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CHAPTER 1

MIGRATORY CONNECTIVITY OF A WIDELY DISTRIBUTED SONGBIRD, THE AMERICAN REDSTART (*SETOPHAGA RUTICILLA*)

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ABSTRACT.—Determining the degree of connectivity between breeding and wintering populations is critical for understanding the ecology and evolution of migratory systems. We analyzed stable hydrogen isotopic compositions in tail feathers (δD_w) collected from 26 sites in 11 countries throughout the wintering range of the American Redstart (*Setophaga ruticilla*), a Nearctic–Neotropical migratory passerine bird. Feathers were assumed to have molted on the breeding grounds, and δD_w was used to estimate breeding origin. Values of δD_w were highly correlated with longitude of sampling location, indicating that breeding populations were generally distributed along the east–west axis of the wintering grounds. Within the Caribbean region, Florida, and Bahamas, δD_w values were negatively correlated with winter latitude, which suggests that American Redstarts exhibit a pattern of chain migration in which individuals wintering at northern latitudes are also the most northern breeders. To identify the most probable breeding regions, we used a likelihood-assignment test incorporated with a prior probability of breeding abundance using Bayes's rule. Expected δD values of feathers from five breeding regions were based on interpolated δD values from a model of continent-wide growing-season δD values in precipitation (δD_p) and were adjusted to account for a discrimination factor between precipitation and feathers. At most wintering locations, breeding assignments were significantly different from expected frequencies based on relative breeding abundance. Birds wintering in eastern and western Mexico had a high probability of breeding in northwest and midwest North America, whereas birds in the Greater and Lesser Antilles were likely to have originated from breeding regions in the northeast and southeast, respectively. Migratory connectivity, such as we report here, implies that the dynamics of breeding and nonbreeding populations may be linked at a regional scale. These results provide a key opportunity for studying the year-round ecology and evolution of spatially connected populations in a migratory species. Received 12 September 2005, accepted 25 May 2006.

RESUMEN.—Es importante determinar el grado de conectividad entre las poblaciones en reproducción y las poblaciones en invernada, para entender la ecología y evolución de los sistemas migratorios. Analizamos la composición isotópica de hidrógeno estable (δD_w) en plumas de la cola de *Setophaga ruticilla*, una especie de ave migratoria Neártica–Neotropical, colectadas a lo largo de las áreas de invernada en 26 sitios en 11 países. Se admitió que las plumas habían crecido en los sitios de anidación y δD_w se usó para estimar el origen de nacimiento. Los valores de δD_w estuvieron altamente correlacionados con la longitud de las localidades muestreadas, lo que indica que las poblaciones en reproducción estuvieron, por lo general, distribuidas a lo largo del eje este-oeste de los sitios de invernada. Los valores de δD_w , dentro de la región caribeña, Florida

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y Bahamas, estuvieron negativamente correlacionados con la latitud invernal, lo que sugiere que *Setophaga ruticilla* presenta un patrón de migración en cadena en el cual los individuos que pasan el invierno en latitudes más norteñas también son los que se reproducen más al norte. Para identificar las regiones de reproducción más probables, utilizamos una prueba de probabilidad de asignación incorporada con una probabilidad a priori de abundancia reproductiva usando la regla de Bayes. Los valores esperados de δD de las plumas de cinco regiones de reproducción se basaron en valores interpolados de δD de un modelo de crecimiento estacional de valores de δD , a lo largo del continente, en la precipitación (δD_p) y se ajustaron para explicar un factor de discriminación entre la precipitación y las plumas. En la mayoría de las localidades de invernada, las asignaciones reproductivas fueron significativamente diferentes de las frecuencias esperadas basadas en la abundancia relativa de reproductores. Las aves que invernaron en el este y oeste de México tuvieron una alta probabilidad de reproducirse en el noroeste y medio oeste de América del Norte, mientras que las aves en las Antillas mayores y menores probablemente se originaron en zonas de reproducción en el noreste y sureste, respectivamente. La conectividad migratoria, como la que reportamos aquí, involucra que la dinámica de las poblaciones en reproducción y fuera de la temporada reproductiva puede estar ligada en una escala regional. Estos resultados ofrecen una oportunidad clave para el estudio del ciclo anual ecológico y evolutivo de las poblaciones conectadas espacialmente en especies migratorias.

ONE OF THE primary obstacles to understanding the ecology and evolution of migratory animals is the inability to determine the degree to which breeding and nonbreeding periods are geographically linked (Myers et al. 1987, Holmes and Sherry 1992, Dolman and Sutherland 1995). Long-distance migration is a widespread phenomenon among birds. In the northern hemisphere, for example, well over half of temperate-breeding species spend their stationary nonbreeding season in the tropics (Rappole 1995, Newton and Dale 1997). Knowledge about the degree of connectivity between breeding and nonbreeding populations, unfortunately, exists for only a few birds, most of which are large-bodied geese, ducks, and coastal waders (see reviews in Alerstam 1990, Bairlein 2001). Passerines, in contrast, are typically wide-ranging, short-lived, and small-bodied, characteristics that make them difficult to track year-round with conventional techniques. Nonetheless, passerines constitute the majority of global avian diversity (Sibley and Monroe 1990) and represent most of the estimated 10 billion individuals that migrate between the tropics and northern temperate zones each year (Moreau 1972, Alerstam 1990).

Determining migratory connectivity is essential for understanding the factors that limit and regulate migratory species throughout their annual cycle (Holmes and Sherry 1992, Dolman and Sutherland 1995, Sherry and Holmes 1996). In the past few decades, several migratory passerines have declined in all or parts of their breeding range (Sauer and Droege 1992,

Peterjohn et al. 1995). Potential limiting factors have been identified during the breeding (e.g., Robinson et al. 1995, Rodenhouse et al. 2003), wintering (e.g., Baillie and Peach 1992, Sillett et al. 2000, Marra and Holmes 2001), and migration (e.g., Moore et al. 1995, Sillett and Holmes 2002) periods. We are just now beginning to uncover how events within these periods can carry over to affect individual success in subsequent seasons (Marra et al. 1998; Gill et al. 2001; Norris et al. 2004a, b; Saino et al. 2004), which implies that population abundance is controlled by the interaction of events throughout the annual cycle (Sherry and Holmes 1996, Norris 2005). Without knowing the degree of connectivity between breeding and nonbreeding areas, however, it is impossible to understand fundamental biological processes of migratory animals, such as how population dynamics in one season are connected to population dynamics in a subsequent season (Marra et al. 2006). Understanding patterns of connectivity may also reveal important insights about other facets of migratory biology, such as the evolution of migration, genetic structuring, and life-history trade-offs (Webster et al. 2002, Marra et al. 2006).

Stable isotope techniques have improved our ability to link breeding and wintering populations (Chamberlain et al. 1997, Hobson and Wassenaar 1997, Kelly et al. 2002). Stable hydrogen isotopes ($^2\text{H}/^1\text{H}$: δD), in particular, are a valuable geographic marker in North America because of their strong correlation with continent-wide patterns of precipitation (Cormie et al. 1994,

Bowen and Revenaugh 2003). Hydrogen isotopic compositions are transferred through a primary producer to higher-order consumers (Cormie et al. 1994), including birds (Chamberlain et al. 1997, Hobson and Wassenaar 1997). Many migratory passerines undergo a complete molt on the breeding grounds before migration (Pyle 1997) and, because feathers are metabolically inert after they are grown, hydrogen isotopes sampled from feathers on the wintering grounds can provide a signature of breeding location (Chamberlain et al. 1997, Hobson and Wassenaar 1997, Wassenaar and Hobson 2000a).

Recent studies using stable isotopes have shown promise for uncovering patterns of migratory connectivity over large geographic ranges. Black-throated Blue Warblers (*Dendroica caerulescens*), for example, are dispersed along a longitudinal axis of the West Indies, where eastern wintering populations are more likely to breed at southern temperate latitudes and western populations are more likely to breed at northern latitudes (Rubenstein et al. 2002). In the eastern hemisphere, stable isotope analysis has shown that two subspecies of Willow Warblers (*Phylloscopus trochilus trochilus* and *P. t. acredula*) segregate on their African wintering grounds in accordance with a migratory divide on the breeding grounds in Scandinavia (Chamberlain et al. 2000).

Here, we present an analysis of the migratory connectivity of the American Redstart (*Setophaga ruticilla*; hereafter "redstart"), a Nearctic–Neotropical migratory songbird, which has a transcontinental range on both the breeding and nonbreeding grounds. With the exception of a small number of band recaptures (Fig. 1A), the degree of connectivity and migration patterns in redstarts between the breeding and nonbreeding grounds are essentially unknown. We analyzed hydrogen isotopic compositions from individuals captured on 26 sites in 11 countries across the wintering range (Fig. 1B and Table 1). We used assignment tests derived from Bayes's rule to predict the breeding origin of redstarts sampled across their stationary nonbreeding range. The broad distribution of this species also allowed us to investigate general patterns of migration. Using general linear models, we examined whether breeding populations were spatially correlated with longitudinal and latitudinal axes of the nonbreeding grounds. This allowed us to examine poorly known patterns of migration,

such as leap-frog or chain migration (Lundberg and Alterstam 1986, Boland 1990).

METHODS

Study species.—American Redstarts are small (9 g) Nearctic–Neotropical migratory passerines that breed in mixed deciduous–coniferous forests throughout North America, from British Columbia to Newfoundland and as far south as Louisiana (Sherry and Holmes 1997, Sauer et al. 2004; Fig. 1A). During the stationary nonbreeding period, individuals occupy a variety of habitats, including mangrove forests, lowland forests, and dry forests primarily in Mexico, Central America, northern South America, the Caribbean, the Bahamas, and southern Florida (Fig. 1A). Low densities occur in Bermuda, Ecuador, and Peru (Sherry and Holmes 1997, D. R. Norris and P. P. Marra pers. obs.).

Winter sampling sites.—We collected tail feathers (third rectrix; $n = 188$) from redstarts across their stationary nonbreeding range (60.6–105.7°W and 9.3–32.2°N; Fig. 1B and Table 1). Individuals were lured into a mist net using a taxidermy mount of a redstart along with a playback consisting of male song from the breeding grounds and chip notes recorded on the nonbreeding grounds. Most feathers were collected between 2001 and 2004, with the exception of Dominican Republic (1997; $n = 11$) and Belize (1999; $n = 10$). We defined *a priori* three distinct wintering regions on the basis of island–mainland classification and geographic proximity: (1) the "Caribbean," including all sampling sites in the Caribbean, as well as the Bahamas and the southern tip of Florida; (2) "middle America," including sites in Central America and Mexico; and (3) "Bermuda," which we believed was far enough away from other locations to be classified separately. Within regions, we defined 12 wintering locations that were essentially separate countries, but with eastern and western Mexico split because of geographic distance and the separation of the locations by the Sierra Madre mountains. Each wintering location typically had multiple *sites* which were specific areas where redstarts were sampled (listed in Table 1).

To test for year effects, we collected feathers in multiple years from eastern Mexico (2001–2003) and Jamaica (2001, 2003). Stable hydrogen isotopic compositions from feathers sampled on the wintering grounds (δD_w) were not significantly different between years (eastern Mexico: $F = 0.13$, $df = 2$ and 24 , $P = 0.88$; Jamaica: $F = 0.01$, $df = 1$ and 16 , $P = 0.91$), so data were pooled. Table 1 shows sample sizes grouped by sex and age classes (after hatch year [AHY] and hatch year [HY]).

For the purposes of this paper, we refer to any individual in the first year of life, starting from the approximate time they were born (May–July), as an

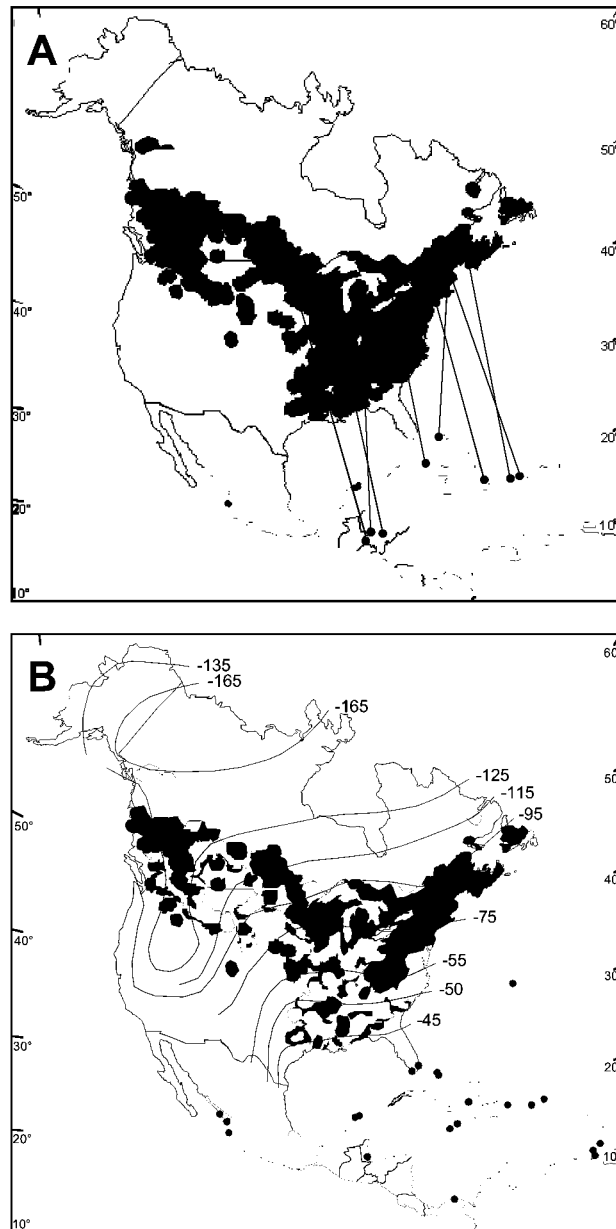


FIG. 1. (A) Banding locations of American Redstarts on breeding grounds (dark gray; Sauer et al. 2004) and recovery points on wintering grounds (light gray; Sherry and Holmes 1997) connected by a straight line ($n = 8$; data from Bird Banding Laboratory, Canadian Wildlife Service, 1924–2002). (B) Contour lines with δD values of songbird feathers (from Wassenaar and Hobson 2001; δD values are uncorrected for differences in atmospheric hydrogen exchange but corrected for the discrimination factor between precipitation and feathers; see text) overlaid with breeding density of American Redstarts (from Breeding Bird Survey [BBS]). Low breeding densities are light gray, high breeding densities are black. Five shades correspond to BBS density categories (number of individuals per 24.5 km survey route). Projection for both maps is Lambert Zenithal Equal-Area. Black dots indicate the location of sampling sites on the wintering grounds.

TABLE 1. Stable hydrogen isotopic compositions (mean \pm SE) of feathers (δD_w) sampled in each region, country, and site and their geographic coordinates, along with age (after hatch year [AHY] and hatch year [HY]) and sex of American Redstarts.

| Country | δD_w (mean \pm SE) | Site | Latitude (°N) | Longitude (°W) | AHY ^a | | HY ^a | | Total |
|-------------------------------|---------------------------------|------------------|------------------|-------------------|------------------|---|-----------------|---|-------|
| | | | | | M | F | M | F | |
| Middle America region | | | | | | | | | |
| Belize | -96 \pm 4 | Punta Gorda | 16.10 | -88.80 | 2 | 1 | 2 | - | 5 |
| | | Silver Creek | 16.27 | -88.88 | 2 | 2 | 1 | - | 5 |
| Mexico (eastern) ^b | -108 \pm 3 | Celustun | 20.87 | -90.40 | 8 | 7 | 4 | 7 | 26 |
| | | Hampolol | 19.93 | -90.40 | - | 1 | - | - | 1 |
| Mexico (western) ^b | -107 \pm 3 | Puerto Vallarta | 20.62 | -105.25 | 3 | - | - | 1 | 4 |
| | | San Blas | 21.52 | -105.27 | 1 | 3 | 4 | - | 8 |
| | | Santa Cruz | 22.50 | -105.72 | 2 | - | 1 | 1 | 4 |
| Panama | -88 \pm 4 | Bocas del Toro | 9.33 | -82.25 | 6 | 1 | 2 | 1 | 10 |
| Caribbean region | | | | | | | | | |
| Bahamas | -82 \pm 3 | Andros Town | 24.70 | -77.77 | 5 | 4 | 1 | - | 10 |
| | | Stanaird Creek | 24.83 | -77.88 | 2 | 2 | 1 | 2 | 7 |
| Cuba | -94 \pm 4 | Guantanamo Bay | 20.15 | -75.21 | 5 | 5 | 2 | 1 | 13 |
| Dominican Republic | -70 \pm 4 | Jarabacoa | 19.12 | -70.63 | 5 | 1 | 4 | 1 | 11 |
| Jamaica | -79 \pm 2 | Black River | 18.02 | -77.85 | 6 | 5 | 1 | - | 12 |
| | | Coleyville | 18.20 | -77.52 | 2 | 2 | 2 | 1 | 7 |
| | | Windsor | 18.37 | -77.62 | - | 1 | - | - | 1 |
| Puerto Rico | -78 \pm 3 | Cabo Rojo | 18.09 | -67.15 | 2 | - | 1 | 1 | 4 |
| | | Ceiba | 18.27 | -65.65 | 2 | 4 | 2 | 1 | 9 |
| | | Maricao | 18.18 | -66.98 | 1 | - | 1 | - | 2 |
| | | Rio Abajo | 18.43 | -66.39 | - | 2 | - | - | 2 |
| | | Utuado | 18.27 | -66.70 | - | - | 2 | - | 2 |
| | | Vieques | 18.15 | -65.45 | - | 1 | 1 | - | 2 |
| Trinidad and Tobago | -48 \pm 2 | Parlatuvier (TO) | 11.30 | -60.65 | 5 | 1 | - | - | 6 |
| | | Cacandee (TR) | 10.55 | -61.43 | 1 | 2 | 3 | 1 | 7 |
| | | Oropuche (TR) | 10.60 | -61.10 | 1 | - | 1 | - | 2 |
| USA (Florida) | -84 \pm 2 | Flamingo | 25.14 | -80.93 | 9 | 2 | 7 | - | 18 |
| Bermuda | | | | | | | | | |
| Bermuda | -85 \pm 4 | Hamilton | 32.29 | -64.78 | - | - | 5 | 5 | 10 |

^aAHY = after hatch year (>1 year old); HY = hatch year (<1 year old).

^bEastern and western Mexico were treated as different "countries" because of the large distance between locations.

HY bird. Similarly, AHY birds are individuals in the second year of life or later. This is different from the conventional definition of these age classes, in which individuals are classified as HY up to and including 31 December of the year in which they were born, after which they are classified as AHY (Pyle 1997). Using the conventional definition would make the presentation of our results difficult to interpret, because first-year male redstarts were sampled throughout the wintering season but retained female-like plumage until they molted after their first breeding season (Sherry and Holmes 1997). Males with female-like plumage, therefore, would be placed in different age categories based on the time they were sampled.

Stable isotope analysis.—Stable hydrogen isotope ratios ($^2\text{H}/^1\text{H} = R$) are reported in delta (δ) notation, in per-mil units (‰), where $\delta = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1,000$ and R_{standard} is the hydrogen isotope ratio of Vienna standard mean ocean water (V-SMOW). Feathers were cleaned of surface oils using a 2:1 chloroform:methanol solution and left to air dry. Because a fraction of the hydrogen in feathers rapidly exchanges with ambient moisture (Wassenaar and Hobson 2000b), feathers were equilibrated with local atmosphere for 72 h to ensure that all samples had an equal opportunity to exchange with the local atmosphere. To control for potential seasonal differences in atmospheric moisture of δD values in the laboratory, all analyses were performed within a span of two months in 2004. We cut a small portion (approximately 0.1–0.15 mg) from the tip of each tail feather (third rectrix), loaded them separately into silver capsules, and heated them at 100°C for 24 h to remove potential surface water. After the capsules were crushed, they were loaded into a reduction furnace (Finnigan TC/EA, Thermo Electron Corporation, Waltham, Massachusetts) at 1,450°C, and introduced on-line to an isotope-ratio mass spectrometer (Finnigan MAT Delta Plus XL). We ran three in-house standards (mean \pm SD): brucite (from University of Michigan; $-89 \pm 4.4\text{‰}$, $n = 13$), Georgia kaolinite clay ($-56 \pm 5\text{‰}$, $n = 49$), and domestic chicken (*Gallus gallus domesticus*) tail feathers ($-93 \pm 2.5\text{‰}$, $n = 12$). All standards closely matched values previously run in the laboratory. In addition to these standards, we ran duplicates (within the same run) of tail feather from the same individual redstart ($n = 21$), which produced a mean difference of 3.1‰ (± 0.5 SE).

Statistical analyses and assignment test.—We evaluated broad-scale migration patterns using general linear regression models (GLM: analysis of covariance with interaction effects) with δD values from feathers (δD_w) as the dependent variable. First, we examined the effects of age, sex, and wintering longitude (plus two-way and three-way interactions between all variables) on δD_w sampled across the entire wintering range. Given that latitude and longitude were weakly correlated ($r^2 = 0.14$, $P < 0.0001$, $n = 178$), we chose to include longitude in

the primary model, because longitude encompassed a much larger degree range (45°W, range: -61°W to -106°W) than latitude (16°N, range: 9°N to 25°N [excluding Bermuda]). However, we compared *post hoc* univariate models (ordinary least-squares regression) with both latitude and longitude as separate predictor variables. Second, given our results in the longitudinal analysis of all sites, we examined the effect of sex, age, and latitude (plus interactions) on δD_w within each of the two wintering regions. The purpose of this analysis was to explore whether the predictability of latitude increased when δD_w was examined separately between the Caribbean and middle America regions. In all cases, we used univariate regression analysis to display the relationship between the significant predictor variables generated from the GLMs and δD_w values. Values of δD_w were normally distributed within each region and for all sites combined (Shapiro-Wilks' test for normality, $P > 0.05$). All data are reported as means \pm SE, and all tests were considered significant at $\alpha \leq 0.05$.

To examine specific breeding origins of redstarts sampled on the wintering grounds, we applied a likelihood assignment test incorporating Bayes's rule (Royle and Rubenstein 2004). In general, this procedure produced two types of assignments to estimate breeding origin: the first is based on likelihood analysis of δD values, and the second combines the likelihood analysis with relative breeding abundance using Bayes's rule. This approach uses relative breeding abundance as a prior probability and combines it with the observed data (δD values from feathers sampled on the nonbreeding grounds: δD_w) to determine the posterior probability of the most likely breeding origin for each individual. Below we outline the steps for these assignment tests.

First, we defined five breeding regions (northwest [NW], midwest [MW], northeast [NE], central-east [CE], and southeast [SE]) based on a combination of breeding density data from the Breeding Bird Survey (BBS; Sauer et al. 2004; Fig. 1A) and continent-wide patterns of δD (Wassenaar and Hobson 2001; Fig. 1B). More specifically, boundaries between the NW, MW, and NE regions were chosen on the basis of three core areas of high breeding density in the northern range (Fig. 1A). *A priori*, we also knew that these areas would yield distinct δD values in precipitation (Fig. 1B). Boundaries between the NE, CE, and SE regions were chosen on the basis of known latitudinal differences in δD values between these areas (Fig. 1B); each region also had an area of high breeding density, judging from BBS data.

Next, to estimate the probability distribution of δD values from feathers in each breeding region (δD_b), we estimated probability distributions of δD in precipitation (δD_p) within each breeding region and adjusted these distributions to account for isotopic discrimination between δD_p and δD_b . Means and standard deviations of δD_p values were extracted from an equal-area

grid (North American Lambert equal-area projection) of long-term average growing-season δD_p (growing season defined as months with mean temperature $>0^\circ\text{C}$; Bowen et al. 2005) using the SPATIAL ANALYST extension of ARCGIS, version 9.0 (ESRI, Redlands, California). Isotopic discrimination factors between δD_p and the δD of passerine feathers (δD_f) have been estimated previously on the basis of data for North American songbirds that span much of the redstart breeding range (e.g., Hobson and Wassenaar 1997). Here, we use a discrimination factor of -19% between precipitation and feathers derived from the Hobson and Wassenaar (1997) data set by Bowen et al. (2005). These were the same growing-season precipitation grids used for assignment tests of redstarts in the present study. However, because neither the calibration data set of Hobson and Wassenaar (1997) nor the redstart data reported here have been corrected for exchangeable hydrogen, we expected that a systematic offset exists between the absolute δD_f values in each study, as a result of differences in the δD values characteristic of atmospheric moisture in the different geographic locations where the feathers were analyzed. Therefore, we applied a final correction to the isotope discrimination factor to account for expected geographic differences between values analyzed in our lab (Kingston, Ontario) and the location of analysis for the calibration data (Saskatoon, Saskatchewan). Assuming that δD values in ambient moisture are correlated with δD_p values, we used estimates of the mean annual δD_p values at each site (Saskatoon: -118% ; Kingston: -69% ; see Acknowledgments; Bowen and Revenaugh 2003) to approximate the difference in δD values for atmospheric moisture at each lab (49%). Assuming that 13% of feather hydrogen is exchangeable under laboratory conditions (Chamberlain et al. 1997), δD values measured here should be $\sim 6\%$ heavier than those measured by Hobson and Wassenaar (1997) because of hydrogen exchange with atmospheric moisture. Adjusting the estimated discrimination factor upward by 6% gave a best-estimate discrimination factor of -13% . Although we believe that the discrimination factor incorporating the 6% adjustment is most appropriate, we note that the percentage of difference in assignments (see calculations below) made using discrimination factors of -13% and -19% was only 9% (17 of 188 individuals). We also acknowledge that the use of a "global" value assumes that there are no regional differences in discrimination between δD_p and δD_f , but we have no *a priori* hypothesis to suggest how this would vary over large geographic areas, and regression lines suggest that residuals between δD values in precipitation and feathers are normally distributed (Chamberlain et al. 1997, Hobson and Wassenaar 1997).

Given information on the mean and SD of δD_b for each breeding region (Table 2), we then calculated likelihood-based assignments for each individual sampled on the wintering grounds (δD_w). The estimated

TABLE 2. Relative breeding abundance (proportion of birds estimated from Breeding Bird Survey [BBS] data) and stable hydrogen isotopic compositions in feathers (δD_b : mean \pm SD) from five *a priori* defined breeding regions of American Redstarts in North America. See Figure 3 for delineation of breeding areas.

| Breeding region | $f(b)^a$ | δD_b^b (mean \pm SD) |
|-------------------|----------|-----------------------------------|
| Northwest (NW) | 0.251 | -118.5 ± 13.6 |
| Midwest (MW) | 0.224 | -102.3 ± 14.2 |
| Northeast (NE) | 0.381 | -77.5 ± 5 |
| Central-east (CE) | 0.113 | -63.4 ± 5.9 |
| Southeast (SE) | 0.031 | -50.8 ± 7.8 |

^a Relative breeding abundance from BBS data; see text.

^b Estimate of stable hydrogen isotope values in feathers from growing-season δD in precipitation; see text.

probability distribution of y (where $y = \delta D_b$) for each breeding area can be expressed by $f(y|b)$; where $b = \text{NW, MW, NE, CE, SE}$. An individual sampled on the wintering grounds yields a value of y^* (where $y^* = \delta D_w$), and the likelihood of it originating from a given breeding region can be evaluated by $f(y^*|b)$, given $y^* = y$. Assuming y is normally distributed with a mean (μ_b) and standard deviation (σ_b) estimated from above, the likelihood corresponding to y^* is:

$$f(y^*|\mu_b, \sigma_b) = \frac{1}{\sqrt{2\pi}\sigma_b} \left[-\frac{1}{2\sigma_b^2}(y^* - \mu_b)^2 \right] \quad (1)$$

Individuals sampled on the wintering grounds, therefore, generate a probability of origin for each breeding region, and the most likely breeding origin is the one that has the largest $f(y^*|b)$.

In terms of probability assignments, however, the most likely breeding origin will also be influenced by the relative abundance between breeding regions ($f(b)$; Royle and Rubenstein 2004). In such cases, $f(b)$ may be considered a prior probability (i.e., the probability that a random individual on the wintering grounds originates from a breeding area [b] in the absence of any information about δD_w). To estimate $f(b)$, we downloaded interpolated abundance data assigned to each BBS vector grid cell within the study area (Sauer et al. 2004) and calculated the mean cell value within each breeding region using ARC GIS. We then calculated $f(b)$ by dividing the mean value for each breeding region by its total area (Table 2).

Using the conditional probability $f(b|y^*)$, $f(b)$ can be incorporated into the assignment test as a prior probability using Bayes's rule:

$$f(b|y) = \frac{f(y|b)f(b)}{f(y)} \quad (2)$$

Where $f(y)$ is a normalizing constant:

$$f(y) = \sum_b f(y|b)f(b) \quad (3)$$

Here, $f(y|b)$ is the likelihood assignment outlined above, and $f(b)$ is the relative abundance for each breeding region. For each individual, the assignment yields probabilities of origin for each breeding region, where the most likely origin (denoted hereafter as \hat{b}) is the breeding region with the largest $f(b|y^*)$.

Using goodness-of-fit, we tested the frequency distribution of \hat{b} , $f(\hat{b})$, for each wintering location against the null hypothesis that individuals have an equal probability of breeding in a given region (i.e., $H_0: f(\hat{b}) = f(b)$). For some breeding regions, expected frequencies were less than one, so we used Fisher's exact test (Zar 1996). We combined data from Panama and Belize because these locations had the same sample size ($n = 10$) and $f(\hat{b})$. We also compared $f(\hat{b})$ between locations from middle America and the Caribbean using a 2×5 contingency-table chi-square test. Because different numbers of individuals were sampled at each location, we adjusted for equal sample sizes by calculating $f(\hat{b})|n = 10$. However, we recognize that this adjustment may not accurately represent the sample distribution, because of potential differences in abundance between nonbreeding sites.

RESULTS

A general linear model that included age, sex, and wintering longitude of each sampling site (see Table 1), plus interactions, explained 50% of the variation in δD_w ($F = 23.0$, $df = 7$ and 170 , $P < 0.0001$). Longitude was the only significant predictor variable ($F = 135$, $df = 1$ and 170 , $P < 0.0001$; all others: $P > 0.05$; Fig. 2A), but age approached significance ($F = 3.3$, $df = 1$ and 170 , $P = 0.07$), with HY individuals ($-89 \pm 3\text{‰}$) having slightly but not significantly lighter δD_w values compared with AHY individuals ($-84 \pm 2\text{‰}$). To examine the robustness of this model, we re-ran it, excluding six sites lying on the extreme ends of the longitudinal gradient (located in western Mexico and Trinidad-Tobago). The model still explained a significant portion of the variation ($r^2 = 0.33$, $F = 9.65$, $df = 7$ and 139 , $P < 0.0001$), and longitude was again the best predictor variable ($F = 6.91$, $df = 1$ and 139 , $P < 0.0001$). Although latitude was also a significant predictor of δD_w ($r^2 = 0.13$, $P < 0.0001$, $n = 178$), it explained a much smaller portion of the variance compared with longitude ($r^2 = 0.48$; see Fig. 2A).

Next, we examined the effect of age, sex, and wintering latitude, plus interactions on δD_w values within each major geographic wintering

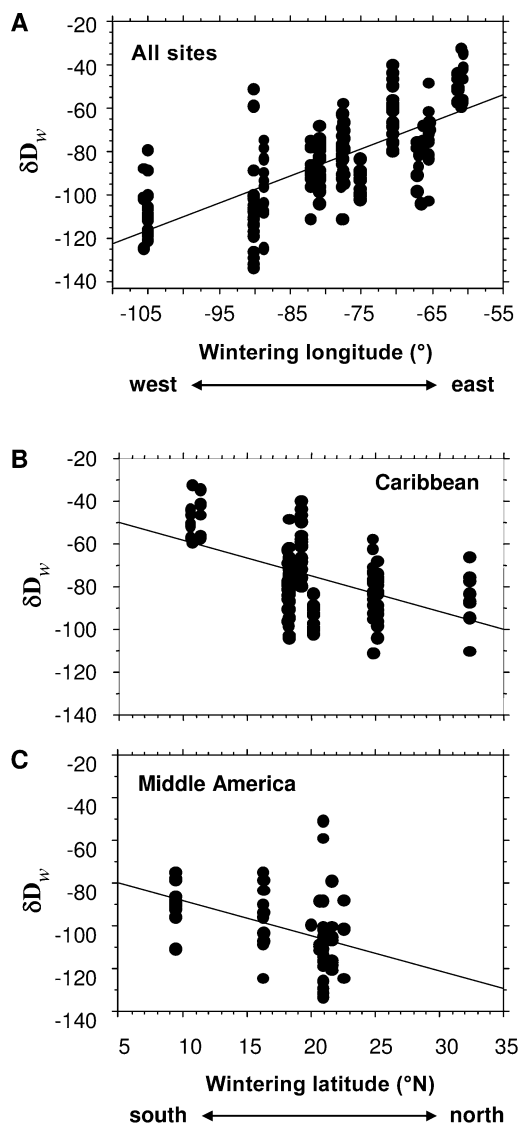


FIG. 2. Relationship between stable hydrogen isotopic compositions in tail feathers of American Redstarts sampled on wintering grounds (δD_w) and (A) longitude of winter sampling site (all sites combined, Bermuda excluded; $r^2 = 48$, $P < 0.0001$, $n = 178$), and latitude of winter sampling sites within (B) the Caribbean (including Florida and the Bahamas; $r^2 = 0.36$, $P < 0.0001$, $n = 115$), and (C) middle America (including eastern and western Mexico; $r^2 = 0.18$, $P < 0.0005$, $n = 63$). Feathers were assumed to be grown at or near the breeding grounds. Results from the general linear models that include latitude and longitude (separately) and additional independent variables (age, sex, and interactions) are presented in the text.

region (Caribbean and middle America). The GLM explained 38% of the variation in δD_w for the Caribbean ($F = 8.8$, $df = 7$ and 107 , $P < 0.001$) and 26% of the variation in δD_w for middle America ($F = 2.74$, $df = 7$ and 55 , $P = 0.02$). In both cases, latitude was the only significant predictor variable (Caribbean: $F = 33.5$, $df = 1$ and 107 , $P = 0.0003$; middle America: $F = 12.0$, $df = 1$ and 55 , $P = 0.001$). The relationship between δD values and latitude was negative (Fig. 2b, C), indicating that individuals at lower wintering latitudes tended to breed farther south than populations at higher wintering latitudes.

For assignment tests, each individual ($n = 188$) was considered to have come from the breeding region with the highest $f(b|y^*)$, denoted as \hat{b} . Overall, the confidence in assignment for \hat{b} (i.e., the probability of originating from \hat{b} in relation to the other four breeding regions) was high: 55% (104 of 188) of \hat{b} assignments had a 0.9 or higher probability of assignment, 69% (129 of 188) were 0.8 or higher, and only 12% (22 of 188) were lower than 0.6 (none were lower than 0.5). Interestingly, the incorporation of relative breeding abundance using Bayes's theorem changed only 5.9% (11 of 188) of the \hat{b} assignments when compared with the likelihood-

only approach that did not consider relative abundance (see above). The likelihood-only approach also did not decrease the confidence of \hat{b} assignments: 49% (92 of 188) of \hat{b} assignments had a 0.9 or higher probability of assignment, 66% (124 of 188) were 0.8 or higher, and only 9% (16 of 188) were lower than 0.6 (none were lower than 0.5).

Nine of the 12 (75%) wintering locations (i.e., countries, but with Panama and Belize combined and Western and Eastern Mexico split; see above) had $f(\hat{b})$ distributions significantly different than expected from complete mixing (i.e., if distribution equals relative abundance, $f(b)$; $P \leq 0.05$; Table 3 and Fig. 3). Two of the three locations that were not significant had $P \leq 0.10$ (Western Mexico and Bahamas), with Bermuda the only region with $P > 0.10$ (Table 3). Cuba and Trinidad and Tobago both had $>90\%$ of \hat{b} assignments from a single breeding region, and all locations had $>50\%$ from one region. After adjusting for unequal sample sizes between regions, locations grouped into middle America and the Caribbean both had significantly different $f(\hat{b})$ distributions than expected (Table 3). The $f(\hat{b})$ distributions between these regions were also significantly different ($\chi^2 = 81.3$, $df = 4$, $P < 0.0001$).

TABLE 3. Breeding region with the highest frequency of assignment (maximum \hat{b}) for each wintering region (bold) and wintering location. Values of chi-square (χ^2) and P are from Fisher's exact goodness-of-fit test of $f(\hat{b})$ versus the expected frequency, $f(b)$, with $df = 4$ for all tests.

| Country | Maximum \hat{b} (Percentage of total) ^a | Goodness-of-fit test ^b | |
|------------------------------------|---|-----------------------------------|-----------|
| | | χ^2 | P |
| Middle America ^c | MW (48) | 10.36 | 0.04 |
| Belize ^d | MW (60) | 8.39 | 0.04 |
| Mexico (eastern) | NW (52) | 17.10 | 0.002 |
| Mexico (western) | MW (50) | 7.61 | 0.10 |
| Panama ^d | MW (60) | 8.39 | 0.04 |
| Caribbean ^{c,e} | NE (40) | 28.34 | >0.0001 |
| Bahamas | NE (47) | 8.08 | 0.09 |
| Cuba | MW (92) | 15.87 | 0.003 |
| Dominican Republic | NE (55) | 11.54 | 0.02 |
| Jamaica | NE (60) | 9.95 | 0.04 |
| Puerto Rico | NE (52) | 9.45 | 0.05 |
| Trinidad and Tobago | SE (93) | 32.10 | >0.0001 |
| USA (Florida) | NE (50) | 9.56 | 0.05 |
| Bermuda | NE (50) | 4.90 | 0.30 |

^a Maximum \hat{b} is the breeding region with the largest number of \hat{b} assignments.

^b Observed, $f(\hat{b})$ versus expected frequencies, relative breeding abundance: $f(b)$; see Table 2.

^c Adjusted for equal sample sizes within each country; see text for details.

^d Panama and Belize grouped for goodness-of-fit test.

^e "Caribbean" includes Florida and Bahamas but not Bermuda.

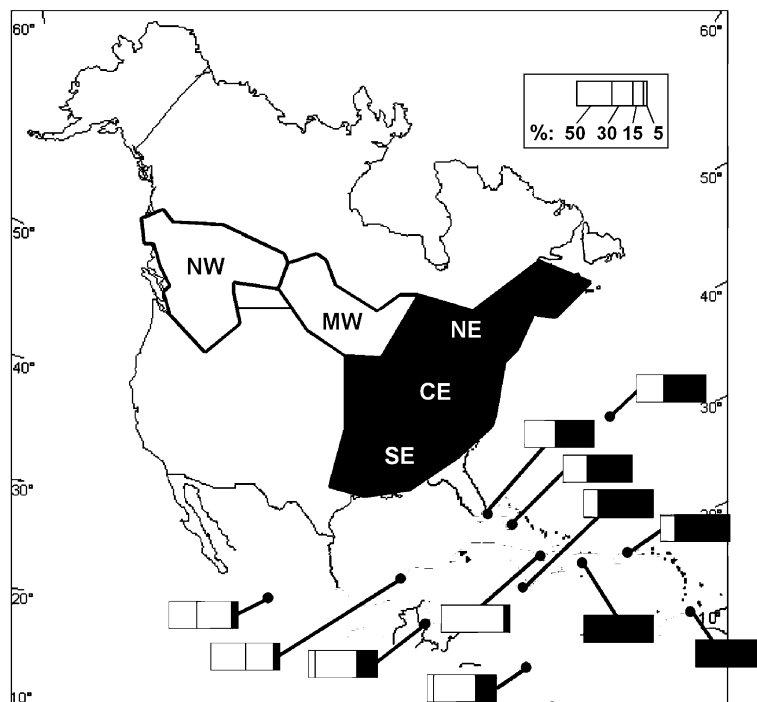


FIG. 3. Distribution of the most likely breeding region $f(\hat{b})$ from likelihood-based Bayesian assignment tests for individuals at each wintering country (eastern and western Mexico are separate). Bars indicate proportion of individuals assigned to each breeding region (rounded to the nearest 5%; see legend for reference).

DISCUSSION

Our results provide important and unique insight into the migratory connectivity and patterns of migration for a long-distance Nearctic–Neotropical songbird over its entire breeding and nonbreeding range. Over a broad scale, redstart populations show a strong degree of clinal variation between eastern and western wintering regions. Stable hydrogen isotopic compositions from feathers sampled on the wintering grounds (δD_w) were highly correlated with the longitude of sampling location (Fig. 2), which implies that western populations originated from northwest breeding areas and that eastern populations were from eastern and southern breeding areas. Results from assignment tests support this general pattern and provide more specific estimates of breeding origin. The distribution of most likely breeding regions, $f(\hat{b})$, was significantly different between individuals wintering in middle America or in the Caribbean; redstarts wintering in middle America were most likely to have originated

from the northwest and midwest breeding regions, whereas individuals from the Caribbean were most likely to have bred in northeast, central-east, and southeast regions (Fig. 3). These results agree with data from band recoveries suggesting that birds wintering in Central America bred west of the Great Lakes and individuals wintering in the Caribbean bred east of the Great Lakes (Fig. 1A). The degree of connectivity between the breeding and wintering grounds along the longitudinal axis implies that redstarts, in general, minimize migration distances by traveling primarily along a north–south axis between breeding and wintering sites. Strong east–west clinal variation has been reported in several species of migratory birds, including Yellow Warblers (*D. petechia*; Clegg et al. 2003), Willow Warblers (Chamberlain et al. 2000), Pink-footed Geese (*Anser brachyrhynchus*; Alerstam 1990, Madsen et al. 1999), and White Storks (*Ciconia ciconia*; Bairlein 2001). Kelly and Hutto (2005) provide support for east–west clinal variation in migration patterns of New World wood-warblers.

We also found broad patterns of connectivity related to latitude. The correlation between δD_w values and nonbreeding latitude for individuals in the Caribbean suggests that redstarts in the eastern range exhibit a regional pattern of chain migration. First identified by Nilsson (1858, cited in Alerstam and Hedenström 1998), this pattern occurs when populations retain the same latitudinal sequence on the breeding and nonbreeding grounds. Results from assignment tests in redstarts suggest that populations at southern wintering latitudes (Trinidad and Tobago, Dominican Republic) breed in the central-east and southeast United States, whereas birds from the most northern nonbreeding locations in the Greater Antilles and continental United States (Florida, Cuba, Jamaica, Bahamas) breed primarily in the northeast United States and eastern Canada (from the Great Lakes to the Atlantic coast; Fig. 3). Chain migration has recently been documented in a raptor (Sharp-shinned Hawks [*Accipiter striatus*]; Smith et al. 2003) but, to our knowledge, this is the first evidence in a North American passerine bird. Pienkowski et al. (1985) proposed that chain migration could arise when larger individuals from northern breeding latitudes (Bergman's rule) out-compete individuals from southern latitudes for northern wintering sites. We found no evidence for this hypothesis in redstarts. In fact, among AHY males in the Caribbean, body size (unflattened wing chord) was negatively related to wintering latitude ($r^2 = 0.25$, $P < 0.001$, $n = 73$) and positively related to δD_w values ($r^2 = 0.19$, $P = 0.008$, $n = 37$), which suggests that larger individuals tended to occupy southern latitudes on both the nonbreeding (latitude of sampling site) and breeding grounds (δD_w values).

Our results also provide important information on the degree of connectivity between specific geographic areas on the breeding and nonbreeding grounds. If redstarts showed complete mixing at a given wintering location (i.e., country), we would have expected the breeding origin distribution, $f(\hat{b})$, to be similar to expected frequencies based on $f(b)$. However, we found that, in most countries (83%, 10 of 12), $f(\hat{b})$ was significantly ($P < 0.05$) or marginally ($P \leq 0.10$) different from expected (Table 3). In particular, individuals from Trinidad and Tobago showed a high degree of connectivity with the southeast breeding region (93% of assignments), Cuba with

the midwest region (93%), and Jamaica with the northeast (60%). In the remaining countries, >75% of individuals originated from only two breeding regions—from the Caribbean: Bahamas (northeast and central-east: 83%), Dominican Republic (northeast and central-east), Florida (midwest and northeast: 94%), and Puerto Rico (northeast and central-east: 76%); and from middle America: Belize (midwest and northeast: 90%), Panama (midwest and northeast: 90%), eastern Mexico (northwest and midwest: 91%), and western Mexico (northwest and midwest: 88%). Although we split eastern and western Mexico *a priori*, the two locations showed remarkably similar assignment distributions, most of the individuals from both areas originating from the western portion of the breeding range.

It is possible that δD_w values may underestimate the number of breeders at northern latitudes. Recent evidence from a δD analysis of marked individuals returning to our breeding site in Ontario indicate that ~40% of redstarts two years or older (AHY) molt their tail feathers at staging areas south of the breeding grounds, the frequency of which may be related to the timing and amount of parental care adults provide at the end of the breeding season (Norris et al. 2004b). In the present study, lower δD_w values of AHY birds compared with those of HY birds (though the difference was nonsignificant; $P = 0.07$) also suggests that some adult birds may be molting south of their breeding sites (assuming that all HY birds molt on or near their natal sites). It is possible, for example, that some individuals assigned to northeast breeding regions could have bred in the midwest and that those assigned to the midwest actually bred in the northwest. This could explain why we observed relatively few individuals assigned to the northwest breeding region (12% of assignments vs. 25% expected from breeding abundance) and a relatively high number of individuals assigned to the midwest breeding region (36% vs. 23% expected). Alternatively, the relatively low number of birds assigned to northern and western breeding regions may be attributable to incomplete sampling coverage on the wintering grounds (i.e., likely in Mexico and Central America).

We found that application of relative breeding abundance as an *a priori* probability of breeding origin, $f(b)$, changed <6% of the number of assignments (\hat{b}) compared with likelihood-only

assignments. This suggests that the size and shape of the breeding areas we delineated were appropriate to confidently assign individuals based on large differences in δD_b between these regions. If, for example, regions were subdivided into smaller areas, we would expect significantly lower power of assignment and a greater influence of $f(b)$. Although $f(b)$ did not change many of the assignments, we strongly recommend that future studies incorporate relative abundance, because large differences in density between regions may significantly influence the probability of origin.

We recognize, however, that in some cases estimation of $f(b)$ may be difficult. Here, we used data from the BBS, which is a convenient and accessible resource for estimating relative abundance of North American species. In addition to the fact that there is no equivalent data set for the tropical or south-temperate regions, the northern limit of the BBS precludes the estimation of $f(b)$ for many northern breeding species. Even in our study, there are almost certainly redstart populations breeding north of the BBS limit (Sherry and Holmes 1997). However, we believe that these populations likely comprise a small fraction of global population size because we failed to detect many individuals with extremely negative δD_w values that would be indicative of northern breeders (especially in the east). For this reason, and because there are no survey data available to help us delineate range boundaries in this region (an essential prerequisite for accurately estimating δD values of precipitation), we excluded the boreal areas from our analysis, but we caution that this could influence the outcome of breeding assignments, and future studies should take this into consideration.

Given our broad delineation of breeding regions, we found stable hydrogen isotopes to be a useful marker for assigning individuals to predefined areas of origin. However, we note the following potential sources of error. First, although evidence suggests that individuals incorporate δD values in feathers from the location where they were grown (Chamberlain et al. 1997, Hobson and Wassenaar 1997), we still lack independent data (i.e., from band recaptures or radiotelemetry) that can confirm the accuracy of this technique in passerines. Second, the resolution to assign birds to their correct origin will depend on natural and

analytical variability in δD . Natural sources may include temporal variability within seasons (i.e., when feathers were grown), annual variability (comparisons of δD values across years), and individual variability (δD values within the same feather; Roziński et al. 1993, Farmer et al. 2003). One must also incorporate the underlying analytical variability, which is typically an order of magnitude higher for hydrogen than for either carbon or nitrogen. These sources of variability in δD will likely limit the ability to assign origins of migratory animals to broad regions. Third, we assumed a "global" discrimination factor between precipitation and feathers. Although past evidence suggests that discrimination factors likely do not vary regionally, Lott and Smith (2006) showed geographic variation between δD values in precipitation and raptor feathers. The mechanisms by which this occurs are still unclear, but we anticipate that future studies will examine the validity of this assumption.

As many have noted, the use of additional stable isotopes (e.g., strontium, nitrogen; Chamberlain et al. 1997, Rubenstein et al. 2002), genetic markers (e.g., microsatellites, mitochondrial DNA, amplified fragment length polymorphisms [AFLPs]; Milot et al. 2000, Wennerberg et al. 2002, Kelly et al. 2005), or trace elements (Szép et al. 2003) may increase the power of assignment tests. The challenge will be to understand whether and how additional markers vary across the breeding ranges of redstarts and other migratory species. For stable hydrogen isotopes, variation of δD values in precipitation in North America (Bowen and Revenaugh 2003, Bowen et al. 2005) is well documented and can be used to infer migration movements, as we have done here. However, we still have a poor understanding of how other markers vary across continental scales. Even a single additional marker with relatively moderate resolution would likely contribute important information when combined with δD (e.g., Clegg et al. 2003, Kelly et al. 2005).

The spatial structure found between breeding and wintering area implies that redstart populations are geographically linked, at least on a regional scale. Most Nearctic–Neotropical migratory birds exhibit asynchronous fluctuations in abundance on North American breeding grounds (Sauer and Droege 1992, Peterjohn et al. 1995). This suggests that populations

within specific breeding regions may be linked to specific wintering locations. Simulation models have shown that the ability to accurately predict population size when habitat is lost at a given wintering or breeding location will be highly dependent on the degree of connectivity between these areas (Dolman and Sutherland 1995, Marra et al. 2006). The ability to link changes in habitat on the nonbreeding grounds or on migration routes with population abundance on the breeding grounds, therefore, will be a critical step toward understanding the factors that influence the population dynamics of migratory birds across their entire range (Norris 2005, Webster and Marra 2005). Connecting winter habitat loss with breeding abundance will be especially important for species, such as redstarts, whose reproductive success on the breeding grounds is correlated with the quality of habitat occupied on the tropical wintering grounds (Norris et al. 2004a).

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