.0 ± 0.4</td>
<td>1.0 to 3.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2001</td>
<td>36</td>
<td>1.9 ± 0.3</td>
<td>0.5 to 2.5</td>
</tr>
<tr>
<td></td>
<td>Wing length (mm)</td>
<td>2000</td>
<td>58</td>
<td>104.0 ± 3.1</td>
<td>95.0 to 111.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2001</td>
<td>36</td>
<td>104.0 ± 2.9</td>
<td>99.0 to 110.5</td>
</tr>
<tr>
<td></td>
<td>Mass (g)</td>
<td>2000</td>
<td>57</td>
<td>50.2 ± 6.2</td>
<td>34.9 to 66.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2001</td>
<td>36</td>
<td>50.1 ± 5.5</td>
<td>39.5 to 62.7</td>
</tr>
<tr>
<td>Gray Catbird</td>
<td>Fat score</td>
<td>2000</td>
<td>73</td>
<td>1.9 ± 1.3</td>
<td>0.0 to 4.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2002</td>
<td>83</td>
<td>1.2 ± 0.8</td>
<td>0.0 to 4.0</td>
</tr>
<tr>
<td></td>
<td>Muscle score</td>
<td>2000</td>
<td>73</td>
<td>2.1 ± 0.3</td>
<td>1.0 to 3.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2002</td>
<td>83</td>
<td>1.8 ± 0.5</td>
<td>0.5 to 2.5</td>
</tr>
<tr>
<td></td>
<td>Wing length (mm)</td>
<td>2000</td>
<td>73</td>
<td>86.7 ± 2.1</td>
<td>82.7 to 90.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2002</td>
<td>83</td>
<td>87.5 ± 3.2</td>
<td>74.0 to 99.0</td>
</tr>
<tr>
<td></td>
<td>Mass (g)</td>
<td>2000</td>
<td>73</td>
<td>86.7 ± 2.1</td>
<td>29.7 to 47.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2002</td>
<td>80</td>
<td>35.8 ± 2.9</td>
<td>29.5 to 47.6</td>
</tr>
</tbody>
</table>

birds most likely originated from the northern and eastern portions (Fig. 2). Similar to Swainson’s Thrushes, probable origins of the Wood Thrush population were not greatly affected by the assumed discrimination values (Fig. 2).

GRAY CATBIRD

We determined a significant effect of day ($F_{26,156} = 2.0, P = 0.01$), year ($F_{1,156} = 13.4, P < 0.001$), and fat score ($F_{1,156} = 10.9, P = 0.001$) on feather $\delta D$ in our GLM model ($F_{39,156} = 3.1, P < 0.001$). There was a strong effect of year driving these relationships (Table 1), and we found that in 2000, catbirds had higher fat scores ($F_{1,155} = 18.6, P < 0.001$), higher muscle scores ($F_{1,155} = 18.6, P < 0.001$), and higher body mass ($F_{1,155} = 8.2, P = 0.005$) than in 2002 (Table 2), and ultimately originated from more northerly locations, with lower feather $\delta D$ values ($F_{1,155} = 36.9, P < 0.001$). For both years, we found no significant relationship between feather $\delta D$ values and day ($r^2 < 0.1, P > 0.69$) or muscle score ($r^2 < 0.01, P > 0.39$).

Our GIS analysis suggested that 75% of the HY population sampled stemmed from a narrow belt extending roughly from the Carolinas to eastern Oklahoma (Table 3, Fig. 3). Furthermore, a trend toward higher abundance in

TABLE 3. Descriptive statistics and tolerance limits of feather deuterium isotope ($\delta D$) values of Swainson’s Thrushes, Wood Thrushes, and Gray Catbirds calculated with 95% confidence and used to depict probable natal origins of birds caught at a stopover site at Ft. Morgan Peninsula, Alabama, 2000–2002.

<table>
<thead>
<tr>
<th>Species</th>
<th>$n$</th>
<th>Mean ± SD $\delta D$ (%)</th>
<th>50% tolerance limit $\delta D$ (%)</th>
<th>75% tolerance limit $\delta D$ (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Lower</td>
<td>Upper</td>
<td>Lower</td>
</tr>
<tr>
<td>Swainson’s Thrush</td>
<td>109</td>
<td>-133.2 ± 24.7</td>
<td>-139.7</td>
<td>-126.7</td>
</tr>
<tr>
<td>Wood Thrush</td>
<td>56</td>
<td>-56.4 ± 13.7</td>
<td>-61.4</td>
<td>-51.4</td>
</tr>
<tr>
<td>Gray Catbird</td>
<td>159</td>
<td>-68.9 ± 12.7</td>
<td>-74.5</td>
<td>-63.3</td>
</tr>
</tbody>
</table>
the eastern portion of the zone of probable origin suggested most birds likely originated from the Carolinas or central portions of Mississippi, Alabama, and Georgia (Fig. 3). Sensitivity analysis suggested that changes of ±3% resulted in approximately ±100 km change to the estimated zones of origin (Fig. 3).

DISCUSSION

At the continental scale, the results of our isotopic mapping and analysis showed that feather δD measurements placed the expected population origin consistently within the latitudinal range of each species’ known breeding distribution. Swainson’s Thrushes had the most negative feather δD values, corresponding well with their more northerly distribution (see also Kelly et al. 2005). Wood Thrushes and Gray Catbirds, in turn, had more positive δD values, placing them at more southerly latitudes, again consistent with their known breeding ranges. However, within these expected ranges, we were able to define much more narrow probable regions of origin for the subpopulations moving through our sampling stations, thus providing graphical map-based depictions of migratory connectivity or defined “catchment” areas (Wassenaar and Hobson 2001, Dunn et al. 2006, Hobson et al. 2006). These regions, representing where 50%–75% of the population likely originated, became a template that could be subjected to additional GIS queries aimed at further elucidating regions or habitats of important production. We suggest that this approach could be widely adopted as a tool to recommend important conservation actions based on real connectivity versus broad range-wide management prescriptions.

Recent concern in the literature (Bowen et al. 2005, Hobson 2005, Lott and Smith 2006) regarding the assumption of tissue-specific hydrogen isotopic offset between precipitation and feathers (−25%) prompted our sensitivity
FIGURE 2. Probable breeding origins of Wood Thrushes migrating through a stopover site at Ft. Morgan Peninsula, Alabama, 2000–2002, based on 50% and 75% tolerance limits (TL) of the feather δD distribution calculated for a 95% confidence level and assuming a precipitation to feather discrimination value of −25‰. Sensitivity to discrimination values was assessed by depicting 75% TLs for precipitation to feather discrimination values of −22‰ (northernmost band) and −28‰ (southernmost band). Inset is a 3-D side view depicting magnitude of changes in abundance along the east–west axis of the area encompassed by the 50% and 75% TLs, and scaled to the same east–west axis as the TLs. The map was generated using a modified version of the GIS-based model for δD in precipitation (Meehan et al. 2004) and an interpolated surface of Wood Thrush abundance from the North American BBS.

analyses. The results of our GIS definition of the areas of origin showed the estimation to be relatively robust to this discrimination, suggesting that for many passerines this assumption may be of less concern than other potential sources of bias or error. The extent of the defined area of origin would have been affected to a far greater degree had different summary statistics been used to portray this area. Tolerance limits tend to be more conservative and depict a broader zone than what would be portrayed by statistics relating to the mean (e.g., 95% CI). Careful consideration should be given to study objectives when selecting which
FIGURE 3. Probable breeding origins of Gray Catbirds migrating through a stopover site at Ft. Morgan Peninsula, Alabama, 2000–2002, based on the 50% and 75% tolerance limits (TL) of the feather δD distribution calculated for a 95% confidence level and assuming a precipitation to feather discrimination value of −25‰. Sensitivity to discrimination values was assessed by depicting 75% TLs for feather to precipitation discrimination values of −22‰ (northernmost band) and −28‰ (southernmost band). Inset is a 3-D side view depicting magnitude of changes in abundance along the east–west axis of the area encompassed by the 50% and 75% TLs, and scaled to the same east–west axis as the TLs. The map was generated using a modified version of the GIS-based model for δD in precipitation (Meehan et al. 2004) and an interpolated surface of Gray Catbird abundance from the North American BBS.

When comparing origins of different samples, confidence intervals may be appropriate. However, we suggest the use of tolerance limits for depiction of areas of origin corresponding to a capture site.

For all three species, we found that timing of passage through the sampling sites was not correlated with feather δD value or derived latitude of origin. This contrasts with some previous isotopic studies. For instance, feather δD analyses revealed that Wilson’s Warblers (Wilsonia pusilla) in western North America used a “leapfrog” migration pattern and that distance to the wintering grounds affected migratory timing in fall but not spring (Kelly et al. 2002, see also Smith et al. 2003). However, the Swainson’s Thrush was the only species showing a broad potential range of latitudinal origins for which differential timing of migration might be expected. Previous studies have noted the possibility of increased feather δD values for this species due to molt occurring further south than breeding sites (Wassenaar...
and Hobson 2001, see also Kelly et al. 2005). However, since our sample was only of HY birds, this was not a factor in the assignment of origins. Both Wood Thrushes and Gray Catbirds were clearly from much more geographically discrete regions. Body fat similarly was not associated with timing of passage through the stopover site or latitude of origin. However, we did determine a significant year effect in potential origins of Gray Catbirds that were in better condition in 2002 and apparently derived from more northerly areas. This result points to the possibility of regional changes in productivity among years and suggests that stable isotope analysis can provide a means of identifying spatial correlates of body condition as well as timing of migration. However, there are other possible explanations for the year effect we saw in Gray Catbirds. It is possible that both years involved the same areas of origin for the population but precipitation was more enriched in deuterium during the growing season of 2000 than 2002. Drought conditions can also cause heat stress in birds, which results in enrichment in the body hydrogen pool of individual HY birds, leading to higher feather δD values (McKechnie et al. 2004, Wunder et al. 2005, Powell and Hobson 2006). This may result in birds from a single area of origin appearing to derive from more southern locations during years of heat stress.

A major problem with the application of feather δD values is that, for much of the North American continent, it provides only broad latitudinal information about origin. However, as argued recently by Hobson (2005), the application of additional information can further constrain probable origins for most species. The most obvious first step is to restrict analysis to an appropriate species of interest having a fairly narrow longitudinal range. Secondly, where applicable, additional information such as BBS relative abundance data can serve as a probability surface that can constrain origins by defining where the species no longer or rarely occurs within its hypothetical breeding range, and, more importantly, by suggesting likely origins based on population hotspots. Statistically, the use of such an abundance surface to weight likely sources of origin becomes a Bayesian approach. Royle and Rubenstein (2004) first developed this method in their analysis of feather isotope data from Black-throated Blue Warblers ("Dendroica caerulescens") distributed across most of their range. Such quantification of derived probability of origin based on prior knowledge of relative abundance represents an important development (Wunder et al. 2005). We feel our approach provides a useful alternative to that of Royle and Rubenstein (2004), by portraying likely origins as a continuously varying probability surface, rather than arbitrarily delineating subpopulations from which prior probabilities are calculated. However, with all such approaches, there are pitfalls. Most importantly, the Bayesian approach, and the GIS depiction we used here to portray likely origins using BBS data, assumes that probability of capture is directly correlated with relative abundance of singing males (i.e., as fundamentally recorded by the BBS dataset).

The assumption here that areas of high abundance represent the most likely “source” populations assumes that relative abundance (as derived from the BBS data) is directly linked to reproductive success (Vickery et al. 1992, Bock and Jones 2005). This has yet to be verified for most species. However, combining abundance and isotope data allows the formulation of spatially explicit hypotheses and predictions regarding the dynamics of metapopulations. Here, we delineated likely origins of HY birds, and so provide information on regions of production associated with our specific capture locations. For Wood Thrushes and Gray Catbirds, the BBS data provide a method to stratify origins into regions of high and low breeding density for the east-central and southeastern United States, respectively. Using conventional mark-recapture approaches, this provides a means to test whether birds produced in these zones are indeed represented according to breeding abundance at the stopover sites.

The careful delineation of avian areas of origin corresponding to specific capture locations for birds during migration will provide a new means to test how well BBS abundance surfaces correspond to productivity estimates based on the Monitoring Avian Productivity and Survivorship (MAPS) datasets for North America (Desante et al. 2001). In addition, changes in area-specific productivity estimates based on the stable isotope data could be correlated with changes in land cover within
the delineated areas of origin using GIS analysis. Our approach was based entirely on depicting origins at the population and not the individual level. This seems appropriate when the samples are derived from a single sampled population with a normal distribution in feather δD values. However, when this is not the case, and the sampled population represents discrete source populations with differing δD distributions, it would be more appropriate to assign each individual to origin on the feather δD basemap and then depict the frequency of abundance of individuals spatially. Finally, the use of additional stable isotope markers or trace elements to improve delineation of areas of origin is encouraged (Hobson et al. 1999, Rubenstein et al. 2002, Hobson 2005) but will require substantial ground-truthing to establish their usefulness as additional GIS layers, particularly at continental scales.

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LITERATURE CITED


