Joel D. Blum · E. Hank Taliaferro
Richard T. Holmes

Determining the sources of calcium for migratory songbirds using stable strontium isotopes

Abstract We investigated natural variations in the stable isotopic composition of strontium (a surrogate for calcium) in the bones of a single species of breeding migratory songbird, as well as in their eggshells, egg contents, and food sources. We use this information to determine the sources of calcium to these migratory songbirds and their offspring. Samples were collected from two locations in the northeastern USA (Hubbard Brook, NH, and Downer Forest, VT.) that differed in soil geochemistry. The mean $^{87}Sr/^{86}Sr$ ratios of food items (caterpillars and snails), eggshells, and egg contents were indistinguishable within each site, but significantly different between the two sites. Mean $^{87}Sr/^{86}Sr$ ratios for the bones of adult females were significantly different between the two sites, but values were significantly lower than those of food items and eggshells at each site. Two of four adult individuals studied at each site had $^{87}Sr/^{86}Sr$ ratios lower than the entire range of values for local food sources. Mixing calculations indicate that up to 60% of skeletal strontium and calcium was derived from foods consumed in the winter grounds where lower $^{87}Sr/^{86}Sr$ ratios predominate. At each study site, the $^{87}Sr/^{86}Sr$ ratio of eggshells differed significantly between clutches, but the mean clutch $^{87}Sr/^{86}Sr$ ratios were unrelated to the skeletal $^{87}Sr/^{86}Sr$ ratio of the laying adult. These findings suggest that strontium (and hence calcium) for eggshell production in this species is derived predominantly from local food sources in breeding areas. Thus, reductions in available calcium in northern temperate ecosystems due to the influences of acid deposition could be potentially harmful to this and other species of migratory bird.

J.D. Blum (✉)
Department of Geological Sciences, University of Michigan, Ann Arbor, 425E. University Avenue, MI 48109, USA
e-mail: jdblum@umich.edu
Tel.: +1-734-6153242, Fax: +1-734-7634690

E.H. Taliaferro · R.T. Holmes
Department of Biological Sciences, Dartmouth College, Hanover, NH 03755, USA

Introduction

Investigations of natural variations in the stable isotopic composition of strontium in the environment have proven useful in tracing the various sources of nutrient base cations in forest ecosystems (Gosz et al. 1983; Graustein and Armstrong 1983; Åberg et al. 1989; Miller et al. 1993; Bailey et al. 1996; Blum and Erel 1997; Kennedy et al. 1998; Vitousek et al. 1999) and have recently been used in studies of elephant (*Loxodonta africana*; Koch et al. 1995), Atlantic salmon (*Salmo salar*; Kennedy et al. 1997, in press), and migratory songbird (*Dendroica caerulescens;* Chamberlain et al. 1997) movements. Strontium isotopes provide a fundamentally different type of tracer than the light stable isotopes (e.g., those of hydrogen, carbon, nitrogen, and oxygen) that are more commonly used in biological applications, because variation in the $^{87}Sr/^{86}Sr$ ratio is determined by radioactive decay in rocks over geological time scales and is unaffected by the mass-dependent isotope fractionation that results in variations in the light stable isotope ratios (e.g., Graustein 1989).

Strontium is a non-nutrient trace element that tends to follow calcium as a trace constituent during nutrient uptake, internal distribution, and excretion within organisms (Elias et al. 1982; Graustein 1989; Sillen 1992; Gierth et al. 1998; Blum et al. 2000) and can thus be used as a tracer of various inputs of calcium to ecosystems and food webs. In this study, we used stable strontium isotope ratios to determine the sources of calcium to a breeding migratory songbird, the black-throated blue warbler (*D. caerulescens*: Parulidae) and its offspring, in two forest ecosystems in the northeastern USA. We have previously reported (Blum et al. 2000) a study of the degree of biological fractionation of Ca/Sr ratios in the soil-plant-invertebrate-bird food chain at the same study sites. This report adds additional data on the $^{87}Sr/^{86}Sr$

and Ca/Sr ratios of insects, eggshells, and egg contents, and focuses specifically on two objectives: (1) determining the proportion of calcium in adult bones that was derived from foods in the breeding areas versus the winter areas, and (2) confirming agreement with the prevailing literature that the calcium used in the formation of egg contents and eggshells in this migratory species is derived from local food sources in the breeding area. Our findings are relevant to many of the issues raised by Drent and Woldendorp (1989) and Graveland and van der Wal (1996) concerning the possibility that anthropogenically caused decreases in available calcium in forests might affect the availability of this nutrient for temperate breeding birds.

Materials and methods

Samples were collected between 5 and 19 June 1996 from two study sites – one at the Charles Downer State Forest (Downer Forest) in Sharon, Vermont, and another at the Hubbard Brook Experimental Forest (Hubbard Brook) in West Thornton, New Hampshire. Details of the bedrock geology, soil development, and vegetation types at these study sites are given by Blum et al. (2000). Black-throated blue warblers arrive at the sites after migration from the Caribbean region in mid to late May and immediately begin nest building. They generally begin laying clutches of four to five eggs (one per day) within 2 weeks of arrival at the breeding sites (Holmes 1994). Hubbard Brook is the site of a long-term ecological study of black-throated blue warblers (e.g., Holmes et al. 1996) and a second site was chosen at Downer Forest because of its naturally higher calcium content and the lower $^{87}Sr/^{86}Sr$ ratios of its soils (see Blum et al. 2000). Extensive observation of the feeding habits of black-throated blue warbler and analyses of gut contents suggests that larval Lepidoptera are the main food sources (Holmes 1994), although during egg-laying they probably take small snails as an additional source of calcium (R.T. Holmes, unpublished data). There is no evidence for the ingestion of other calcareous items such as vertebrate bones or calcareous grit. At each site, all samples were collected within a circular sampling area with a diameter of ~400 m. Four female black-throated blue warblers were followed at each site until their nests were found. After they had completed their clutches, the adult females and all of their eggs were collected under permit from federal and state agencies and with procedures approved by the Institutional Animal Care and Use Committee of Dartmouth College. Caterpillars (Families: Geometridae and Notodontidae) were collected from four sites on each plot near the locations of the nests; nine caterpillars from Hubbard Brook and eight caterpillars from Downer Forest were analyzed. Six snails were collected from beneath cardboard sheets placed on the forest floor at Hubbard Brook and one at Downer Forest.

Adult female warblers were dissected and their femurs removed and cleaned. Eggs were stored frozen and then broken open allowing easy separation of egg contents (yolk, albumen, and embryo) from shells. All samples were stored in the fresh frozen state, then dried overnight at 105°C. Caterpillars and egg contents were ashed in acid-washed quartz crucibles at 500°C. All samples were digested in ultra-pure nitric and hydrochloric acids, evaporated to dryness, and then redissolved in ultra-pure 5% nitric acid for analysis. Solutions were diluted to appropriate concentration ranges, spiked with a yttrium internal standard, and analyzed with an accuracy of ±3% for the concentration of calcium and strontium using a Finnigan magnetic sector inductively coupled plasma mass spectrometer calibrated with appropriate analytical standards. A second aliquot of each solution containing 1,000 ng of strontium was eluted through ion-specific cation exchange columns using Sr-Spec resin. Approximately 75 ng of each pure strontium fraction was loaded onto a tungsten filament with Ta_2O_5 powder. Total procedural blanks were <40 pg strontium and thus negligible. Filaments were loaded into a Finnigan MAT 262 thermal ionization mass spectrometer (TIMS) for isotope ratio measurement. $^{87}Sr/^{86}Sr$ ratios were normalized to a $^{86}Sr/^{88}Sr$ ratio of 0.1194 (to eliminate mass-dependent isotope fractionation) and over 100 isotope ratios were measured for each sample, yielding a mean $^{87}Sr/^{86}Sr$ ratio for each sample with an analytical uncertainty of less than ±0.00002 (2 SD; Table 1). The mean $^{87}Sr/^{86}Sr$ value obtained for 32 replicate analyses of inter-laboratory calibration standard NIST-987 was 0.71026±0.00002 (2 SD).

Results and discussion

Comparison of $^{87}Sr/^{86}Sr$ ratios between the two sites

The range of measured $^{87}Sr/^{86}Sr$ ratios of food items, eggshells, egg contents, and adult bones were completely non-overlapping between the two study sites (Fig. 1, Table 1). Mean $^{87}Sr/^{86}Sr$ ratios of food items, eggshells, and egg contents at Hubbard Brook were 0.7191 (SD=0.0013, n=15), 0.7191 (SD=0.0007, n=16), and 0.7190 (SD=0.0006, n=8), respectively, and at Downer Forest were 0.7132 (SD=0.0003, n=9), 0.7129 (SD=0.0006, n=17), and 0.7128 (SD=0.0002, n=6), respectively (Table 1). The mean $^{87}Sr/^{86}Sr$ ratios of food items, eggshells, and egg contents were higher at Hubbard Brook than at Downer Forest by 0.0059, 0.0062 and 0.0062, respectively. Mean $^{87}Sr/^{86}Sr$ ratios of adult female warblers were also higher at Hubbard Brook (0.7170, SD=0.0020, n=4) than at Downer Forest (0.7121, SD=0.0013, n=4), but by a smaller difference of 0.0049 (Table 1). These differences in $^{87}Sr/^{86}Sr$ ratios between the two sites primarily reflect the different compositions and ages of the geological substrate on which soils at each location have developed, and the transfer of these characteristic $^{87}Sr/^{86}Sr$ ratios through the food web from soil to forest vegetation to invertebrates to birds (Blum et al. 2000).

$^{87}Sr/^{86}Sr$ ratios of food sources and eggs within each site

The mean $^{87}Sr/^{86}Sr$ ratios that we measured in food sources were indistinguishable from values of eggshells at both Hubbard Brook (P=0.96, F=0.003, df=29) and Downer Forest (P=0.13, F=2.43, df=25) (Fig. 1). The variation in $^{87}Sr/^{86}Sr$ ratios of food items, however, were larger at Hubbard Brook (SD=0.0013, n=15) than at Downer Forest (SD=0.0003, n=9). A similar trend of greater variability in the $^{87}Sr/^{86}Sr$ ratios at Hubbard Brook compared to Downer Forest was also found for soils and vegetation (Blum et al. 2000). Nevertheless, the variation in $^{87}Sr/^{86}Sr$ ratios of eggshells from Hubbard Brook (SD=0.0007, n=16) was approximately the same as at Downer Forest (SD=0.0006, n=17), suggesting that by feeding on multiple food items, the adult birds homogenize the $^{87}Sr/^{86}Sr$ ratios of individual food items (Fig. 1). At Hubbard Brook, where we had a significant number of both snail and caterpillar analyses, we found

Fig. 1 $^{87}Sr/^{86}Sr$ ratios of female adult black-throated blue warbler bones, eggshells, and food items ($\triangle$ caterpillars, $\triangledown$ snails) from Hubbard Brook, NH, and Downer Forest, VT. *Shaded areas* connect values for female adults with values of the eggshells from their clutch. The analytical uncertainties of each individual analysis are smaller than the width of the eggshell symbol
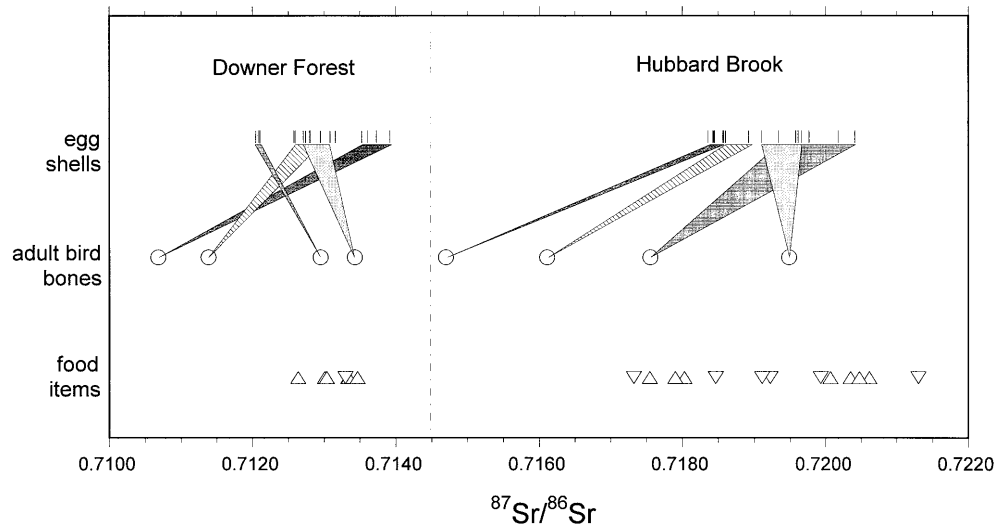

Table 1 Range, mean, and standard deviation of Ca/Sr (mg/µg) and $^{87}Sr/^{86}Sr$ ratios for the various sample types

			Ca/Sr			$^{87}Sr/^{86}Sr$		
		n	Range	Mean	SD	Range	Mean	SD
Food item: caterpillars	Hubbard Brook	9	0.29–1.36	0.66	0.35	0.71755–0.72062	0.71908	0.00140
	Downer Forest	8	0.29–0.63	0.44	0.13	0.71264–0.71347	0.71317	0.00029
Food item: snails	Hubbard Brook	6	0.50–0.81	0.61	0.13	0.71733–0.72130	0.71923	0.00111
	Downer Forest	1	–	0.42	–	–	0.71330	–
Adult bird bones	Hubbard Brook	4	2.30–3.65	2.96	0.69	0.71470–0.71948	0.71696	0.00205
	Downer Forest	4	0.97–3.62	2.36	1.11	0.71068–0.71343	0.71211	0.00129
Eggshells	Hubbard Brook	16	0.60–1.77	0.90	0.35	0.71843–0.72018	0.71912	0.00068
	Downer Forest	17	0.44–1.15	0.74	0.24	0.71205–0.71392	0.71285	0.00059
Egg contents	Hubbard Brook	8	0.79–2.94	1.49	0.77	0.71825–0.71947	0.71900	0.00057
	Downer Forest	6	0.73–1.23	0.75	0.28	0.71262–0.71309	0.71281	0.00018

that the $^{87}Sr/^{86}Sr$ ratios of caterpillars and snails were indistinguishable ($P=0.85$, $F=0.39$, $df=13$), and displayed a similar degree of variability (caterpillars: SD=0.0014, $n=9$; snails: SD=0.0011, $n=6$).

The mean $^{87}Sr/^{86}Sr$ ratios of eggshells differed significantly among the clutches within each site (Hubbard Brook: $P<0.001$, $F=22$, $df=15$; Downer Forest: $P<0.001$, $F=66$, $df=16$). This suggests that heterogeneity in the $^{87}Sr/^{86}Sr$ ratios of food sources between each bird's territory was reflected in the isotopic composition of their eggshells. Differences in the $^{87}Sr/^{86}Sr$ ratios of eggshells within each clutch were also measured. The maximum range in $^{87}Sr/^{86}Sr$ ratios within clutches varied from 0.00006 to 0.00107 (3–50 times the analytical uncertainty of the isotope ratio measurements). The $^{87}Sr/^{86}Sr$ ratio of an individual egg would be expected to represent the average value of food ingested by the adult female during the 1-day egg-laying period; thus, these within-clutch variations may reflect small changes in the foraging area of the females from day to day within their territories. Although the contents of only a subset of the eggs were analyzed, a linear regression of the data revealed that the $^{87}Sr/^{86}Sr$ ratios of eggshells are highly correlated to those of the egg contents at both Hubbard Brook and Downer Forest ($r=0.96$ and 0.90, respectively).

$^{87}Sr/^{86}Sr$ ratios of adult birds

Adult female warblers had $^{87}Sr/^{86}Sr$ ratios significantly lower than their food sources at Hubbard Brook ($P=0.020$, $F=6.90$, $df=17$) and Downer Forest ($P=0.030$, $F=6.23$, $df=12$). Adults also had $^{87}Sr/^{86}Sr$ ratios significantly lower than their eggshells at Hubbard Brook ($P=0.001$, $F=13.8$, $df=19$) and marginally lower than their eggshells at Downer Forest ($P=0.089$, $F=3.21$, $df=20$). Half of the adult females at each site had $^{87}Sr/^{86}Sr$ ratios lower than the entire range of values for food sources in their summer habitats. This is probably due to a portion of the strontium in their bones being derived from winter habitats where $^{87}Sr/^{86}Sr$ values of food sources are expected to be lower than in the summer sites. Black-throated blue warblers winter in the Caribbean Islands (especially the Greater Antilles) and coastal regions of the Yucatan Peninsula (Holmes 1994). The geologic substrate in these regions (Mascle and Letouzey 1990) is predominantly Cretaceous and Tertiary marine limestone (calcium carbonate) with $^{87}Sr/^{86}Sr$ of 0.707–0.709 (Burke et al. 1982), and volcanic, plutonic, and volcanoclastic silicate rocks with $^{87}Sr/^{86}Sr$ of 0.704–0.706 (Frost et al. 1998). Maritime ecosystems, such as those of the Caribbean, also receive significant

proportions of their plant-available strontium (and calcium) from marine aerosols with $^{87}Sr/^{86}Sr$ of 0.709, and thus vegetation and foodweb $^{87}Sr/^{86}Sr$ ratios are strongly influenced by the marine value (e.g., Miller et al. 1993; Kennedy et al. 1998; Vitousek et al. 1999). Thus, $^{87}Sr/^{86}Sr$ values of plants and insects from the Caribbean region would be expected to range from 0.704 to 0.709.

Given the estimates of $^{87}Sr/^{86}Sr$ ratios in the winter areas discussed above, and using the average measured values for food sources in the northern breeding areas, we can calculate the proportion of winter strontium in the bones of the adult females (x_{winter}) that we collected in early summer at Hubbard Brook and Downer Forest using the following mass balance equation:

$$x_{winter} = [(^{87}Sr/^{86}Sr)_{bone} - (^{87}Sr/^{86}Sr)_{summer}]$$
$$/[(^{87}Sr/^{86}Sr)_{winter} - (^{87}Sr/^{86}Sr)_{summer}]$$

The proportion of strontium from the winter site calculated in this way should be equivalent to the proportion of calcium from the winter site, provided that food sources have similar Ca/Sr ratios in the winter and summer habitats. We consider this a very good assumption and note that even though Hubbard Brook and Downer Forest have contrasting soil Ca/Sr ratios, these differences are diminished up the food web leading to indistinguishable values for insects and snails (Blum et al. 2000).

For the two adult birds at Hubbard Brook that had $^{87}Sr/^{86}Sr$ ratios below the range of values for Hubbard Brook food sources (Fig. 1), we calculated that the proportion of winter strontium (and calcium) in these individuals was 30–45% and 20–30%, respectively, based on the average Hubbard Brook summer diet with $^{87}Sr/^{86}Sr$ of 0.7191 and using the estimated range of values for winter food of 0.704–0.709. Similarly, for the two adult birds at Downer Forest that had $^{87}Sr/^{86}Sr$ ratios lower than Downer Forest food sources (Fig. 1), we calculated that the proportion of winter strontium is 20–40% and 30–60%, respectively, based on the average Downer Forest summer diet with $^{87}Sr/^{86}Sr$ of 0.7132 and using the same range of values for winter food of 0.704–0.709.

The two additional birds from each site had $^{87}Sr/^{86}Sr$ ratios within the ranges observed for food sources and eggs at each summer site. These adult females may have either (1) spent the winter in a habitat with higher $^{87}Sr/^{86}Sr$ ratios than the range of values we estimated, (2) retained less of the winter strontium in their skeletal tissues during the period since their arrival at the breeding area due to earlier arrival, or (3) represent younger birds whose bone Sr isotope values are biased toward breeding sites where bones were fist formed. In these calculations we also cannot account for the isotopic contribution of food consumed during migration, which could also influence summer isotopic values. The general correlation between the mean $^{87}Sr/^{86}Sr$ of the adult's bones with the food in each of the two breeding sites we studied, strongly suggests that the strontium (and calcium) in adult bones in early summer is derived in large part from foods consumed since their arrival on the breeding sites

in early to mid May, but our calculations show that some birds still retain up to 60% of their strontium (and calcium) from winter sites as late as mid to late June.

Our results demonstrate that calcium incorporated into the bones of black-throated blue warblers is a mixture of calcium derived from foods in their nesting and wintering areas. The cycling time of calcium through migratory passerines is not known, but based on this study we can say that it is long enough that four of the eight birds we analyzed retained a significant winter $^{87}Sr/^{86}Sr$ signal (20–60% of skeletal calcium) 2–4 weeks after arrival at nesting areas and after cycling large quantities of calcium through their bodies during egg production.

Does skeletal calcium contribute to egg formation?

Because many migratory birds finish migration only 1–2 weeks before laying their first egg, and because some bird species are known to store calcium as medullary bone prior to egg-laying (e.g., Mueller et al. 1964; Gilbert 1983; Dacke et al. 1993), we considered whether calcium stored in the skeletons of passerines might contribute to shell formation. Several workers have pointed out that a clutch of eggs contains approximately the same amount of calcium as the entire skeleton of most small passerines and have also used calculations of the calcium budgets of great tits (Graveland and Van Gijzen 1994) and house sparrows (Ankney and Scott 1980; Krementz and Ankney 1995) to suggest that birds with large calcium demands for egg-laying relative to body size store little or no calcium in their skeletons before egg-laying. Similar arguments comparing estimated amounts of calcium in the skeleton with the amount utilized in egg production have also been made for the black-throated blue warbler (H. Taliaferro, R.T. Holmes, J.D. Blum, unpublished data). Pahl et al. (1997) used a radiographic method to determine that several resident passerine species do not remobilize calcium from their leg bones. In the study reported here, we investigated the possibility that strontium isotopes can be used to place constraints on the sources of calcium used in the production of bird bones and eggs.

If skeletal strontium were a major contributor of strontium during egg formation we might expect the $^{87}Sr/^{86}Sr$ ratios of adult female bones within each site to match closely the $^{87}Sr/^{86}Sr$ ratios of the eggs they produce. For example, adults with the lowest skeletal $^{87}Sr/^{86}Sr$ ratios at a given site would be expected to produce eggs with $^{87}Sr/^{86}Sr$ ratios lower than birds with higher skeletal $^{87}Sr/^{86}Sr$ ratios. We did not observe this pattern with black-throated blue warblers. In fact, the female from Downer Forest that had the lowest bone $^{87}Sr/^{86}Sr$ ratio produced eggs with the highest $^{87}Sr/^{86}Sr$ values at that site, whereas a female from Downer Forest with a relatively high bone $^{87}Sr/^{86}Sr$ ratio produced eggs with the lowest $^{87}Sr/^{86}Sr$ values at that site (Fig. 1).

Similarly, if skeletal strontium were a major contributor of strontium during egg formation, we might also ex-

pect that the first egg laid in a clutch would have an $^{87}Sr/^{86}Sr$ ratio closer to that of the female's skeleton than to those of subsequent eggs. House sparrows are known to alter their diet to include materials higher in calcium only after production of the first eggshell of their clutch (Ankney and Scott 1980; Pinowska and Krasnicki 1985). For each of the eight birds we studied, all eggs in the clutch were analyzed. Although we do not know the order in which specific eggs were laid, none of the birds produced eggs with outlier $^{87}Sr/^{86}Sr$ ratios (see Fig. 1).

The $^{87}Sr/^{86}Sr$ data discussed above do not suggest an important contribution of skeletal strontium to eggshells. However, in this instance we must consider the implications for the possible contribution of calcium separately from strontium, because the Ca/Sr ratios of the bird skeletons were significantly higher than those of the food sources (Table 1). Equations describing the effect of mixing two reservoirs with different Ca/Sr and $^{87}Sr/^{86}Sr$ ratios on the $^{87}Sr/^{86}Sr$ ratio of a mixture are given in Faure (1986) and Capo et al. (1998). For our data, the higher mean Ca/Sr ratios of bones compared to food items (Table 1) results in a situation where the $^{87}Sr/^{86}Sr$ ratio of a mixture is less sensitive to additions of calcium from bone than from additions of calcium from food items. For example, in a mixture where 50% of the calcium came from bone and 50% of the calcium came from food items, only 15% of the strontium would come from the bone (assuming that Ca and Sr were mobilized from bone in proportion to their concentration ratio). As a result of the small amount of bone strontium compared to bone calcium in such a mixture, the $^{87}Sr/^{86}Sr$ ratio would be relatively insensitive to the presence of the bone calcium.

To calculate a maximum shift in $^{87}Sr/^{86}Sr$ that we might expect from such a mixture, we used the $^{87}Sr/^{86}Sr$ ratio from the bird with the lowest $^{87}Sr/^{86}Sr$ ratio at each site. We calculated that an eggshell derived from 100% food items with an average food item $^{87}Sr/^{86}Sr$ ratio would differ in $^{87}Sr/^{86}Sr$ ratio from an eggshell derived from 50% bone calcium by 0.0008 at Hubbard Brook and by 0.0004 at Downer Forest. These calculated shifts represent 40% and 20% of the range of eggshell $^{87}Sr/^{86}Sr$ values at Hubbard Brook and Downer Forest, respectively, and illustrate that the ecosystem variability in the $^{87}Sr/^{86}Sr$ of food items at each study site could surpass the effect of calcium addition by mobilization from bone unless there is a large (i.e., >~50%) proportion of calcium derived from bone. If one were testing for a small contribution of calcium from food items with the majority coming from bone, then the $^{87}Sr/^{86}Sr$ ratio would be extremely sensitive to small additions of calcium. However, in this case where the majority of calcium comes from food items, the $^{87}Sr/^{86}Sr$ ratio is insensitive to small additions of calcium. Thus we cannot unequivocally rule out the possibility of small bone calcium additions from $^{87}Sr/^{86}Sr$ ratios alone. However, as discussed above, arguments based on the relative amounts of calcium in an adult skeleton versus a clutch of eggs make this possibility very unlikely.

Implications and potential applications

This study of stable strontium isotopes in a bird species is the first of its kind; it sheds light on several important ecological processes and demonstrates the potential of strontium isotopes in studies of animal ecology. In two small forested plots we have determined the variation in the $^{87}Sr/^{86}Sr$ ratio of food sources, eggshells, and egg contents. We have demonstrated that the $^{87}Sr/^{86}Sr$ ratios of adult females collected in mid to late June generally reflect the $^{87}Sr/^{86}Sr$ ratios of their summer food sources, although the skeletons of some females contain up to 60% strontium from winter food sources. Thus, the $^{87}Sr/^{86}Sr$ signal in adult skeletons may be utilized in conjunction with deuterium and carbon isotope measurements in the manner suggested by Chamberlain et al. (1997) to ascertain the general location of summer habitats for birds arriving in winter grounds after migration, but with the caveat that skeletal values may be shifted toward lower $^{87}Sr/^{86}Sr$ ratios due to inputs from winter habitats during the previous winter. The turnover time of skeletal strontium in migratory passerines is not well known and requires further study. Thus we recommend that for migratory studies, bird bones be sampled immediately after arrival at a new habitat if information is sought on the $^{87}Sr/^{86}Sr$ ratio of the habitat from which they migrated. We have verified that feathers contain sufficient strontium for isotopic analysis (J.D. Blum, unpublished data) but further study will be necessary to determine if they are useful for migratory studies. Our finding that small-scale variations in the $^{87}Sr/^{86}Sr$ of food sources in forests are preserved in eggs (and egg contents) suggests that stable strontium isotopes may prove to be useful in dispersion studies of animals, particularly in areas where distinct geological contacts create boundaries in the $^{87}Sr/^{86}Sr$ of plants and their consumers.

We found using $^{87}Sr/^{86}Sr$ ratios that very little strontium is contributed from adult skeletons to their eggs, but due to the higher Ca/Sr ratio of bones compared to food items we found that $^{87}Sr/^{86}Sr$ ratios are not sensitive to small additions of calcium from bones to eggs. Thus we are unable to use this method alone to test whether long-distance migrant birds remobilize significant quantities of calcium from their bones. However, we concur with the results of Ankney and Scott (1980), Krementz and Ankney (1995), and Graveland and Van Gijzen (1994) that bird skeletons do not contain enough calcium to be important sources of calcium for egg-laying. We further suggest that reductions in available calcium in the northeastern USA due to the influences of acid deposition (Likens et al. 1998) could be potentially harmful to breeding birds, as suggested by Drent and Woldendorp (1989) for the Netherlands, because they are dependent on sources of calcium in their breeding habitats to meet the calcium demands of egg-laying.

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