LINKING BREEDING AND WINTERING GROUNDS OF BICKNELL'S THRUSHES USING STABLE ISOTOPE ANALYSES OF FEATHERS

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ABSTRACT.—Previous studies have shown that natural abundance of deuterium (D), and to a lesser extent ^{13}C, in feathers of migrant songbirds in North America can be used to infer geographic origins of molt. We used that approach to investigate whether Bicknell's Thrush (*Catharus bicknelli*) populations could be segregated on the breeding grounds at six sites in eastern North America to evaluate contributions from the breeding areas to wintering populations. Further, we tested our isotopic model using feathers from hatching-year migrant Swainson's Thrush (*Catharus ustulatus*) and Gray-cheeked Thrush (*Catharus minimus*) moving through southern Manitoba and Ontario and found that δD values were consistent with northerly boreal forest natal sites in northwestern and central Canada. Despite a strong latitudinal gradient in δD of average growing season precipitation over the breeding range, we found considerable overlap in δD values of Bicknell's Thrush among all breeding sites. No strong pattern in $\delta^{13}C$ values of feathers with latitude was apparent. Nevertheless, the more negative δD values of feathers from wintering birds in the Dominican Republic compared to breeding area samples suggested that birds from more northerly locations in North America contributed to this population of wintering birds. High variance in feather δD values within breeding populations also suggested high natal dispersal, considerable movement of birds among island habitats on the breeding grounds, or both. Even higher variances in feather δD values from small study areas on the wintering grounds, compared to similar-sized areas in the breeding range, suggest that many different breeding populations mix in winter habitat. *Received 1 November 1999, accepted 8 August 2000.*

UNLIKE OTHER MEMBERS of the genus *Catharus*, Bicknell's Thrush (*Catharus bicknelli*) occupies a limited breeding distribution in North America, extending from southern Quebec and the Maritime Provinces south to New England and New York (Ouellet 1993, Atwood et al. 1996). Within that region, the species occurs in isolated, dense patches of conifer-dominated stands and is restricted to high-elevation sites in the U.S. portion of its range. Less is known about the status of Bicknell's Thrush on its wintering grounds, which are restricted to the Greater Antilles (Ouellet 1993; C. Rimmer, K. McFarland, and J. Goetz unpubl. data). It is believed that the species' winter range is allopatric from that of other *Catharus*. Degradation of suitable montane forest habitat in the United States due to development and atmospheric

pollution, loss of habitat from intensive forestry in the Canadian Maritime Provinces, and the removal of over 90% of the mesic forests on the species' wintering grounds have resulted in serious conservation concerns (Rosenberg and Wells 1995, Atwood et al. 1996, Rimmer et al. 1998).

Of fundamental importance to the conservation of migratory songbirds like Bicknell's Thrush is the ability to link breeding, wintering, and stop-over sites, especially because several species, including adult Bicknell's Thrush, are philopatric to wintering as well as breeding sites (Greenwood and Harvey 1982, Rappole et al. 1983, 1992; Holmes and Sherry 1992). Such information would facilitate conservation efforts to target specific populations and to coordinate those efforts at key locations (Myers et al. 1987, Moore and Simons 1992). One poorly understood component of the life history of most migratory songbirds is the degree of dis-

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persal among breeding sites by both adults and first-time breeders (i.e. natal philopatry). That becomes of conservation interest when birds are forced to move among a small number of widely dispersed islands of habitat or when birds form metapopulations where individuals move between source and sink populations (Donovan et al. 1995). The only means of obtaining such information is through the careful tracking of individuals. Previous approaches for small songbirds have met with little success, because conventional methods of marking birds with bands or transmitters have been largely ineffective. The use of molecular techniques (Avise 1992, Moore and Simons 1992, Wenink et al. 1994) or behavioral characters (e.g. DeWolfe and Baptista 1995) has shown some promise. More recently, however, measurement of naturally occurring stable isotopes of H in bird feathers has provided a major breakthrough in the way migratory birds can be tracked in North America (Hobson and Wassenaar 1997, Kelly and Finch 1998). That research has shown that stable isotopes can be applied to a broad range of long distance migratory organisms, including insects (Wassenaar and Hobson 1998, Hobson 1999, Hobson et al. 1999).

The deuterium (D) abundance in a pool of H is expressed by the isotopic D/H ratio, or more commonly by its δD value, which becomes more negative with decreasing D abundance (see below). The basis of the stable H-isotope approach is that deuterium in rainfall shows characteristic patterns across the North American continent (Fig. 1), with a strong gradient from more positive δD values in the American Southeast to more negative δD values in the Northwest. Because plants obtain most of their H from rainfall, their tissues reflect similar continental D/H patterns as observed in precipitation (Cormie et al. 1994a, b). Although the H-isotopic composition of herbivorous insects and insectivorous birds are undoubtedly influenced by factors other than food, including the isotopic composition of drinking water and ambient water vapor (see flowchart in Ayliffe and Chivas 1990) patterns of growing-season average D/H in precipitation are strongly reflected up the foodweb to birds (Hobson and Wassenaar 1997). Because feathers are metabolically inert following formation, the H content of feathers directly reflects that of the local
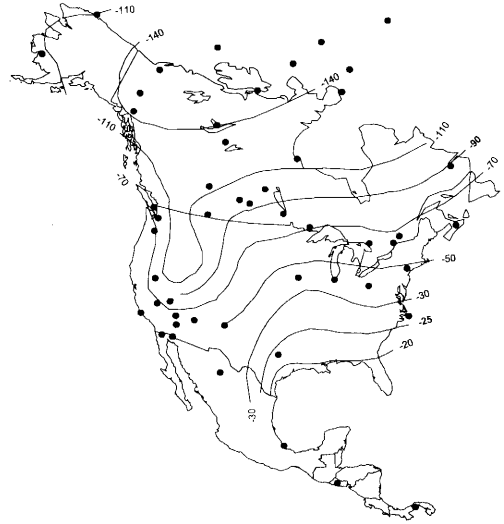

FIG. 1. Patterns of growing-season average δD values in precipitation. Contours are based on compilations of data by Hobson and Wassenaar (1997). Dots refer to long-term precipitation sampling stations.

food web where feathers were grown. Fortunately, most species of migrant songbirds in North America molt flight feathers each year on or close to their breeding grounds before departing for wintering areas. Thus, flight feathers carry a H-isotopic signal of their breeding ground location for a full year following feather formation (Hobson 1999). Wassenaar and Hobson (2000) recently confirmed that strong continental H-isotopic effect by measuring δD values in feathers of Red-winged Blackbirds (*Agelaius phoeniceus*) along an interior continental gradient in δD.

The goal of this study was to investigate patterns of stable-isotope distributions in feathers of Bicknell's Thrush from known breeding and wintering locations. Results were used to evaluate the usefulness of the stable-isotope technique as a means of (1) linking breeding origins of Bicknell's Thrush with wintering sites, and (2) establishing evidence for movement of individuals among breeding sites. Previous research in New England showed the presence of a north–south isotopic gradient in feathers of Black-throated Blue Warblers (*Dendroica caerulescens*; Chamberlain et al. 1997), but it was unknown if such a gradient would hold for birds such as Bicknell's Thrush that occupy both high- and low-elevation sites. We also com-
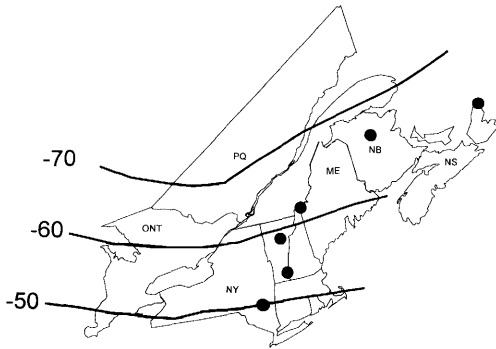
FIG. 2. Locations of sampling sites for Bicknell's Thrush on the breeding grounds and overlay of interpolated precipitation average δD contours as described in Figure 1. Sites are from south to north: Catskills, NY; S. Green Mountains, VT; N. Green Mountains, VT; Mt. Megantic, Quebec; New Brunswick; and Cape Breton (Table 1).

pared the stable-isotope values in feathers of hatch-year individuals of both Gray-cheeked (*Catharus minimus*) and Swainson's (*Catharus ustulatus*) thrushes as they migrated in the fall through two migration monitoring stations in southern Canada. We predicted that the more northerly natal origins of those species compared with Bicknell's Thrush would result in more depleted feather δD values. Our ultimate goal was to begin to develop an isotopic database for Bicknell's Thrush that could be used to link breeding and wintering sites and so provide a tool to assist with effective conservation of that species.

METHODS

We obtained single rectrices of Bicknell's Thrushes from breeding locations in Quebec (45°27′N, 71°09′W), New Brunswick (47°14′N, 66°45′W), Cape Breton (47°00′N, 60°43′W), northern Vermont (44°31′N, 72°48′W), southern Vermont (43°05′N, 72°55′W), and New York (42°10′N, 74°13′W), during May–July in 1995–1998 (Fig. 2), and from wintering sites in the Dominican Republic during November–March 1995–1998. Birds were captured using mist nets and playback of conspecific songs, and were banded. One rectrix (R5) was removed before release and stored in a paper envelope. Individuals were aged by presence of buffy greater covert tips, shape of collected rectrix (Collier and Wallace 1989, Pyle 1997), or both. Similarly, outer rectrices of Swainson's and Gray-cheeked thrushes were obtained in 1997 from hatching-year (HY) birds as they migrated through Delta Marsh Bird Observatory in southern

Manitoba (50°11′N, 98°19′W) and Long Point Bird Observatory in southern Ontario (42°34′N, 80°15′W).

Obtaining information on geographic origins where feathers were grown is possible through the stable-isotopic analysis of H in feathers (Hobson and Wassenaar 1997). However, a portion of H in feather keratin is bound to N or O and thus forms weak bonds capable of exchange with ambient H in water vapor (Schimmelmann 1991). To eliminate effects of H exchangeability, we equilibrated our feather samples with steam under controlled conditions using a modification of the method described by Schimmelmann (1991) and more fully detailed in Wassenaar and Hobson (2000). Briefly, H-isotopic exchangeability for feathers was first quantified by an isothermal (130 ± 0.1°C) static equilibration with steam having a wide range of H-isotopic values (−135 to +525‰) for 2 h and then measured the total H δD values (Schimmelmann 1991, Hobson et al. 1999). After equilibration of samples, all water vapour was removed cryogenically from individual sample breakseal tubes. Samples were then sealed under vacuum and combusted at 850°C in the presence of cupric oxide, followed by cryogenic separation of CO_2 from H_2O. An aliquot of the CO_2 was used for $\delta^{13}C$ measurements using standard methods. The water from feather combustion was reduced to H_2 gas on hot Zn, and D/H ratios were measured on a Micromass Optima® dual inlet isotope-ratio mass spectrometer at the National Water Research Institute, Saskatoon. Stable H-isotopic results are reported in parts per thousand deviation from the Vienna Standard Mean Ocean Water Standard (VSMOW), and normalised to the VSMOW/SLAP (Standard Light Antarctic Precipitation) scale. Sample reproducibility was better than ±2.0‰

All δD values for Bicknell's Thrush are reported for nonexchangeable H. A simple two-end-member isotopic equilibration procedure was used to calculate the proportion of exchangeability, f_e, for feathers based on equilibration with steam:

$$f_e = (\delta D_{TA} - \delta D_{TB}) / ((\delta D_{WA} - \delta D_{WB})(1 + \epsilon_{x-w}/1000)) \quad (1)$$

where f_e is the fraction of exchangeable H, δD_T is the total H-isotopic composition, δD_w is the H-isotopic composition of the steam, ϵ_{x-w} is the isotopic fractionation factor in permil between water and exchangeable organic H, and A and B subscripts refer to isotopically different and widely separated equilibration waters (Schimmelmann et al. 1999). The nonexchangeable H-isotopic composition, δD_n, was determined from:

$$\delta D_n = (\delta D_t - (f_e \, \alpha \, \delta D_w))/(1 - f_e) \quad (2)$$

where f_e is determined from Equation (1), δD_t is the H-isotopic composition of the feather equilibrated with steam δD_w, and α is the isotopic fractionation factor between steam and the exchangeable H. The

TABLE 1. Summary of stable isotope values (mean ± SE) of rectrices obtained from breeding and wintering Bicknell's Thrush and for fall migrant hatch-year Swainson's and Gray-cheeked thrushes moving through southern Canada.

Species	Location	Age/Status[a]	n	δD (‰)	δ^{13}C (‰)
Bicknell's Thrush	New Brunswick	B	13	-80.3 ± 2.3	-22.6 ± 0.2
	Cape Breton	B	9	-67 ± 2.7	-23.8 ± 1.2
	Mt. Megantic, Quebec	B	4	-62 ± 2.0	-22.3 ± 0.3
	N. Green Mountains, VT	B	19	-74 ± 1.5	-22.0 ± 0.1
	S. Green Mountains, VT	B	10	-64 ± 1.2	-22.5 ± 0.2
	Catskills, NY	B	9	-62 ± 3.7	-21.9 ± 0.1
	Dominican Republic	W	83	-86 ± 1.7	-22.2 ± 0.1
Gray-cheeked Thrush	Delta Marsh Bird Observatory	HY (FM)	12	-127 ± 3.5	-22.4 ± 0.3
Swainson's Thrush	Delta Marsh Bird Observatory	HY (FM)	29	-140 ± 2.9	-23.2 ± 0.1
	Long Point Bird Observatory	HY (FM)	17	-118 ± 5.6	-23.3 ± 0.2

[a] B: breeding, W: wintering, HY (FM): hatching-year fall migrant.

isotopic fractionation between steam and exchangeable organic H at the equilibration temperatures used was estimated to be about 80‰ (α = 1.080) (Schimmelmann et al. 1999).

To investigate the correlation between δD in Bicknell's Thrush and local rainfall during the growing season, we used contours of weighted average growing season D in precipitation for eastern North America using the most recently available data (Hobson and Wassenaar 1997). Contours were constructed by kriging weighted summer precipitation δD values at arbitrary 10‰ intervals (Fig. 1). We then used those contours and compared them to feather values of after-second-year (ASY) individuals to assess the usefulness of the isotope technique in investigating origins of Bicknell's Thrush. We used ASY birds in that comparison because they were more likely to be associated with the site where feathers
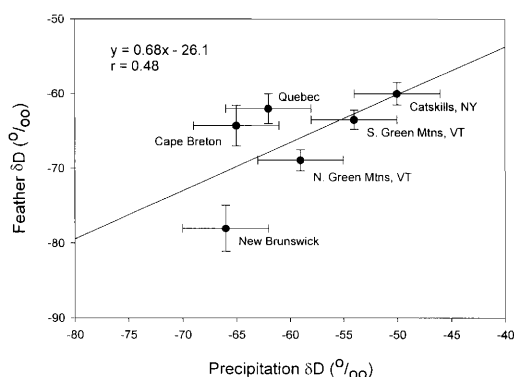
FIG. 3. Relationship between nonexchangeable feather δD values for ASY Bicknell's Thrush and average growing season precipitation δD inferred for each site. Error bars are standard error. Variance associated with the x-axis is from an arbitrary overall estimate of error in precipitation data and interpolation (see Wassenaar and Hobson 2000).
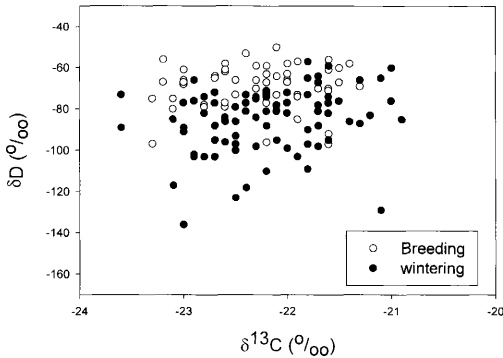
were collected because of high levels of philopatry in ASY individuals on both wintering and breeding areas (McFarland and Rimmer unpubl. data). It should be noted that feather δD values are expected to differ by a constant value from growing-season average precipitation values at the sites where feathers were grown because of isotopic fractionation effects (Hobson and Wassenaar 1997, Wassenaar and Hobson 2000).

RESULTS

Bicknell's Thrush from the six breeding sites ranged significantly in feather stable-isotope values (MANOVA, Wilk's Lambda = 4.6, P < 0.001). That effect was driven primarily by differences in feather δD values (ANOVA, F = 7.6, df = 5 and 59, P < 0.001) compared with δ^{13}C values (F = 2.2, df = 5 and 59, P = 0.07; Table 1). In contrast to previous studies (Chamberlain et al. 1997, Hobson and Wassenaar 1997, Wassenaar and Hobson 2000), we found a weaker relationship between ASY feather δD values on the breeding grounds and the average growing-season precipitation δD values for those sites (r = 0.48, P < 0.05, Fig. 3). That relationship was weakened further if both SY (second year) and ASY birds were included (r = 0.35, P < 0.05), which suggests that younger birds dispersed more between natal sites and subsequent breeding sites.

Feathers from Bicknell's Thrush (HY, SY, and ASY) wintering in the Dominican Republic were significantly more depleted in δD values compared with those measured on the breeding grounds (t = 48.3, df = 1 and 145, P < 0.001; Table 1, Fig. 4), but we detected no difference between feather δ^{13}C values from

FIG. 4. Distribution of Bicknell's Thrush nonexchangeable feather δD and δ¹³C values from breeding and wintering grounds.

breeding and wintering sites ($t = 2.0, P = 0.16$). Variation in feather δD values at two small (~20 ha) study plots in the Baoruco Mountains, Dominican Republic differed significantly from those at two similar sized plots in the Green Mountains, Vermont (homogeneity of coefficients of variation, $\chi^2 = 18.59$, df = 3, $P < 0.001$; Table 2).

Feather δD values for Swainson's and Gray-cheeked thrushes moving through the two migration monitoring stations were consistently more depleted than those of Bicknell's Thrush on its breeding and wintering grounds (Table 1) and corresponded well to their expected breeding locations in boreal forests of northern Canada and possibly Alaska (Fig. 1).

DISCUSSION

Our stable-isotope analyses of feathers from breeding and wintering Bicknell's Thrushes demonstrate how this approach to tracking migratory birds can provide information previously not obtainable using conventional techniques (see review by Hobson 1999). By analyzing feathers of birds captured on their wintering grounds, it may be possible to infer general geographic origins of molt of otherwise unmarked individuals. However, the utility of that method depends to a large extent on the presence of significant isotopic differences among sites of interest. We predicted that because Bicknell's Thrushes were sampled over a north–south gradient in precipitation δD and because previous isotopic studies in that general region confirmed a strong linkage between feather δD and that of precipitation (Chamberlain et al. 1997), thrushes breeding at sites ranging from New Brunswick to the Catskill Mountains in New York would similarly reflect that environmental isotopic gradient. Although that was generally not the case, our analyses suggest that many individuals wintering in the Dominican Republic may have originated from more northern (e.g. Canadian) portions of their range. A decoupling of the feather δD and precipitation δD values for Bicknell's Thrushes would also be consistent with dispersal between molting origins the previous year and their current breeding areas.

Several factors can influence local δD values of precipitation and cause departures from the general continental averages shown in Figures 1 and 2. Importantly, those isotopic contour maps do not take into account local climatic effects, particularly those related to elevation and proximity to coastlines. In general, precipitation falling at the base of mountains or along coastlines is enriched in D compared to that falling at higher elevations or further inland (Dansgaard 1961, Zeigler 1988). Such processes may have contributed to local decoupling of the strong latitudinal gradient in precipitation δD found elsewhere through the central portion of the continent (Hobson and Wassenaar 1997, Wassenaar and Hobson 2000). It is also not clear how such isotopic patterns can vary

TABLE 2. Comparison of δD (‰) values of rectrices from Bicknell's Thrush at two small study areas in the Baoruco Mountains, Dominican Republic (Pueblo Viejo and Palo de Agua) with two areas in the Green Mountains, Vermont, USA (Mt. Mansfield and Stratton Mountain). Each study plot covered approximately 20 ha.

Location	n	Mean ± SE	Minimum	Maximum	Coefficient of variation[a]
Pueblo Viejo	21	−82 ± 3.2	−117	−57	−0.179
Palo de Agua	21	−86 ± 3.8	−129	−64	−0.203
Mt. Mansfield	19	−73 ± 1.6	−92	−64	−0.091
Stratton Mountain	10	−64 ± 1.2	−70	−59	−0.057

[a] Homogeneity of coefficients of variation, $\chi^2 = 18.59$, df = 3, $P < 0.001$.

among years, particularly during El Niño and La Niña years.

Another contributing factor to the lack of isotopic differences among breeding sites may have been movement of individuals among sites. Feathers sampled from individuals at breeding sites were grown the previous year. Those species with high natal and breeding-site fidelity will show a fairly strong relationship between feather δD and local precipitation average δD. However, in cases where individuals move among sites between years, such a relationship is less likely to exist. The relatively high within-site variance of feather δD values of Bicknell's Thrush in our study provides evidence for considerable dispersal between sites where birds molted their flight feathers the previous year and their breeding site at the time of sampling. Such dispersal was more evident when birds of all age categories were considered compared with just ASY birds. Previous studies of patterns of δD in bird feathers from several species and across larger geographical gradients have shown much lower within-sample variance in δD values among individuals (Chamberlain et al. 1997, Hobson and Wassenaar 1997). Between-year dispersal might be expected for species breeding in small, isolated habitat fragments that select ephemeral, mid-succession forest stands within those habitat islands (Ouellet 1993, Atwood et al. 1996, K. McFarland and C. Rimmer unpubl. data).

Direct observations of SY birds dispersing corroborates with the isotopic data. Eight years of banding at several sites in the Green Mountains, Vermont, have yielded one intermountain dispersal by an SY male. That individual was banded in 1995 and was believed to have been unmated. It was recaptured in 1997, 1998, and 1999 on another mountaintop to the east separated by 18 km of unsuitable habitat. Several instances of between-year movements of 1–2 km in breeding home range locations of SY individuals have also been observed within an intensively studied, larger habitat island (Mt. Mansfield, Vermont; K. McFarland and C. Rimmer unpubl. data). The banding returns generally suggest high breeding philopatry among ASY birds and higher incidence of natal and SY dispersal among breeding sites. Isotopic data are generally consistent with that interpretation.

Despite absence of strong isotopic segregation among breeding sites we measured, wintering birds sampled from the Dominican Republic were more depleted in feather D than birds from breeding grounds for the same sampling years. We suggest two possible explanations for that pattern. First, it is possible that those wintering birds originated, on average, from more northern locations than we measured. Further evidence for that hypothesis was provided by our isotopic measurements for Gray-cheeked and Swainson's thrushes whose feather δD values were typical of more boreal locations. The bulk of the wintering population in the Dominican Republic may have originated from sites at the northern limits of the species range, possibly suggesting previously undocumented source populations of Bicknell's Thrush. Our isotope data suggest that source populations just north of New Brunswick, possibly in southern Newfoundland, or a few hundred kilometers north of the Quebec sampling site of Mount Megantic are possible (Y. Aubry pers. comm.; Wassenaar and Hobson unpubl. data). Because D in rainfall tends to be depleted with altitude, a second possibility is that the wintering population was derived primarily from higher-altitude sites within the central range of the species, namely high peaks of the Adirondacks, White Mountains, or mountains of Maine. Currently, our understanding of the true isotopic precipitation map for the breeding grounds of Bicknell's Thrush is too coarse to evaluate between-season variability and effects of local topography. We recommend that future studies attempt to increase sampling to include both higher-altitude sites and possible breeding sites to the north of our sampling sites, particularly in southern Quebec.

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