



BREEDING DESTINATIONS AND SPRING MIGRATION PATTERNS OF SWAINSON'S THRUSH (*CATHARUS USTULATUS*) AT A COSTA RICAN STOPOVER SITE

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ABSTRACT.—Stable-isotope analysis of feathers has become a useful tool for examining migration patterns and annual connectivity of migratory songbird populations. We used this approach, combined with molecular sex-identification, to examine expected breeding destinations and migration ecology of Swainson's Thrush (*Catharus ustulatus*) at a spring stopover site on the Osa Peninsula of Costa Rica. The number of individuals passing through the site increased in late March and peaked in mid-April before declining toward late April. Plumage and expected feather-deuterium (δD_f) values for North America indicated that most individuals had probably bred or fledged in west-central regions of the boreal forest and western mountains, rather than farther north in the Yukon and Alaska or in eastern regions of Canada and the United States. Average δD_f values differed little between males and females, indicating similar breeding destinations, though females tended to show greater variability. The δD_f values of second-year and after-second-year birds differed only slightly, which suggests that most adults molted near the breeding grounds. Timing of migration through the site was not related to breeding latitude as inferred from feather δD . We also found little relation between the energetic reserves carried by individuals and their expected breeding destination, possibly because the reserves carried at this stage have little relation to the total reserves needed by northern breeders for the final stage of migration. Received 28 April 2006, accepted 14 March 2007.

Key words: breeding destinations, *Catharus ustulatus*, Costa Rica, deuterium, migration ecology, stable isotopes, Swainson's Thrush.

Destinos de Cría y Patrones de Migración de Primavera de *Catharus ustulatus* en un Sitio de Escala en Costa Rica

RESUMEN.—Los análisis de isótopos estables de las plumas se han convertido en una herramienta útil para examinar los patrones de migración y la conectividad anual de las poblaciones de aves canoras migrantes. Utilizamos este enfoque, combinado con la identificación molecular del sexo, para examinar los destinos de cría esperados y la ecología de migración de *Catharus ustulatus* en un sitio de escala de primavera en la Península de Osa, Costa Rica. El número de individuos que pasan a través del sitio incrementa a fines de marzo y tiene un pico a mediados de abril, antes de disminuir hacia fines de abril. El plumaje y los valores esperados de deuterio en las plumas (δD_p) para América del Norte indicaron que la mayoría de los individuos habían probablemente criado o emplumado en las regiones del centro-oeste del bosque boreal y de las montañas del oeste, en lugar de más al norte en Yukon y Alaska, o en las regiones del este de Canadá y los Estados Unidos. Los valores promedio de δD_p difirieron poco entre machos y hembras, indicando los mismos destinos de cría, aunque las hembras tendieron a mostrar mayor variabilidad. Los valores de δD_p de las aves del segundo año y posteriores difirieron muy poco, lo que sugiere que la mayoría de los adultos mudaron cerca de los sitios de cría. La fecha de migración a través del sitio no estuvo relacionada con la latitud de cría inferida a partir del δD de las plumas. También encontramos poca relación entre las reservas energéticas de los individuos y sus destinos esperados de cría, posiblemente porque las reservas que portaban en este período tienen poca relación con las reservas totales necesarias de los migrantes para la fase final de la migración.

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MIGRATORY BIRDS FACE a multitude of factors that affect their survival and fitness during the breeding season (Robinson et al. 1995), during migration (Sillert and Holmes 2002), and on the wintering grounds (Latta and Faaborg 2002). Recently, more emphasis is being placed on elucidating how different factors can interact temporally and spatially to influence individuals and populations (Webster and Marra 2005). A fundamental step in this process is the establishment of connections between disparate regions and habitats used by migrants during the annual cycle—their so-called “migratory connectivity.” However, our knowledge of connectivity has generally been restricted to larger species such as waterfowl, raptors, and some shorebirds, whereas relatively little is known about the connectivity of migratory songbird populations. The recent development of stable-hydrogen-isotope ($^2\text{H}/^1\text{H}$, measured as δD) analysis of feathers of North American migrants to approximate latitudinal origins of molt (Hobson 2005) has provided an important new tool that will especially benefit studies of those species too small to be tracked using satellite technology or other extrinsic markers.

Mean growing-season deuterium (^2H) abundance in rainfall follows a characteristic pattern across North America, becoming more depleted from southeast to northwest and from low to high elevations (Meehan et al. 2004). Shallow-rooted plants obtain most of their hydrogen from rainfall, and δD values in precipitation are incorporated up the food chain into the tissues of birds. Because feathers are metabolically inert after formation and most bird species molt flight feathers on or near the breeding grounds, the isotopic signature in the feather of a bird at a stopover site or on the wintering grounds can help identify the location of the breeding area (Hobson 2005). Adult and juvenile songbirds show fidelity to their breeding and natal areas (Greenwood and Harvey 1982, Gardali et al. 2003, Sedgwick 2004); therefore, these analyses can also suggest where an individual sampled outside the breeding period will likely breed in the following season.

Deuterium measurements have helped link the breeding and wintering areas of various North American (reviewed by Hobson 2005) and European (Bearhop et al. 2005) songbirds and, more recently, have been used to answer important questions about the ecology and evolution of songbirds. For example, Kelly et al. (2002) used feather δD to show that, in fall, Wilson’s Warblers (*Wilsonia pusilla*) from northern populations passed through a stopover site in New Mexico earlier than those from southern populations (see also Smith et al. 2003, Kelly 2006, Paxton et al. 2007). Such isotopic analyses may also be helpful in examining how the distance traveled to a stopover site or the remaining distance to the breeding or wintering grounds affects the energetic reserves carried during migration (Lindström and Alerstam 1992, Hobson et al. 2007).

We used δD measurements to identify expected breeding destinations and migration patterns of Swainson’s Thrushes (*Catharus ustulatus*) passing through the Osa Peninsula of Costa Rica during spring migration. Swainson’s Thrush is a Neotropical migrant, and recent genetic studies have identified two distinct clades with separate breeding sites, migratory routes, and wintering locations. Individuals of the coastal clade (russet-backed group) breed along the Pacific coast of North America and migrate through the western United States to winter in Mexico and northern Central America, whereas birds of the continental clade (olive-backed group) breed across the boreal forest and migrate through eastern

North America to wintering grounds in South America (Evans Mack and Yong 2000, Ruegg and Smith 2002). Less is known about the degree to which different breeding populations within each clade use similar wintering sites or migratory routes. Our goals were to examine (1) the expected breeding destinations of individuals passing through the study site and (2) how the inferred breeding latitude affects timing of migration in males and females and the energetic reserves carried during migration.

METHODS

Study area and capture methods.—We conducted field work on the northwest tip of the Osa Peninsula, Costa Rica, during spring migrations of 2002–2005 (Fig. 1). The Osa Peninsula is 1,093 km² and contains a mixture of tropical wet forest, premontane wet forest, and tropical moist forest (Holdridge 1967). Annual mean temperature is 27°C. Average annual precipitation is 5,500 mm, with dry and wet seasons occurring in December–April and May–November, respectively. Our 3-ha study area (8°50′N, 83°40′W) was located ~10 km north of Corcovado National Park and ~5 km west of the town of Drake Bay. The forest in this region is premontane wet forest and tropical wet forest (Sanchez-Azofeifa et al. 2002). Habitat at the study site was primarily secondary forest, 15 to 25 years in age, with primary forest along the eastern and southern edges.

Migrating Swainson’s Thrushes were caught using 12 to 15 mist nets (12 m, 30-mm mesh) set up each day for ~6 h beginning at dawn. Study periods ran from 28 March to 29 April 2004 and from 30 March to 29 April 2005. Preliminary studies at the site in 2002 and 2003 were conducted outside these periods (2002: 17 March to 12 April; 2003: 15 April to 10 May) and indicated that nearly all Swainson’s Thrushes migrate through the study area from late March to late April (Fig. 2). Because the data from 2002 and 2003 do not span the entire migratory period, we used only the 2004 and 2005 data in most analyses. Swainson’s Thrushes are very rare in the study area during winter (D. M. Collister unpubl. data), and nearly all individuals caught during the present study were almost certainly passage migrants. After capture, individuals were fitted with a federal band, measured (mass and wing length), checked for fat (Helms and Drury 1960), and aged as second-year (SY) or after-second-year (ASY) on the basis of plumage, feather shape and wear, and wing morphology (Pyle 1997). We also classified all individuals into coastal (russet-backed) or continental (olive-backed) groups on the basis of plumage (Pyle 1997, Evans Mack and Yong 2000). In 2004, we collected a tail feather (rectrix 5) from every fifth individual caught throughout the season.

Stable-isotope analyses.—Feathers were cleaned of surface oils using a 2:1 chloroform:methanol solution and then dried in a fume hood. Stable-isotope assays were performed at Environment Canada in Saskatoon, Saskatchewan (National Hydrology Research Center). Stable hydrogen isotopes of feathers (δD_f) were measured using the comparative equilibration method described by Wassenaar and Hobson (2000). Briefly, δD measurements on feathers and keratin standards were made on H_2 derived from high-temperature flash pyrolysis of feathers and continuous-flow isotope-ratio mass spectrometry (CF-IRMS). Repeated analyses of calibrated in-house keratin reference materials yielded an external repeatability of better than $\pm 2\%$. Measurements are reported in

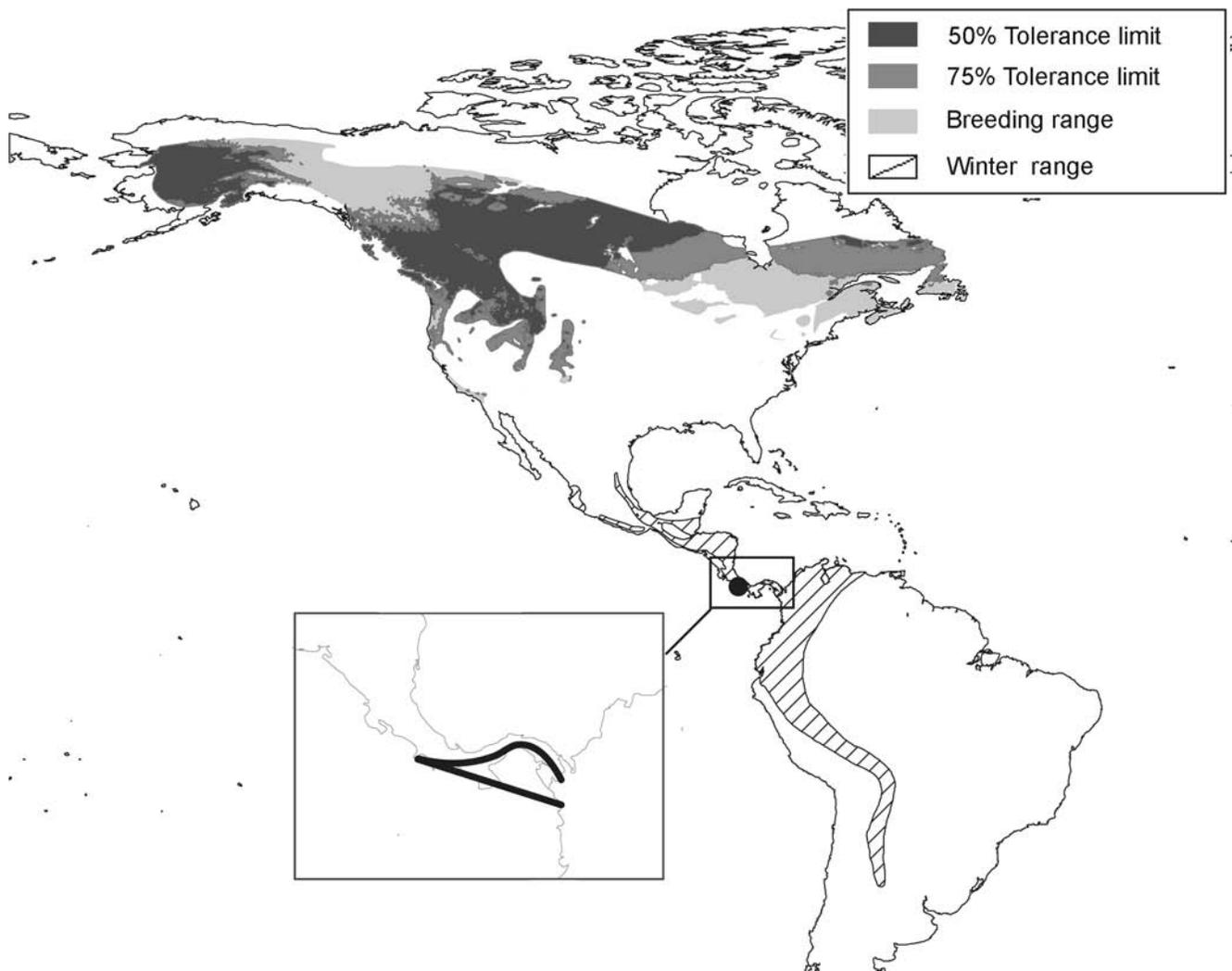


FIG. 1. Expected breeding destinations of Swainson's Thrushes migrating through the study site on the Osa Peninsula, Costa Rica (study site denoted by solid circle). Tolerance limits indicate the percentage of the population expected to lie within the indicated distributions at 95% confidence. Light shading indicates the remaining breeding range outside the 75% tolerance limit, and the dashed area indicates the winter range. The inset map shows the study region in more detail, with two possible routes by which Swainson's Thrushes wintering in South America may reach the study site.

the delta-notation based on the Vienna Standard Mean Ocean Water (VSMOW).

Genetic analyses.—Swainson's Thrush is sexually monomorphic, and individuals included in the isotope analysis were sexed using molecular markers. DNA was extracted from the basal tip of the calamus and the umbilical clot (Horváth et al. 2005) of individual feathers using the QiAMP Microkit (Qiagen, Valencia, California). We employed the sex-identification primers, P2 (5'-TCTGCATCGCTAAATCCTT-3') and P8 (5'-CTCCCAAGGATGAGRAAYTG-3') developed by Griffiths et al. (1998). Polymerase chain reaction (PCR) conditions were modified from Bush et al. (2005), along with a modification in the P2 primer sequence to allow for IRD labeling. Ten microliters of template DNA were used in a 17- μ l PCR mixture containing 100 ng of each primer, 0.16 mM dNTPs, 1.5mM MgCl₂, 50mM KCl, 10mM Tris-HCl pH 8.3, 0.1% Triton X-100, BSA 0.8 μ g/ μ l, 1 μ M of a 700

or 800 IRD label (Li-COR), and 0.5 units AmpliTaq (Roche). The PCR profiles followed Griffiths et al. (1998) and consisted of a 1.5-min denaturation step at 94°C, 35 cycles of 30-s denaturation at 94°C, 45-s annealing at 52°C, and a 45-s extension at 72°C. The program finished with a final cycle of 60 s at 52°C and a final extension for 5 min at 72°C. The PCR fragments were fractionated on 7% polyacrylamide gels in automated sequencers (LiCor 4200, LiCor, Lincoln, Nebraska). Both negative and positive controls were included in all series of PCR reactions. Negative controls included extraction blanks and PCR blanks. For positive controls, we used plucked feathers and skin from Swainson's Thrush and Varied Thrush (*Ixoreus naevius*) specimens of known sex that were obtained from the salvage collection at the Cowan Vertebrate Museum, University of British Columbia, and had died during the breeding season. Varied Thrushes were sexed by plumage (Pyle 1997), whereas Swainson's Thrushes were sexed by dissecting

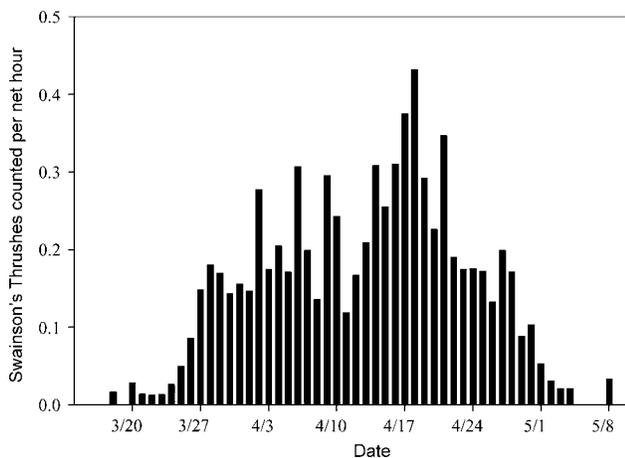


FIG. 2. Spring migration phenology of Swainson's Thrushes on the Osa Peninsula, Costa Rica, from 2002 to 2005. We averaged the number per net hour where the same day was surveyed in multiple years.

and identifying the reproductive organs. Reproducibility of the analysis was 100% and was determined from 14 randomly chosen individuals subject to replicate PCR reactions.

Breeding destinations.—Approximate breeding destinations in the current year were inferred from the previous molt location of ASY birds and the natal site of SY birds, assuming that individuals show reasonable fidelity to their previous breeding and natal sites, respectively (Greenwood and Harvey 1982, Gardali et al. 2003, Hoover 2003, Sedgwick 2004). In North America, the deuterium approach is sensitive to latitudinal differences on the order of 2° of latitude (Wassenaar and Hobson 2006). To accommodate isotopic discrimination from precipitation to feather δD values (Hobson and Wassenaar 1997), we adjusted all values by -25‰ and used these for further analyses. Recent evidence suggests that a constant discrimination factor may not apply to all taxa or regions (Wunder et al. 2005, Lott and Smith 2006); however, a value of -25‰ was a best estimate for passerines given our current knowledge. Hobson et al. (2007) showed that the methods used here are robust to slight deviations in the δD_p to δD_f fractionation, and we believe our assumptions regarding destinations and previous molt origins to be reasonable and on the order of ~ 220 km of latitude for the central portion of the species' range. Expected destinations were identified using a georeferenced, altitude-corrected data set of expected average growing-season deuterium in precipitation (δD_p ; Meehan et al. 2004). This data set is available online (see Acknowledgments) as a raster grid file and was incorporated into ArcGIS 9.0 (ESRI, Redlands, California). To identify expected destinations, we first calculated the 50% and 75% tolerance limits, which refer to the percentage of the population expected to fall within a particular range at 95% confidence. Our data tended to be right-skewed; therefore, we used a nonparametric tolerance limit, which does not require a normal distribution for the population (Murphy 1948). We used the "reclassify" function where cells within the tolerance limits were assigned a one, whereas those outside were left blank. These reclassified rasters were converted to polygon feature layers and incorporated onto the base map along

with a georeferenced breeding-distribution map for Swainson's Thrush (see Acknowledgments). We then restricted the feature layers to those locations within the breeding range.

Statistical analysis.—We used general linear models (GLMs) to examine differences in δD_f values by age and sex and to test whether timing of migration and energy stores were predicted by expected breeding latitude. The latter analyses assume that individuals moving to different regions do not differ considerably in behavior (other than differences in timing). We report the results of GLM test statistics and the beta estimates for significant slope terms. We examined fat scores and the residuals from a regression of mass against wing length as an index of energetic condition. The use of residuals for condition requires linear relationships between size and mass, and independence of energy reserves in relation to body size (Schulte-Hostedde et al. 2005). Plots of the mass–wing length residuals revealed an equal distribution across the range of wing lengths, which suggests a linear relationship, and no evidence that overall size influenced condition. Males and females were combined for this analysis because the sexes do not differ in mass when corrected for wing length, which suggests that they fall along the same size continuum (analysis of covariance, wing: $F = 25.61$, $P < 0.001$; sex: $F = 1.56$, $P = 0.22$). Statistical analyses were conducted using R, version 2.3.1 (see Acknowledgments).

RESULTS

Migration patterns.—Across the four years, the number of migrating individuals caught per net hour increased rapidly in late March and remained high for approximately three weeks, before declining in late April (Fig. 2). Nearly all individuals appeared to have passed through by the end of the first week in May. However, only a single year was available to infer abundance at the onset and completion of migration in late March and early May, respectively, whereas three to four years were available for the peak periods in April. In 2004 and 2005, respectively, 546 (average = 0.22 birds per net hour) and 540 (0.24 birds per net hour) individuals were captured. Within-season recapture rates were low; only nine (0.017%) and seven (0.013%) individuals were recaptured in 2004 and 2005, respectively. A single tail feather was collected from 109 individuals for isotope and genetic analysis in 2004. These included 51 and 28 SY and ASY individuals, respectively, and 30 individuals whose age could not be determined (UK). Genetic analysis identified 51 males (21 SY, 14 ASY, 16 UK) and 48 females (25 SY, 14 ASY, 9 UK), and 10 individuals could not be sexed.

Breeding destinations.—There was no difference in the δD_f values (mean \pm SE) of SY and ASY males (SY: $-137 \pm 4.9\text{‰}$; ASY: $-137 \pm 6.1\text{‰}$; $F = 0.001$, $df = 1$ and 33 , $P = 0.98$; Fig. 3), whereas SY females had slightly lower values than ASY females (SY: $-130 \pm 5.8\text{‰}$; ASY: $-127 \pm 7.6\text{‰}$, $F = 0.16$, $df = 1$ and 36 , $P = 0.69$). With age groups combined, males tended toward lower average δD_f values than females (males: $-138 \pm 2.7\text{‰}$; females: $-130 \pm 3.8\text{‰}$; $F = 3.70$, $df = 1$ and 97 , $R^2 = 0.04$, $P = 0.06$). For both sexes, most individuals had values in the range of -120‰ to -160‰ , but a greater proportion of females had δD_f values greater than -120‰ (Fig. 3). Three individuals (SY female, SY male, ASY female) had δD_f values that fell below the known breeding range of

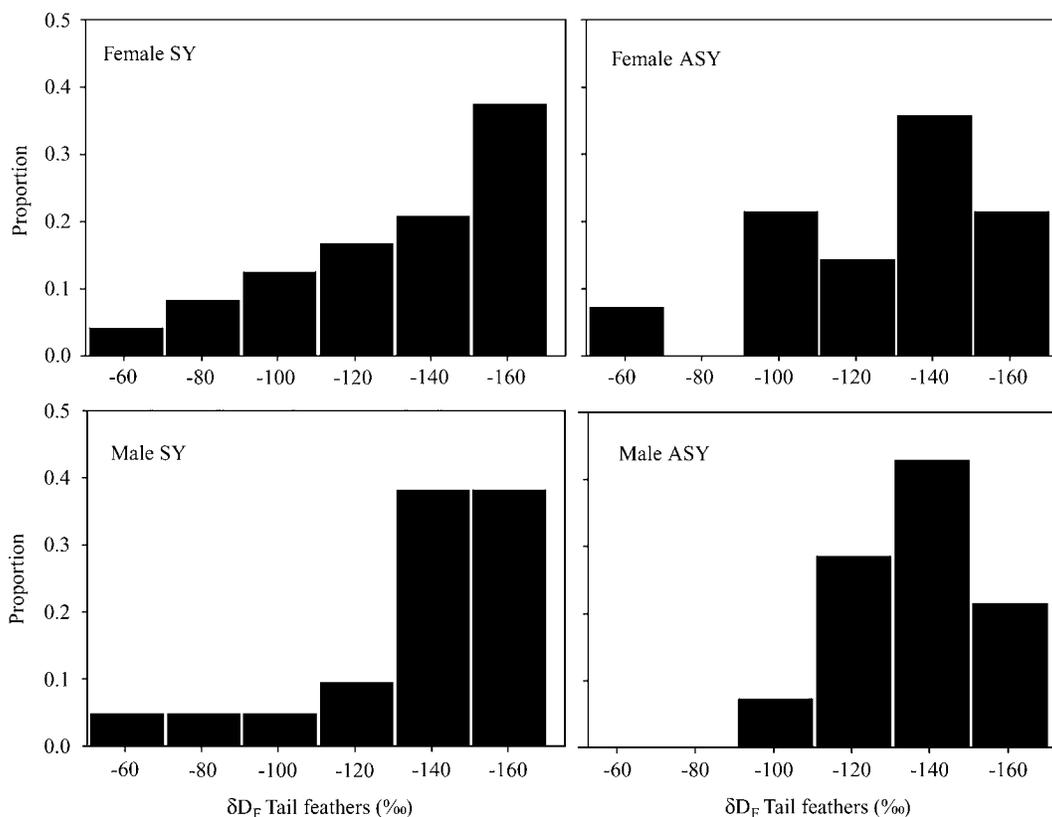


FIG. 3. Frequency distribution of tail-feather δD_f by age and sex for Swainson's Thrushes migrating through the Osa Peninsula, Costa Rica. δD_f values of -80‰ correspond to the approximate southern limit of the continuous breeding range, though small isolated populations exist south of this boundary (Evans Mack and Yong 2000; sample sizes: after-second-year [ASY] female = 14, second-year [SY] female = 24, ASY male = 14, SY male = 21).

Swainson's Thrush, which suggests that these feathers were grown after they had left the breeding area.

According to feather deuterium values, potential breeding destinations encompass a region from the boreal forest of western British Columbia across to eastern Manitoba and the Rocky Mountain range south to approximately Colorado (Fig. 1). Possible destinations based on the isotope approach also included western Alaska and central Québec. Areas of the breeding range that were unlikely included southeastern parts of the range in Ontario, southern Québec and the maritime provinces of Canada, and northern populations in the Yukon Territory and eastern Alaska. Examination of plumage at the time of banding also indicated that all individuals captured were from the continental clade (olive-backed group; Pyle 1997, Evans Mack and Yong 2000). This distinction helps remove west-coast breeding destinations, despite their possibility according to feather deuterium values.

Timing of migration and energy stores in relation to breeding latitude.—We examined timing of migration in relation to expected breeding latitude for sexes separately because, on average, males migrated through the site about six days earlier than females (males: 98.3 ± 1.0 [mean Julian date \pm SE]; females: 104.4 ± 1.2). Among males, we found little relationship between δD_f and date of passage at the study site, which suggests that birds moving to more northern breeding locations were not migrating through the

site earlier ($F = 1.97$, $df = 1$ and 50 , $P = 0.17$, $R^2 = 0.02$). This was also true when we examined male ASY and SY birds separately (ASY: $F = 0.01$, $df = 1$ and 12 , $P = 0.93$, $R^2 < 0.001$; SY: $F = 0.31$, $df = 1$ and 19 , $P = 0.59$, $R^2 = 0.02$). Among females, there was also little relationship between expected breeding latitude and date of passage when considering all ages combined ($F = 1.83$, $df = 1$ and 45 , $P = 0.18$, $R^2 = 0.04$) and known SY birds ($F = 0.41$, $df = 1$ and 22 , $P = 0.53$, $R^2 = 0.02$). However, although the sample size was small, known ASY females showed a tendency for earlier passage of individuals moving to more northern latitudes ($\beta = 0.17$ [95% CI: 0.03–0.31], $F = 6.56$, $df = 1$ and 12 , $P = 0.03$, $R^2 = 0.35$).

Mass–wing residuals showed a strong relationship to fat score (mass–wing residual = $-1.04 + 0.63 \cdot \text{Fat}$, $F = 29.94$, $df = 1$ and 107 , $P < 0.001$, $R^2 = 0.22$); therefore, we chose to use the residuals as an index of migratory condition. Although fat scores provide an index of condition, they are subjective and difficult to use in subsequent statistical analyses (Krementz and Pendleton 1990). Among males, there was no relationship between energetic condition and δD_f whether we considered all ages combined ($F = 1.31$, $df = 1$ and 49 , $P = 0.23$, $R^2 = 0.03$) or separate age groups (ASY: $F = 0.29$, $df = 1$ and 12 , $P = 0.60$, $R^2 = 0.02$; SY: $F = 2.31$, $df = 1$ and 19 , $P = 0.15$, $R^2 = 0.11$). There was also no relationship between energetic condition and δD_f for females (all ages: $F = 0.42$, $df = 1$ and 45 , $P = 0.52$, $R^2 = 0.01$; ASY: $F = 1.19$, $df = 1$ and 12 , $P = 0.30$, $R^2 = 0.09$;

SY: $F = 0.01$, $df = 1$ and 22 , $P = 0.93$, $R^2 = 0.0004$). These findings indicate that for both sexes, birds moving farther north were not carrying greater energetic reserves than their counterparts moving to more southerly latitudes.

DISCUSSION

Breeding destinations and migratory routes.—Recent genetics work has revealed that Swainson's Thrush is split into distinctive coastal and continental clades that diverged during the last glacial maxima (Ruegg and Smith 2002). The coastal clade winters from Mexico to northern Costa Rica and migrates through the western states to breed along the Pacific coast of North America. The continental clade primarily winters in South America from Colombia to northern Argentina, with smaller numbers in southern Costa Rica and Panama (Evans Mack and Yong 2000, Ruegg and Smith 2002, Kelly et al. 2005). Continental migrants move through Central America and enter North America along the Gulf Coast before spreading out to breeding locations across the boreal forest and interior western mountains from Alaska to eastern Canada and the northeastern United States (Yong and Moore 1997, Brewer et al. 2000, Evans Mack and Yong 2000, Ruegg and Smith 2002). Molecular and bioclimatic analyses have indicated range expansion for both the continental and coastal clades since the Pleistocene period. The circuitous migration route used by continental birds breeding in western and central areas of the range may be a historic artifact of the route used during cooler climates when the breeding range was restricted to southeastern North America (Ruegg and Smith 2002, Ruegg et al. 2006).

Although the migratory divide between coastal and continental clades is distinct, the extent to which different breeding populations within each clade use similar migratory routes is not as clear. Individuals passing through our study site on the Osa Peninsula of Costa Rica were of the continental group and were potentially moving to a broad area of the breeding range, but the core region appeared to be the west-central boreal forest of British Columbia to Manitoba and the interior western mountains. By contrast, few individuals appeared to be traveling to southeastern parts of the range in Ontario, Québec, and the Maritime provinces, or to northern parts of the range in the Yukon and eastern Alaska. Although western Alaska and central Québec were possible destinations, we suspect that this is simply attributable to these areas having rainfall δD values similar to those for locations in the core breeding region, especially given that areas adjacent to these regions were unlikely destinations (Fig. 1). Because δD values in North America primarily vary across north-south rather than east-west gradients, this approach is limited in identifying origins of species with broad longitudinal ranges (Wassenaar and Hobson 2001). Approaches that combine isotopic, morphological, and genetic markers may enhance resolution in these cases (Clegg et al. 2003, Hobson 2005, Boulet et al. 2006). The distribution of δD_f values for birds in our study was similar to that of individuals passing through Delta Marsh, Manitoba, in spring, which were also believed to be moving to the west-central boreal forest (Wassenaar and Hobson 2001). By contrast, birds migrating through southeastern Ontario, which likely bred in boreal regions of Ontario and Québec, had a higher proportion of values in the

range of -120% to -70% . We also noted a tendency for females to have slightly higher δD_f values than males. This could indicate differential migration distance of the sexes or a greater likelihood of molt-migration for adult females, because that group had the highest δD_f values. Alternatively, it may simply be a sampling artifact and further examination may be needed.

Individuals that wintered in South America likely reached the study area via one of two routes. First, they may have moved to the northwest coast of South America and made a water crossing, making landfall between the Azuero Peninsula of Panama and the Osa Peninsula of Costa Rica before moving northwest (Fig. 1). They may also have moved to northwest Colombia and into the Darién region of eastern Panama before heading west along the Isthmus. However, this seems less likely, because crossing over to the Pacific side would entail a slight southward movement and a likely crossing of the mountain ranges that run northwest to southeast throughout Central America. A few individuals may also have wintered in southwestern Costa Rica and western Panama, though the species is considered a rare winter resident in the region (Stiles and Skutch 1989). Furthermore, no Swainson's Thrushes were caught during mist-netting studies at the site over three eight-day periods from mid-December to early March of 2005–2006 (D. M. Collister unpubl. data). Using isotopic and genetic markers, Kelly et al. (2005) also suggested that Swainson's Thrushes from western South America likely bred in western areas of North America. If most birds moving along the Pacific coast of Costa Rica are from western and central breeding populations, it is unclear what routes are used by individuals from eastern populations. One possibility is that they winter farther to the northeast in South America and migrate up the east side of Central America. Swainson's Thrushes are common migrants on the Caribbean coast in spring and fall (Galindo et al. 1963, Stiles and Skutch 1989, Ralph et al. 2005). Individuals may also cross the Caribbean, though they are reportedly rare in the West Indies between March and May (Raffaele et al. 1998). Further isotope studies in northern areas of South America and along the Caribbean coast of southern Central America would help resolve potential wintering areas and migration routes of Swainson's Thrushes from west-central and eastern breeding origins.

Some adult Swainson's Thrushes molt during migration (Cherry 1985, Winker et al. 1992), which should be reflected in higher δD_f values than expected on the basis of breeding origin. Consistent with this, Wassenaar and Hobson (2001) found that δD_f values of ASY Swainson's Thrushes in spring were more enriched than those of hatch-year (HY) birds passing through the same sites in fall. By contrast, Kelly et al. (2005) found little evidence that adult Swainson's Thrushes had molted south of the breeding areas. In our study, δD_f values of ASY females were only slightly higher than those of SY females, whereas males of different ages did not differ. Because the δD_f values of the age groups are similar, this suggests that most adults molted on or near the breeding grounds. Given that these individuals were believed to be similar in origin to those passing through southern Manitoba, we are uncertain why these differences exist. The extent of molt-migration may vary annually, perhaps in relation to the onset or cessation of breeding. Extent of late-season reproductive effort and timing of breeding are suggested mechanisms behind variation in the timing of fall molt for American Redstarts (*Setophaga ruticilla*) and flycatchers

(*Empidonax* spp.), respectively (Norris et al. 2004, Rohwer et al. 2005). Swainson's Thrushes typically raise one brood and will renest only if the first is lost early in incubation (Evans Mack and Yong 2000). Thus, in years when breeding begins earlier, a larger proportion of individuals might complete molt on, or very close to, the breeding grounds.

Migration timing in relation to breeding latitude.—Stable-isotope analyses provide a means to test how timing of migration is influenced by previous breeding origin in fall or predicted breeding destination in spring. Early arrival on the breeding grounds often leads to higher reproductive success; thus, individuals can be expected to optimize arrival date with respect to spring conditions (Aebischer et al. 1996, Smith and Moore 2005). On this basis, we might predict a negative relationship between timing of spring migration and breeding latitude if the additional distance to northern breeding grounds requires an earlier departure from wintering areas. In contrast to this prediction, we found little evidence that individuals expected to breed farther north migrated earlier. Only ASY females appeared to show a pattern but, given the small sample size and the lack of a relationship in any other age–sex class, further research is necessary before drawing conclusions for this group. Our findings contrast with those for Wilson's Warblers at five locations in the southwestern United States where previous breeding latitude was related to timing of spring migration (Paxton et al. 2007). Although the strength of the relationship varied among sites, Wilson's Warblers that bred farther south and wintered farther north migrated earliest in spring. A separate study, on Wilson's Warblers in New Mexico, found no relationship between timing of spring passage and breeding latitude, whereas, in fall, individuals from northern breeding populations migrated earlier and wintered farther south than individuals from southern populations (Kelly et al. 2002). Other fall studies have indicated that Yellow Warblers (*Dendroica petechia*) from northern regions also migrate earlier than their southern conspecifics, whereas in Orange-crowned Warblers (*Vermivora celata*) and Common Yellowthroats (*Geothlypis trichas*), individuals from southern breeding areas precede those from the north (Kelly 2006; see also Smith et al. 2003). Along the Gulf Coast, there was no relationship between breeding origin and fall passage dates for Swainson's Thrushes or Gray Catbirds (*Dumetella carolinensis*; Hobson et al. 2007).

Several factors may explain the lack of a relationship between timing of spring passage and breeding latitude in our study. First, these analyses assume that deuterium measurements accurately reflect an individual's breeding destination. Variability in the relationship of δD_p to δD_f may occur across regions and taxa (Wunder et al. 2005, Lott and Smith 2006, Wassenaar and Hobson 2006). These sources of uncertainty could make it difficult to identify a relationship statistically, particularly in spring, when the period of migration is shorter. However, Hobson et al. (2007) found that varying the δD_p -to- δD_f discrimination factor had a minimal effect on depiction of breeding origins using this approach. Ecological factors might also explain our results. One possibility is that distance from the wintering area affects timing in spring, as possibly observed in Wilson's Warblers (Paxton et al. 2007). The individuals in our study may have wintered across a wide range of latitudes from southern Central America to northern Argentina, and passage dates may be influenced by distance traveled to that point. Spring phenology is also delayed with increasing latitude,

and there may be consequences for individuals that arrive too early if they experience inclement weather on the breeding grounds (Brown and Brown 2000). In spring, Swainson's Thrushes migrate at rates of 300 km day^{-1} (Yong and Moore 1997), and it may not be necessary for northern birds to migrate earlier if the rate of travel is sufficient to compensate for the delay in optimal arrival date at higher latitudes. In fact, if spring phenology in northern areas is sufficiently delayed in relation to migration rates, we might predict that birds from southern breeding populations would migrate earliest. It is also possible that northern birds depart wintering areas at the same time as southern birds but migrate faster. If that is the case, the disparity in timing between individuals traveling to different latitudes may still be small by the time they reach an early stopover site such as Costa Rica.

Energetic reserves in relation to breeding latitude.—For most migrants, the energy needed to move between breeding and wintering areas exceeds the amount they can carry, requiring them to make several stopovers *en route* (Hedenström and Alerstam 1997). Different strategies may be used to meet these requirements. One strategy is to begin migration with large reserves, which helps minimize time spent at stopover sites and lowers the likelihood of predation and delayed arrival on the breeding or wintering grounds (Lindström and Alerstam 1992, Bayly 2006). However, high fat loads may affect flight performance. An alternative strategy is for individuals to begin migration with relatively modest energy stores and build them up as required (Schaub and Jenni 2000a). During autumn migration, several European long-distance migrants have the highest energy stores just before crossing the Mediterranean Sea and the Sahara Desert (Schaub and Jenni 2000b, Rubolini et al. 2002). North American wood warblers also tend to carry higher fat stores in the southeastern United States, likely in preparation for crossing the Gulf of Mexico (Kelly and Hutto 2005). Thus, an individual's reserves may be influenced by the distance traveled during migration, the distance that remains, and the location of the stopover site in relation to geographic barriers. The strategy used may also differ among species in relation to diet, density, and the predictability of food sources (Schaub and Jenni 2000a), as well as the different constraints during spring and fall migration (Hedenström and Alerstam 1997).

We found no evidence that males or females moving to more northern breeding areas carried greater energetic reserves than birds moving to more southern latitudes. This contrasts with the findings of an orientation study on Swainson's Thrush in Illinois, where heavier birds had a more westerly orientation than light birds, possibly because they were traveling to more distant areas of the breeding range in Alaska and northwest Canada (Cochran and Wikelski 2005). Regardless of their final destination, the Osa Peninsula will be an early stopover and individuals will not be carrying sufficient reserves to reach the boreal forest of North America. Across much of the spring migration route, Swainson's Thrushes have short stopovers and display migratory restlessness, even with modest energetic reserves that would suggest they use a "feed-by-day, fly-by-night" strategy except when approaching major geographic barriers (Winker et al. 1992; Yong and Moore 1993, 1997; Cochran and Wikelski 2005). Individuals passing through Costa Rica would not likely encounter a barrier until the Gulf of Mexico, so reserves carried at this stage may be more reflective of their requirements through the remaining section of

Central America. The additional energy required by individuals traveling farther north might be more apparent at sites closer to the breeding grounds. Individuals passing through our site may also have wintered across a wide range of latitudes, and distance traveled to that point likely affected reserves, particularly if some had made an ocean crossing from South America before reaching the site.

Our knowledge of migratory connectivity and migration routes of Neotropical migrant species has increased considerably in recent years, in large part thanks to advances in stable-isotope analysis. Most of these studies come from species that mainly overwinter in the Caribbean region, northern Central America, and Mexico (Hobson and Wassenaar 1997, Hobson et al. 2001, Boulet et al. 2006, Norris et al. 2006, Paxton et al. 2007), whereas fewer data exist for species that primarily overwinter in South America. These knowledge gaps impede the conservation of the many Neotropical migrants that overwinter in and migrate through these areas. Increased research emphasis toward regions in southern Central America and South America would provide crucial data for these species, which is particularly important given the rapid and extensive habitat loss occurring throughout many of these regions (Achard et al. 2002).

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