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## The use of isotope tracers for identifying populations of migratory birds

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**Abstract** To determine whether stable isotopes can be used for identifying the geographic origins of migratory bird populations, we examined the isotopic composition of hydrogen (deuterium,  $\delta\text{D}$ ), carbon ( $\delta^{13}\text{C}$ ), and strontium ( $\delta^{87}\text{Sr}$ ) in tissues of a migratory passerine, the black-throated blue warbler (*Dendroica caerulescens*), throughout its breeding range in eastern North America.  $\delta\text{D}$  and  $\delta^{13}\text{C}$  values in feathers, which are grown in the breeding area, varied systematically along a latitudinal gradient, being highest in samples from the southern end of the species' breeding range in Georgia and lowest in southern Canada. In addition,  $\delta\text{D}$  decreased from east to west across the northern part of the breeding range, from New Brunswick to Michigan.  $\delta^{87}\text{Sr}$  ratios were highest in the Appalachian Mountains, and decreased towards the west. These patterns are consistent with geographical variation in the isotopic composition of the natural environment, i.e., with that of precipitation, plants, and soils for  $\delta\text{D}$ ,  $\delta^{13}\text{C}$ , and  $\delta^{87}\text{Sr}$ , respectively. Preliminary analyses of the  $\delta\text{D}$  and  $\delta^{13}\text{C}$  composition of feathers collected from warblers in their Caribbean winter grounds indicate that these individuals were mostly from northern breeding populations. Furthermore, variances in isotope ratios in samples from local areas in winter tended to be larger than those in summer, suggesting that individuals from different breeding localities may mix in winter habitats. These isotope markers, therefore, have the potential for locating the breeding origins of migratory species on

their winter areas, for quantifying the degree of mixing of breeding populations on migratory and wintering sites, and for documenting other aspects of the population structure migratory animals – information needed for studies of year-round ecology of these species as well as for their conservation. Combining information from several stable isotopes will help to increase the resolution for determining the geographic origins of individuals in such highly vagile populations.

**Key words** Stable isotopes · Deuterium · Strontium · Carbon · *Dendroica caerulescens*

### Introduction

Animals that move long distances during their annual cycles, such as many migratory vertebrates, are inherently difficult to track on a seasonal basis. This is especially true for species such as migratory songbirds, which may be too small to carry powerful radio transmitters, which are marked or recovered too infrequently for standard tagging techniques to be useful (Holmes and Sherry 1992), or which lack morphological or molecular variation that could serve as markers for identifying geographic subpopulations (Ball et al. 1988; Wenink et al. 1994). For migratory birds in particular, this absence of markers with which to link breeding and wintering populations impedes understanding of their year-round population dynamics (Sherry and Holmes 1995), and thus hinders development of appropriate conservation strategies (Myers et al. 1987).

Previous investigations have shown that natural variations in the isotopic composition of animal tissues (e.g., bone, muscle, egg shell, feathers) reflect the isotopes in the local environment, e.g., in precipitation, soil type, vegetation and diet (e.g., DeNiro and Epstein 1978; Luz et al. 1990; Mizutani and Wada 1989; Schaffner and Swart 1991; Hobson and Clark 1992). This has led to a number of studies which have used natural variations of isotopic ratios in mammal (van der Merwe et al. 1990;

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Vogel et al. 1990; but see Koch et al. 1995), fish (Nelson et al. 1989; Meyer-Rochow et al. 1992), and arthropod (Fry 1984) tissues to determine their geographical origin. For birds, however, isotopic studies have concentrated mostly on determining feeding habitats and trophic relations rather than on tracing geographic origin (e.g., Mizutani et al. 1990; Hobson and Clark 1992). An exception is a study by Alisauskas and Hobson (1993) which showed that different subpopulations of wintering geese could be identified with carbon isotopes. To our knowledge, isotopes have not been examined systematically to identify subpopulation structure of migratory birds on a large geographic scale.

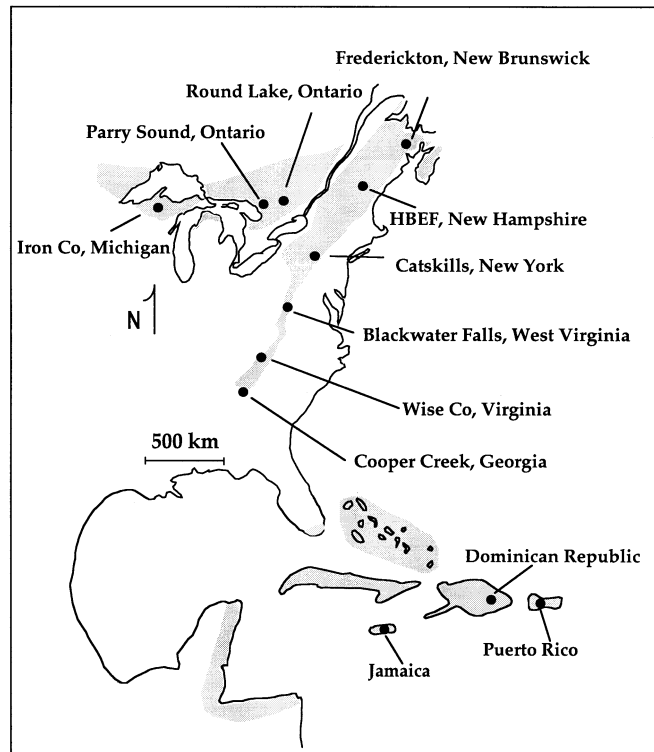
The objective of this study was to test the potential use of stable isotope ratios as regional markers of geographically-widespread, migratory bird populations. In most species of birds, feathers are renewed at least annually, and thus their isotopic composition should reflect that of the foods and water consumed at the time of feather growth (Hobson and Clark 1992; Mizutani et al. 1990, 1992). In our primary study species, the black-throated blue warbler (*Dendroica caerulescens*: Emberizidae, Parulinae), as in many passerine birds, there is a complete molt of all feathers in late summer, on or near their breeding site (Holmes 1994). The breeding range of this North American species extends from Georgia (in the Appalachian Mountains) northward to the maritime provinces of Eastern Canada, and west to Minnesota and southern Ontario. Since this geographic range spans natural gradients in both carbon and hydrogen isotopes in plants (Korner et al. 1991) and surface water (Dansgaard 1964; Sheppard et al. 1969), we hypothesized that hydrogen and carbon isotope ratios in feathers of this species should vary geographically, and should be evident subsequently in feathers obtained from individuals in their Caribbean wintering grounds. We also examined geographic variation in the isotopes of strontium (Sr), measured in bone tissue, to test the prediction that ratios of this element would correspond with those found in regional soil parent materials.

## Materials and methods

To test the hypothesis that the isotopic composition of H and C in black-throated blue warbler feathers vary systematically with latitude, we obtained feathers from 154 individuals of this species collected from nine sites within its temperate breeding range in eastern North America (Fig. 1). We also sampled feathers from 54 black-throated blue warblers from single localities on three Caribbean islands in the central portions of their Neotropical wintering range: Jamaica, Dominican Republic, and Puerto Rico. To test the generality of these findings, we include preliminary data on the isotope ratios in tissues of another north temperate-breeding migratory passerine, the American redstart (*Setophaga ruticilla*), from several localities in North America.

### Feather and bone analyses

Isotopic determinations were made on two or three contour (flank or breast) feathers, and in some cases tail feathers. There was no



**Fig. 1** North-temperate breeding and tropical wintering ranges of the migratory black-throated blue warbler. Locations are indicated from which samples were obtained for isotopic determination

detectable difference in the isotopic composition between tail and contour feathers. Feathers were washed in detergent and water to remove any oils or contaminants and dried at 50°C for 8 h to remove absorbed water.  $\delta^{13}\text{C}$  values were determined on  $\text{CO}_2$  produced by combusting the feather in  $\text{CuO}$  and cryogenically cleaning the  $\text{CO}_2$  on a vacuum extraction line. Analysis was then made on a Finnigan delta E mass spectrometer in the Dartmouth Laboratory for Isotope Tracers in the Environment (D-LITE).  $\delta\text{D}$  values were determined by collecting the water from the  $\text{CuO}$  experiments on zinc, and then converting the water to  $\text{H}_2$  gas by reaction at 500°C (Venneman and O'Neil 1993). Replicate analyses of different feathers from one individual indicated variability of  $\pm 5.0$  for  $\delta\text{D}$  ( $n = 5$ ) and for  $\delta^{13}\text{C} \pm 0.2$  (1 SD,  $n = 9$ ). Feather samples were analyzed for approximately 20 individuals at each of the nine breeding localities. Variation (1 SD) of  $\delta\text{D}$  and  $\delta^{13}\text{C}$  values of feathers from different birds within one locality was  $\pm 10.0$  for  $\delta\text{D}$  and  $\pm 0.5$  for  $\delta^{13}\text{C}$ .

Sr isotopic measurements were made on 2–25 mg samples of bone material. Trace levels of Sr substitute for Ca in the bone hydroxyapatite [ $\text{Ca}_5(\text{PO}_4)_3(\text{OH})$ ] structure yielding a Sr concentration of approximately 50  $\mu\text{g/g}$ . Clean bone fragments were placed into Teflon beakers and repeatedly ultrasonically cleaned in deionized water, dried and weighed. The bones were dissolved in quartz-distilled concentrated  $\text{HNO}_3$ , dried and taken into solution in 1.5 M HCl. Sr was separated from the solution using standard cation exchange procedures (Blum et al. 1994). The Sr isotopic compositions were measured on ~250 ng of Sr using the D-LITE VG-Sector thermal ionization mass spectrometer. For locations where two Sr isotope ratios are given, measurements were made on two individuals. Procedural blanks measured during the course of this study were less than 76 pg Sr, and thus had no detectable influence the Sr isotope measurements. Reported isotope ratios were normalized to  $^{86}\text{Sr}/^{88}\text{Sr} = 0.1194$ . Analyses of NBS-987 during this study yielded  $^{87}\text{Sr}/^{86}\text{Sr} = 0.710274 \pm 0.000016$  (2 SD,  $n = 10$ ).

**Table 1**  $\delta D$  analyses of feathers for equilibration experiments

Day	$\delta D$ analysis			$\delta D$ analysis	
Water:	+320	-58	-320	Water vapor:	+243 -397
4	-51	-71	-99		-64
4	-51	-89	-92		
4	-36	-68	-106		
8	-42	-56	-100		-74 -74
8	-36	-66	-97		
8	-22	-72			
16	-1	-58	-85		-23 -99
16	-4	-55	-94		
16	-19	-75			
24	-15	-71	-90		-25 -83
24		-72			
24		-58			

We report isotopic values in "delta" notation (e.g., Faure 1986), where  $\delta D$ ,  $\delta^{13}C$ , and  $\delta^{87}Sr$  represent the deviation in the  $^2H/^1H$ ,  $^{13}C/^{12}C$ , and  $^{87}Sr/^{86}Sr$  ratios in parts per mil (‰) from reference standards Pee Dee belemnite (PDB) carbonate, standard mean ocean water (V-SMOW), and present-day ocean water (0.70918, Hodell et al. 1989), respectively.

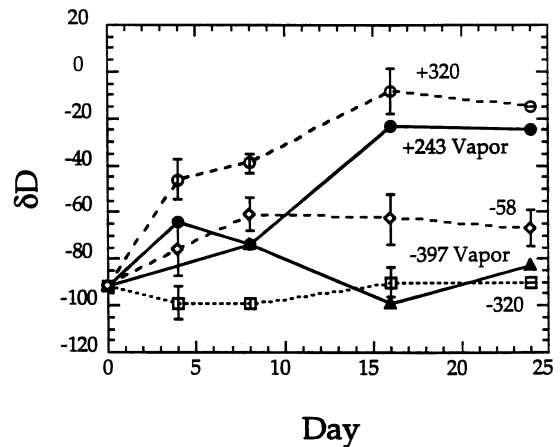
#### Hydrogen isotopic exchange in feather keratin

In this paper, we present hydrogen isotopes values of feathers. Feathers are composed of feather keratin, and the hydrogen and carbon isotopes are incorporated into the keratin structure during growth (Hobson and Clark 1992; Mizutani et al. 1990, 1992). However, 60% of hydrogen in feather keratin is nonexchangeable (e.g., C-H bonded hydrogen), whereas the remaining 40% of the hydrogen (that bonded to oxygen and nitrogen) may potentially exchange with the ambient water after growth. To determine what possible effects the exchangeable hydrogen might have on the hydrogen isotope composition of feathers we performed exchange experiments on feather keratin.

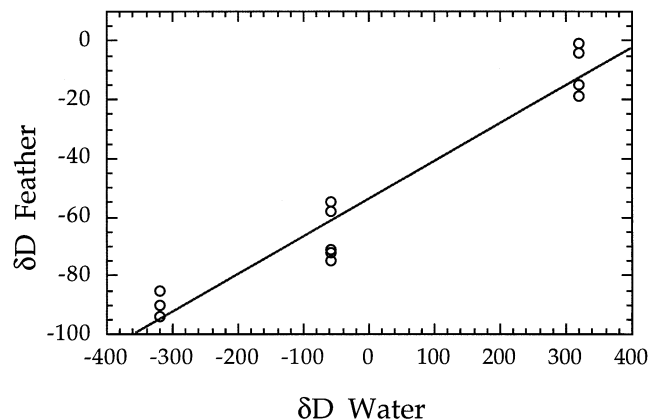
For the hydrogen exchange experiments we used tail feathers from an American redstart ( $210692^{-1}$ ). Analysis of these feathers yield a  $\delta D$  of  $-92 \pm 10‰$  (1 SD,  $n = 10$ ) which is statistically indistinguishable from the  $\delta D$  values of breast feathers measured for this bird ( $\delta D = -92.2 \pm 5‰$ , 1 SD,  $n = 5$ ). Tail feathers were sealed into quartz tubes with 0.5 ml of water of known isotopic composition ( $\delta D = -320, 320$ , and  $-68‰$ ), 500 mg of CuO and 90 mg of granular Cu. These quartz tubes were placed into a water bath kept at a content temperature of  $25^\circ C$  and allowed to exchange for 4, 8, 16 and 24 days. Each of these experiments were run in triplicate. After exchange, the quartz tubes were broken on a vacuum line and the feathers were dried under vacuum. The quartz tubes were then resealed, combusted and the  $H_2O$  and  $CO_2$  were extracted using the procedures outlined above. The results of these analyses are given in Table 1.

To evaluate how fast exchangeable hydrogen of feather keratin would exchange with atmospheric moisture, we conducted several experiments using water vapor generated from a water reservoir of known isotopic composition ( $\delta D = -320$  and  $320‰$ ). For these experiments, we placed 1.5 mg of feather into the head space of quartz tubes that contained water at the lower end. As before, these tubes were sealed and allowed to exchange for 4, 8, 16 and 24 days. The results of these experiments are also presented in Table 1.

These experiments allow us to determine the rate of hydrogen exchange between feather keratin and water/water vapor. For the experiments using waters with  $\delta D$  values of  $-320$  and  $320‰$  relatively large changes in  $\delta D$  values of feathers occurred in the first 8 days but relatively little change occurred after 16 days. These experiments suggest that the rate of hydrogen exchange



**Fig. 2** Rate of hydrogen exchange between feather keratin and  $-320, +320$ , and  $+58‰$  water at  $25^\circ C$ . Also shown are exchange experiments for water vapors of  $-397$  and  $+243‰$  at  $25^\circ C$ . Shown are the mean  $\delta D$  feather values and 1 SD error bars



**Fig. 3**  $\delta D$  in feathers versus  $\delta D$  in waters ( $-320, +320$ , and  $+58‰$ ) equilibrated in the laboratory for 16 and 24 days. The slope of the line gives the percent of exchangeable hydrogen in feather keratin. Values for these experiments are given in Table 1

between feather keratin and water is relatively fast (about 2 weeks) although considerably slower than for many other biogenic compounds (Feng et al. 1993; Schimmelmann et al. 1993; Cormie et al. 1994 a, b). In addition, it is shown in Fig. 2 that the rate of hydrogen exchange is independent of the physical state (liquid versus vapor) of the environmental water. With the exception of the day 8 experiments, the  $\delta D$  of feathers exchanged with liquid water ( $\delta D = 320‰$  or  $-320‰$ ) and water vapor ( $\delta D = 273‰$  or  $-397‰$ ) are statistically indistinguishable. In both cases, the maximum hydrogen exchange occurred within 16 days.

The percent of hydrogen exchange can also be calculated from these experiments. The hydrogen isotopic values of feathers can be divided into two components: an exchangeable and non-exchangeable fraction. If exchangeable hydrogen consists of  $X$  fraction of the total hydrogen, we obtain the following mass balance equation:

$$\delta D_F = X\delta D_2 + (1-X)\delta D_1 \quad (1)$$

where  $\delta D_F$  is the  $\delta D$  value of total hydrogen at the time of formation,  $\delta D_1$  is the  $\delta D$  value of the first reservoir which does not undergo further isotopic exchange after feather growth,  $\delta D_2$  is

the  $\delta D$  value of the exchangeable hydrogen. If the  $\delta D_W$  is the  $\delta D$  value of the equilibration water, and  $\Delta$  is the isotopic discrimination between exchangeable hydrogen of feather and water such that:

$$\delta D_2 = \delta D_W + \Delta \quad (2)$$

Eq. 1 becomes:

$$\delta D_F = X\delta D_W + [(1-X)\delta D_1 + X\Delta] \quad (3)$$

Thus, once the feather has fully exchanged with water (after 16 days) we can calculate the percent of hydrogens exchanged using Eq. 3. The slope of the line on a plot of  $\delta D_F$  versus  $\delta D_W$  will give the percent of exchange (Fig. 3). For these experiments we find an equation of  $\delta D_F = 0.12845\delta D_W + 53.339$  ( $r^2 = 0.967$ ,  $P = 0.001$ ). Thus, the percent of hydrogen exchange is approximately 13%, which is considerably lower than the percent of total exchangeable hydrogen in feathers (~40%). This indicates that about three-fourths to two-thirds of exchangeable hydrogen is not readily accessible by environmental water.

The trends that we observe between  $\delta D$  of black-throated blue warbler feathers and  $\delta D$  of surface waters are not likely to be significantly affected by later post-molt hydrogen exchange for two reasons. First, all of the feathers were analyzed after they were stored in the laboratory for several months. Since the rate of hydrogen exchange is relatively fast, on the order of 2 weeks, the feathers would have equilibrated with laboratory water vapor before they were analyzed. In addition, to further reduce error caused by later hydrogen exchange all hydrogen isotopic analyses were done between February and April of 1994, during which time the water vapor in our laboratory remained relatively constant at approximately  $-159\text{‰} \pm 5.2$  (1 SD,  $N = 19$ ).

Second, the error introduced by hydrogen exchange between laboratory waters and feathers from birds collected in this study is relatively small. This error can be assessed by taking the derivative of Eq. 3, which gives:

$$d\delta D_F = X d\delta D_W \quad (4)$$

where  $d\delta D_F$  is the change in the hydrogen isotope value of the feather that occurs after the feather has equilibrated with laboratory water and  $d\delta D_W$  is the difference between the hydrogen isotopic values of the breeding site and laboratory waters. For example, feathers grown in Georgia ( $\delta D$  water =  $-31\text{‰}$ ), at the extreme southern breeding range, have  $\delta D$  values of approximately  $-68\text{‰}$ . When these feathers equilibrate with waters at Dartmouth ( $\delta D = -81\text{‰}$ ) the  $\delta D$  of the feathers change by  $6.5\text{‰}$ , a change that is less than the analytical uncertainty in the method (approximately  $\pm 10\text{‰}$ ). Thus, for species such as black-throated blue warblers which have a limited geographic range, post-molt hydrogen isotope exchange is not likely to have a significant affect on the analysis.

## Results

### Pattern of hydrogen isotopic ratios in breeding grounds

$\delta D$  values of black-throated blue warbler feathers varied geographically (Tables 2 and 3, Fig. 4), differing by over 30‰ from the southern end of the breeding range in northern Georgia ( $-68 \pm 10\text{‰}$ ) to the northern end in Parry Sound, Ontario ( $-102 \pm 13\text{‰}$ ). In addition,  $\delta D$  values decreased (i.e., became more negative) east to west across the northern part of the breeding range, from New Brunswick ( $-80 \pm 10\text{‰}$ ) to Michigan ( $-98 \pm 10\text{‰}$ ). These patterns have the same general trend with published values for the geographic distribution of  $\delta D$  in surface or rain waters, which decreases with increasing latitude, increasing elevation, and increasing distance from the oceans (Dansgaard 1964; Sheppard et al. 1969; Yurtsever

**Table 2** Isotopic composition of feathers ( $\delta^{13}C$ ,  $\delta D$ ) and bone ( $^{87}Sr/^{86}Sr$ ) of black-throated blue warblers in nine breeding areas in temperate North America and in three wintering sites in the Greater Antilles. See Fig. 1 for site locations

		Location - Black-throated blue warblers											
		Georgia	Virginia	W. Virginia	New York	New Hampshire	New Brunswick	Ontario-Round L.	Ontario-Parry S.	Michigan	Jamaica	Dominican Republic	Puerto Rico
$\delta^{13}C$	$\bar{x}$	-22.1	-23.3	-23.0	-23.1	-24.2	-24.4	-23.8	-23.9	-23.8	-24.1	-23.6	-23.8
	SD	0.6	0.5	0.6	0.5	0.6	0.6	0.6	0.5	0.5	0.9	0.6	1.0
	SE	0.14	0.13	0.14	0.13	0.15	0.14	0.13	0.12	0.13	0.19	0.18	0.22
$\delta D$	$\bar{x}$	-68	-78	-81	-69	-97	-80	-91	-102	-98	-112	-103	-106
	SD	10	14	9	9	11	10	9	13	10	21	7	13
	SE	2.6	3.7	2.2	2.3	3.2	2.3	2.1	3.2	2.6	4.8	2.4	3.1
	<i>n</i>	15	14	17	15	12	19	19	17	15	19	8	17
$^{87}Sr/^{86}Sr$	$\bar{x}$	0.71852 (2) <sup>a</sup>	0.71659 (2)	0.71473 (4)	0.71183 (2)	0.7183 (2)	0.71286 (2)	0.71170 (4)	0.71183 (5)	0.71304 (3)			
	SE	0.71675 (2)	0.71725 (2)	0.71340 (3)	0.71183 (2)	0.71329 (3)	0.71183 (2)	0.71155 (3)	0.71145 (3)				
$^{88}Sr$	$\bar{x}$	13.17	10.45	7.83	5.19	12.87	5.19	3.55	3.74	5.44			
	SE	10.67	11.38	5.95	5.80		5.80	3.74	3.34	3.20			

<sup>a</sup> The 2 SD error of  $^{87}Sr/^{86}Sr$  values in the last decimal place are given in parentheses

1975). The  $\delta D$  values of surface and rain water ranges from a high of approximately  $-31\text{‰}$  in northern Georgia to a low of  $-84\text{‰}$  in southern Ontario (Table 4). The relatively high  $\delta D$  value in warbler feathers from New Brunswick (Fig. 4) are probably due to the close proximity of this site to the Atlantic Ocean and its maritime influences, whereas the lower  $\delta D$  values in Ontario and Michigan are consistent with  $\delta D$  values in continental air masses. Overall, the  $\delta D$  values in black-throated blue warbler feathers were significantly correlated ( $r = 0.86$ ,  $P = 0.001$ , Fig. 5) with those in surface and rain waters at the localities where they were collected. Finally, analyses of feathers from each of seven American redstarts (Table 2) collected in central Alberta yielded a mean  $\delta D$  value of  $-117 \pm 9\text{‰}$ , which is much lower than values for black-throated blue warblers farther east, and matches very closely the expected value from rainwater patterns for that part of North America (Hitchon and Krouse 1972).

The correlation between the  $\delta D$  feathers and surface waters that we observe is consistent with other studies which show that both the  $\delta^{18}O$  (Longinelli 1984; D'Angela and Longinelli 1990, 1993) and the  $\delta D$  (Miller et al. 1988; Cormie et al. 1994) of animal tissue varies as a function of the mean  $\delta^{18}O$  and the  $\delta D$  of surface water. The  $\delta D$  of beetle chitin from eastern North America shows exactly the same geographic variation as the  $\delta D$

of black-throated blue warbler feathers (Fig. 1 in Miller et al. 1988). In the breeding range of black-throated blue warblers, the  $\delta D$  of chitin in beetles varies from a high of  $-55\text{‰}$  in Tennessee to a low of  $-89\text{‰}$  in southern Ontario; and increases to  $-65\text{‰}$  in the New Brunswick area (Miller et al. 1988). The similarity of geographic variation in  $\delta D$  values suggests that the black-throated blue warblers, which are insectivorous, are responding to the variation in  $\delta D$  of the insects.

However, we point out that although it is clear that hydrogen isotopes in bird feathers carry information of the source region, the presence of exchangeable hydrogen in feather keratin can reduce the sensitivity of this technique. In addition, the calibration presented in this paper is only good for the feathers that are equilibrated with Hanover atmospheric moisture. This would significantly limit the general applicability of the calibration and interlaboratory comparisons. We are in the process of developing a better analytical technique that addresses these problems.

Pattern of carbon isotopic ratios in breeding grounds

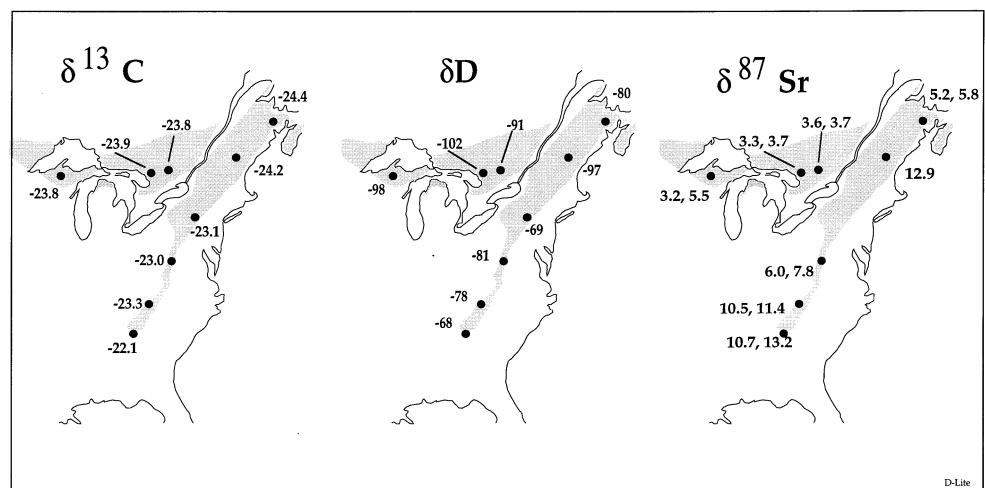
$\delta^{13}C$  in black-throated blue warbler feathers also varied with latitude, from a high of  $-22.1 \pm 0.6\text{‰}$  in Georgia to a low of  $-24.4 \pm 0.6\text{‰}$  in New Brunswick (Table 2, Fig. 4). These values were consistent within each site, as evidenced by the small standard deviations. A similar systematic decrease in  $\delta^{13}C$  with increasing latitude was evident in feathers of American redstarts (Table 3), with those from Louisiana and Mississippi having  $\delta^{13}C$  values of  $-22.4 \pm 0.6\text{‰}$ , whereas birds from New Hampshire had  $\delta^{13}C$  values of  $-23.8 \pm 0.7\text{‰}$ . Values for redstarts from Alberta, however, do not fit this general trend; they had an unusually wide range of  $\delta^{13}C$  values from a high of  $-20.9\text{‰}$  to a low of  $-24.5\text{‰}$  with a mean ( $\pm SD$ ) of  $-22.6 \pm 1.2\text{‰}$  (Table 3).

The systematic decrease in  $\delta^{13}C$  values of black-throated blue warbler feathers we observe is consistent

**Table 3** Isotopic composition of feathers ( $\delta^{13}C$ ,  $\delta D$ ) of American redstarts for three breeding sites

	Location – American Redstarts			
	Mississippi/ Louisiana	New Hampshire	Alberta	Alberta
$\bar{x}$	$\delta^{13}C$ -22.1	$\delta^{13}C$ -23.8	$\delta^{13}C$ -22.6	$\delta D$ -117
SD	0.5	0.7	1.2	9
SE	0.15	0.24	0.45	3.4
n	1	6	7	7

**Fig. 4** Mean  $\delta D$  and  $\delta^{13}C$  in feathers and  $\delta^{87}Sr$  in bones of black-throated blue warblers collected at the localities in Fig. 1



D-Line

**Table 4**  $\delta D$  values of surface water and precipitation

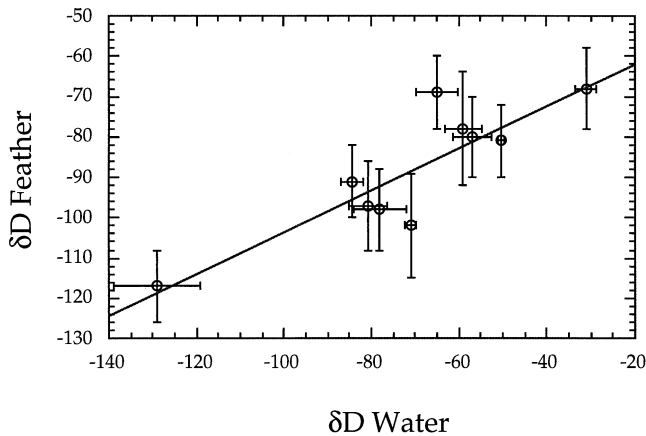
Location	$\delta D$ water	Description	Location	Source
Round Lake, ON	-82.7	river water	Ottawa River at mouth ~60 miles S.E. of site	Yang et al. (1986)
	-83	river water	Ottawa River near Mattawa ~40 miles N.W. of site	Friedman et al. (1964)
	-87.1	rain water	Ottawa IAEA data (1972-1982) ~30 miles east of site	Fritz et al. (1987)
Parry Sound, ON	-72	lake water	Port Carling, Lake Muskoka ~20 miles S.W. of site	Friedman et al. (1964)
	-70	rain water	Univ. of Waterloo isotope laboratory ~100 miles south of site	Miller et al. (1988)
Smithfield Settlement New Brunswick	-60	rain water	IAEA data (weighted mean precipitation $>0^{\circ}$ C) Prince Edward Island. ~100 miles N.E. of site	Miller et al. (1988)
	-53.6 $\pm$ 13.3	rain water	IAEA data (weighted mean precipitation $>0^{\circ}$ C, 1975-83) Truro, Nova Scotia. ~175 east of site	This study
Iron County, MI	-83	river water	Ontonagon River Ontonagon, MI. ~40 miles N.W. of site	Friedman et al. (1964)
	-80	rain water	IAEA data (weighted mean precipitation $>0^{\circ}$ C) Sault Ste. Marie ~150 miles east of site	Miller et al. (1988)
	-70.7 $\pm$ 18.4	rain water	IAEA data (weighted mean precipitation $>0^{\circ}$ C, 1975-1988) Atikokan, ON. ~180 miles N.W. of site	This study
Hubbard Brook Experimental St., NH	-80.8 $\pm$ 4.5	river water	Connecticut River and tributaries in Hanover, NH area July-Aug. 1995. ~80 miles S.W. of site	This study
Catskill Park, NY	-69	river water	Hudson River, near Schuylerville, NY	Friedman et al. (1964)
	-62	stream water	Saratoga, NY both ~60 miles north of site	This study
Wise Co., VA	-51	river water	Holston River, Bluff City, TN ~20 miles east of site	Friedman et al. (1964)
	-50	rain water	Carryville, TN IAEA data ~40 miles S.W. of site	Miller et al. (1988)
Blackwater Falls, WVA	-56	river water	Monongahela River	Friedman et al. (1964)
	-62	river water	Morgantown, WVA ~30 miles NW of site	
Blairsville, GA	-30	lake water	Lake Ocoee, TN	Friedman et al. (1964)
	-33	stream water	Brook of Ocoee	
	-33	river water	Toccoa River all ~40 miles N.W. of site	
	-28	river water	Chattanooga River Chattanooga, TN	Friedman et al. (1964)
Alberta	-129 $\pm$ 10	river water	Stations 82-86 S. McKenzie Basin	Hitchon and Krouse (1972)

with other studies which have shown  $\delta^{13}C$  to decrease with latitude in plants (Korner et al. 1991; Bird et al. 1994) and animals (van Klinken et al. 1994). For example, in the latter study,  $\delta^{13}C$  values in bone differed by approximately 2‰ over 20° latitude in northern Europe. We observed a similar decrease (~2‰ over 20° latitude) in the  $\delta^{13}C$  values in black-throated blue warbler feathers. The underlying cause of this geographic variation in  $\delta^{13}C$  is not well understood. Although it could be related to the proportions of C3:C4 plants in the environment, this seems unlikely to explain the pattern in black-throated blue warblers because this species lives in relatively heavily forested habitats which contain few if any C4 plants. Alternatively, the latitudi-

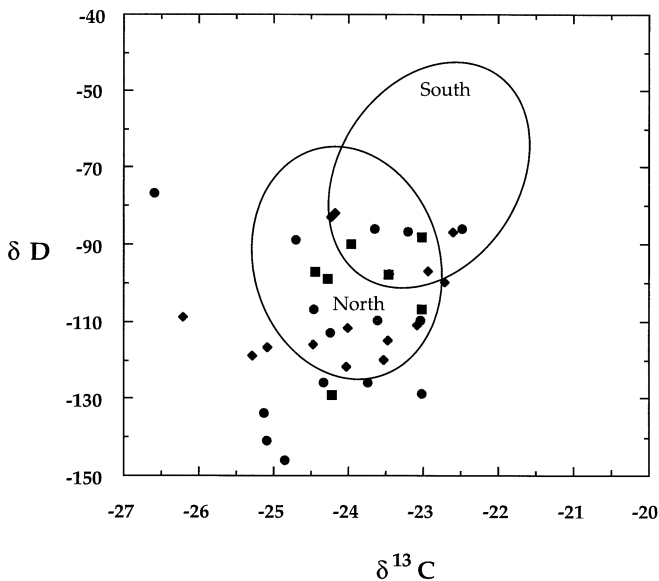
nal variation in  $\delta^{13}C$  values of feathers may reflect natural variation in  $\delta^{13}C$  within C3 plants which vary by approximately 2‰ over this latitudinal gradient (Korner et al. 1991; van Klinken et al. 1994). However, no studies have been made of the regional variation of C isotopes in C3 plants across eastern North America to verify this possibility.

Two-way analysis of hydrogen and carbon isotopes: comparisons of breeding and wintering areas

Plotting  $\delta D$  values in feathers against those for  $\delta^{13}C$  allows further resolution of geographical patterns in the



**Fig. 5** Mean and 1 SD  $\delta D$  values of feathers from 143 black-throated blue warblers versus  $\delta D$  in rain water. Values for waters were either taken from Friedman et al. (1964), Miller et al. (1988), Fritz et al. (1987), or calculated from the oxygen isotope data of Yang et al. (1996) and Hitchon and Krouse (1972), or determined in the laboratory at Dartmouth College, or calculated from IAEA tables. The value of  $-117\text{‰}$  was the mean for feathers collected from American redstarts from Alberta (see Tables 1 and 2)



**Fig. 6**  $\delta D$  and  $\delta^{13}C$  values in feathers of black-throated blue warblers in breeding areas (ellipses) and in winter localities (points). Breeding data are represented by 95% confidence ellipses calculated from the isotopic analyses of feathers from breeding birds in the northern part of the breeding range (Ontario, Michigan, New Hampshire, and New Brunswick) and from the southern breeding area (New York, West Virginia, Virginia, and Georgia). The three wintering localities were in the Greater Antilles: the Dominican Republic (squares), Puerto Rico (diamonds), and Jamaica (dots)

black-throated blue warbler breeding range (Fig. 6). Individuals from areas north of the Catskills in New York typically had lower values in feathers for both  $\delta D$  and  $\delta^{13}C$  than individuals breeding to the south (Fig. 4, Table 2). The 95% confidence ellipses calculated for these two groups of sites provide good separation of northern and

southern breeding populations (Fig. 6), with some overlap due mostly to individuals from maritime New Brunswick with their relatively high  $\delta D$  values.

Figure 6 also includes data on  $\delta D$  and  $\delta^{13}C$  of feathers collected from black-throated blue warblers in several different wintering locations. The values for both isotopes in these wintering birds were relatively low (Table 2, Fig. 6), indicating that most individuals in these samples were from the northern parts of the species' breeding range and few, if any were from the more southerly breeding areas. Furthermore, the variation in isotopic values, as indicated by standard deviations, was generally larger in winter than in breeding sites, especially for  $\delta^{13}C$  (Table 2). In all cases, the samples at each site in both breeding and winter grounds were from warblers occupying very local areas. The wider variation in winter sites probably reflects mixing of individuals from different breeding latitudes. Further sampling of black-throated blue warbler populations from throughout the wintering range will be necessary for determining the degree of mixing of breeding populations that occurs for this particular species, as well as to locate individuals from more southerly breeding populations.

#### Pattern of strontium isotopic ratios in breeding grounds

The two-way analysis of hydrogen and carbon considered above suggests the utility of multiple isotopic systems for separating subpopulations of black-throated blue warblers. To determine if strontium might provide a suitable third axis, we analyzed the Sr isotopic composition of bone fragments from a subset ( $n = 18$ ) of black-throated blue warblers collected from eight of the breeding localities (Table 2, Fig. 4). Bones from two or three individuals per site were analyzed, and the resulting  $\delta^{87}Sr$  values differed more between than within localities, and varied significantly across the breeding range. The  $\delta^{87}Sr$  values of bones from birds along the core of the Appalachian Mountains in Georgia, Virginia, West Virginia, and New Hampshire were high (6.0 to 13.2‰), contrasting with those from the Great Lakes region (Michigan and Ontario) and New Brunswick which were considerably lower (3.2–5.8‰). Although there are no regional surveys of  $\delta^{87}Sr$  in soils or vegetation for comparison, limited data are available on  $\delta^{87}Sr$  in rivers which reflect regional trends in soil  $\delta^{87}Sr$  values. The Susquehanna River predominantly drains the core of the Appalachian Mountains, and has a high  $\delta^{87}Sr$  value of 7.1‰ at its mouth (Fisher and Stueber 1976). The St. Lawrence River has a  $\delta^{87}Sr$  value of 0.4‰ and the St. John River has a  $\delta^{87}Sr$  value of 0.8‰, reflecting the lower soil  $\delta^{87}Sr$  values of the Great Lakes and New Brunswick regions, respectively (Wadleigh et al. 1985). The marked contrast in regional  $\delta^{87}Sr$  values between the Great Lakes/New Brunswick regions and the Appalachians reflects the higher proportion of geologically old crystalline rock in the Appalachians (e.g., Lathrop et al. 1994;  $> 8.6\text{‰}$   $\delta^{87}Sr$ ) relative to low  $\delta^{87}Sr$  limestone

(Burke et al. 1982; 0 to  $-3.4\text{‰}$ ) present in the Great Lakes and New Brunswick regions. The relatively narrow range of  $\delta^{87}\text{Sr}$  values at each locality and the general similarity between  $\delta^{87}\text{Sr}$  values of bone material and regional geology suggest that the  $\delta^{87}\text{Sr}$  of bird bones are largely influenced by the ambient values of their natal sites, although we recognize that bone  $\delta^{87}\text{Sr}$  values probably represent a mixture between  $\delta^{87}\text{Sr}$  values of natal and winter sites.

Based on these data, we suggest that strontium isotopes have the potential for separating black-throated blue warbler individuals that nest along the Appalachian Mountain belt ( $\delta^{87}\text{Sr}$  values of 6.0–13.2‰) from those in the Great Lakes or New Brunswick regions (values of 3.2–5.8‰).  $\delta^{87}\text{Sr}$  samples from more individuals within a site and from more sites will be needed to verify the utility of this isotopic system in separating individuals across their breeding range.

## Discussion

Causes of variation between isotope ratios in birds and the environment.

We found that carbon and hydrogen isotope ratios extracted from bird tissues varied geographically. These isotope ratios, however, differed substantially from those in the environment. For instance, the  $\delta\text{D}$  values of feathers were approximately 10–30‰ lower than the  $\delta\text{D}$  values of local surface waters; and  $\delta^{13}\text{C}$  values of feathers were 3–4‰ higher than the  $\delta^{13}\text{C}$  values of C3 plants in northern forests. These differences probably reflect the carbon and hydrogen isotopic fractionation that occurs through the food chain. It is well known that carbon and nitrogen isotopes become increasingly enriched in the heavy isotope ( $^{13}\text{C}$  and  $^{15}\text{N}$ ) with increasing trophic level (DeNiro and Epstein 1978, 1981). These trophic level studies may provide us a key to understand the carbon isotopic values of the black-throated blue warblers.

Black-throated blue warblers breed mainly in relatively undisturbed, continuous tracts of mixed deciduous/coniferous forests in Eastern North America (Holmes 1994). During the breeding season these warblers are predominantly insectivorous, feeding on Lepidoptera larvae and adults, adult Diptera, spiders, and other arthropods. Thus, the carbon and hydrogen isotopes of the birds feathers should reflect a three-tiered trophic-level structure that begins with C3 plants at the base (level 1), continues with insects (level 2), and ends with the insectivorous birds (level 3). Our carbon isotope data of black-throated blue warblers are consistent with isotopic fractionation with trophic level. It has been shown (Mizutani et al. 1990; Hobson and Clark 1992) that  $\delta^{13}\text{C}$  values of feathers are approximately 3–4‰ higher than the  $\delta^{13}\text{C}$  value of the bird's diet. Since there is no measurable carbon isotopic fractionation between insects and their diet (Fry et al. 1978; Miller 1984), and if we assume that the mean  $\delta^{13}\text{C}$  value in leaves of northern for-

ests is approximately  $-28\text{‰}$  (C.P. Chamberlain, unpublished work; Garten and Taylor 1992) the values for insectivorous black-throated blue warblers should be approximately  $-23$  to  $24\text{‰}$ , which are similar to those we obtained in our analyses.

There are relatively few studies of hydrogen isotope fractionation associated with changes in trophic levels. Those studies that have been done suggest that there is no measurable hydrogen isotope fractionation between the hydrogen in an animal diet and its tissues (Estep and Dabrowski 1980). Experimental studies of bird feathers from red-winged blackbirds (*Agelaius phoeniceus*) (Hobson et al., in press) further demonstrate that the  $\delta\text{D}$  values of feather keratin are similar to the  $\delta\text{D}$  values of their diet. Experimental studies of flour beetles (*Tenebrio molitor*) and American cockroaches (*Periplaneta americana*) (Miller 1984) show a 20–30‰ decrease in  $\delta\text{D}$  of whole body values with respect to their food source. However, in contrast to carbon isotopes, the hydrogen isotopic compositions of tree leaves is much more variable. Further complications also result from the fact that when insects feed on tree leaves, they uptake hydrogen both from leaf water and from plant tissues (e.g., cellulose). It is well known that leaf water is more enriched in deuterium than the source water (soil or stem water) because of isotopic fractionation during transpiration (e.g., Epstein et al. 1977; Allison et al. 1985; Flanagan et al. 1991; Thornburn et al. 1993; Terwilliger and DeNiro 1995). The degree of deuterium enrichment in leaves is a sensitive function of the relative humidity of the air and can vary from 15‰ or less in humid air to 50‰ or greater in dry air. Leaf cellulose is usually depleted in deuterium compared with the source soil water (Epstein and Yapp 1977; White et al. 1994), but can be more enriched (although rare in natural forest) than leaf water if reserved carbohydrates are used for cellulose synthesis (Terwilliger and DeNiro 1995; V.J. Terwilliger, personal communication). Because of these sources of variation, it is difficult to determine the mean hydrogen isotopic compositions of food for the insects that in turn serve as food for birds we studied. At this point we do not know what has caused the 10–20‰ decrease in  $\delta\text{D}$  values of feather keratin relative to the local surface water.

Isotope ratios as population markers.

Although a large amount of work remains to be done in order to understand all of the sources of variation in isotope ratios, the findings of this study show that stable isotope ratios of hydrogen, carbon, and strontium extracted from bird feathers and bones vary systematically with geography within eastern North America. Moreover, these geographic isotopic patterns are consistent with the natural variations of these isotope ratios in surface waters and plants, presumably because of water and food consumption by birds at the time these tissues were produced. These isotopic ratios thus have the potential for serving as population markers. In our attempt to de-



termining the breeding origins of black-throated blue warblers in winter using H and C isotope ratios, we found that individuals in samples from three Greater Antilles islands were from northern breeding populations. Although we lacked material from warblers in the winter ground for analysis of Sr ratios, the addition of such information would help improve our ability to separate sub-populations, particularly species whose breeding range straddles major geographic areas differing in soil parent material  $\delta^{87}\text{Sr}$  values (e.g., the Appalachian mountains versus surrounding regions). Combining information from these isotopes, and possibly additional isotopic systems (e.g., S, O, Nd, Pb), should provide the greatest potential for identifying regional populations. Finally, we point out that one of the benefits of this technique is that, at least for the light stable isotope analyses, only feathers need to be sampled. Thus, the use of C, H, and S isotopes as tracers (all of which are found in feather keratin) require nondestructive sampling and the bird can be captured and released after a feather is removed.

These isotope data suggest a level of resolution that would allow categorization of most breeding individuals in a species with a relatively restricted breeding range, such as the black-throated blue warbler, into one of three regional groups (southern, northern, midwestern/interior), and for a more geographically widespread species like the American redstart, into at least four regional groups (same as above, with the addition of a far western group). Even these levels of resolution would be a major advance in our knowledge of the linkage between breeding and wintering populations in migratory species. The data would be useful for determining whether individuals from local breeding areas remain together in wintering areas or disperse widely, information needed for evaluating the causes of recent population declines in some of these migratory bird species (Robbins et al. 1989; Dolman and Sutherland 1994; Sherry and Holmes 1995).

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