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Tracking habitat use of a long-distance migratory bird, the American redstart *Setophaga ruticilla*, using stable-carbon isotopes in cellular blood

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The successful use of stable isotopes to track migratory animals between different seasons of the annual cycle depends, in part, on the turnover rate of isotopes in sample tissue. We examined whether stable-carbon isotopes in the blood of a long-distance migratory bird, the American redstart *Setophaga ruticilla*, sampled upon arrival to the temperate breeding grounds could be used to track the quality of habitat used the previous season on the tropical wintering grounds. Stable-carbon isotopes in red-blood cells sampled upon arrival ($\delta^{13}C_{RBC}$) were significantly less negative relative to: 1) plasma sampled upon arrival from the same individuals, 2) red-blood cells of redstarts recaptured more than a month later on the breeding grounds, and 3) nestling feathers grown at the same breeding location. $\delta^{13}C_{RBC}$ was also significantly different between sexes, consistent with findings from the wintering grounds where sex-biased habitat use is known to occur. Although individuals likely integrate some isotopic signatures during migration, we provide evidence that cellular blood can be used to track the relative habitat use of migratory birds during the wintering period. Non-destructive methods of sampling stable-isotopes, such as this, are particularly useful because it provides a technique for tracking the patterns of habitat use and/or geographic location of migratory animals. Such approaches allow researchers to understand how events throughout the annual cycle interact to influence population dynamics.

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Stable-isotopes can be a useful tool to track the movements and habitat use of migratory animals throughout the annual cycle. The natural variation of stable isotopes expressed in primary production is driven, in part, by differences in climate (e.g. H, O, N), photosynthetic pathways (e.g. C), and marine vs. terrestrial inputs (e.g. N; Lajtha and Michener 1994, Kelly 2000). Given a known fractionation rate between diet and tissue, isotopic signatures of higher-order consumers, such as birds, can accurately reflect the habitat use and/or geographic location of an individual (Hobson and Clark 1992a). This principle has proven extremely valuable for tracking migratory organisms (Hobson 1999, Webster et al. 2002). Depending on the turnover rate of isotopes in tissues, an individual sampled during one period of the annual cycle can carry an isotopic fingerprint from its previous location thousands of kilometers away.

Tissues, such as feathers, which are metabolically inert after growth, provide an isotopic signal of where they were grown (Hobson and Clark 1992b).

Sampling feathers has been an effective method for tracking some migratory birds (Chamberlain et al. 2000, Kelly et al. 2002, Rubenstein et al. 2002), but many species molt only once a year (Pyle 1997), limiting the amount of potential information that can be gained to a specific period of the annual cycle. Although some metabolically active tissues that have slow turnover rates, such as bone or muscle (Hobson and Clark 1992b, Chamberlain et al. 1997, Marra et al. 1998, Hobson and Wassenaar 1997), can provide long-term information, they often require that the individual be destroyed, thus preventing researchers from collecting subsequent ecological and life-history data.

In this paper, we examine the utility of using stable-carbon isotopes in cellular blood to track the habitat use of a long-distance migratory bird, the American redstart *Setophaga ruticilla*. Redstarts are 8 g Neotropical-Nearctic migrants that winter in the Caribbean, Central America, and northern South America and breed in deciduous and mixed forest throughout North America (Sherry and Holmes 1997). High and low quality winter habitats yield distinct $\delta^{13}C$ values (Marra et al. 1998), reflected through differences in photosynthetic pathways and plant-water use efficiency (O'Leary 1981, Farquhar et al. 1989). Individuals incorporate these values in their system through consumption of insects found in these habitats. By sampling $\delta^{13}C$ in muscle of individuals arriving on the breeding grounds, Marra et al. (1998) found that earlier arriving individuals were more likely to originate from higher quality winter habitat (i.e. have more negative $\delta^{13}C$ values). Sampling muscle, however, required whole specimens and did not allow for subsequent measurement of reproductive success. Alternatively, non-destructive methods have the potential to provide further ecological and life history data of individuals after they are sampled.

One such method involves sampling blood from migratory birds as they arrive onto breeding areas (Morrison and Hobson 2004). A critical assumption of this technique is that individuals must retain an isotopic signature reflective of the wintering grounds. Diet-switching experiments on crows, quails and doves have shown that the half-life of stable-isotopes in red-blood cells was approximately one month, significantly longer than the half-life of plasma (2–3 days; Hobson and Clark 1993). More recently, experiments have shown that the turnover rates in whole blood (red-blood cells and plasma combined) of small passerines with higher metabolic rates may be as little as one week (Pearson et al. 2003, Hobson and Bairlein 2003).

Our goal was to determine if $\delta^{13}C$ in red-blood cells of redstarts sampled upon arrival to the breeding grounds ($\delta^{13}C_{RBC}$) contained signatures from the tropical wintering grounds. Because higher turnover rates have been found in plasma compared to red-blood cells in other species (Hobson and Clark 1993), we hypothesized that $\delta^{13}C$ in plasma ($\delta^{13}C_{PL}$) upon arrival would be more depleted (i.e. reflect typical breeding ground values), relative to $\delta^{13}C_{RBC}$ (which should reflect winter habitats). Furthermore, we hypothesized that $\delta^{13}C_{RBC}$ between sexes should be significantly different due to sex-biased habitat use on the wintering grounds (Parrish and Sherry 1994). Male redstarts occupy primarily high quality habitat that is ^{13}C depleted, whereas females occupy primarily low quality habitat enriched with ^{13}C (Marra et al. 1998, Marra 2000). Since sexual habitat segregation does not occur on the breeding grounds (Sherry and Holmes 1997), we predicted no effect of sex on $\delta^{13}C_{PL}$.

Based on stable-hydrogen isotope analysis and band recovery data, evidence suggests that individuals breeding in northeastern North America over-winter primarily in the Greater Antilles (Holmes and Sherry 1992, Norris et al. In Prep). For wintering ground values, therefore, we analyzed whole blood samples from individuals caught in two typical Caribbean habitats: mangroves ($\delta^{13}C_{MANG}$), and dry scrub forest ($\delta^{13}C_{SCRUB}$). To represent breeding ground $\delta^{13}C$ values, we sampled: 1) red-blood cells of individuals recaptured greater than a month after arrival to breeding grounds ($\delta^{13}C_{RECAP}$), and 2) nestling feathers grown at the same breeding site ($\delta^{13}C_{NTL}$).

Methods

Field data

Prior to the breeding season, we sampled redstarts in two habitats (mangroves and dry forest-scrub) between 15 January and 15 March, 2002 at a 20 ha study plot near Luana Pt., Jamaica (see Marra and Holmes 2001 for details on study site). Individuals were lured into mist nets using a playback and model. We extracted 10–40 μL of blood from the brachial vein, placed it on ice until it was frozen at −20°C (within 4 hours).

Later in the year, during the breeding season (May to July), redstarts were sampled on a 60 ha forest plot at the Queen's University Biological Station, Chaffey's Lock, Ontario, Canada (44°34′N, 76°19′W). We monitored arrival date by conducting daily (06.00–12.00 EST) surveys between 1 May to 15 June. Males sing immediately upon arrival. To record the arrival date of females, we monitored each male daily for 15–20 minutes. In addition to visual identification, changes in male behaviour, such as decreased song rate, song-type switching (MacNally and Lemon 1985), chip notes, and close mate guarding were reliable indicators that a female was present. Once a female was sighted, we confirmed her presence the following day (Norris et al. 2004).

Individuals (n = 67, 52 males, 15 females) were caught within 7 days of arrival in mist nets using conspecific playback and a mounted redstart model. All individuals

were banded with a unique combination of colour leg bands and a U.S. Fish and Wildlife Service band. We extracted 10–40 μL of blood from the brachial vein and placed it on ice until it was centrifuged (within 4 hrs) for 8 min at 14 000 r.p.m. Red blood cells and plasma were immediately separated and then frozen (−20°C). A subset of males (n = 11) were recaptured between 21 June and 16 July and bled using the same methods described above. All recaptured individuals were sampled at least 30 days after their initial capture. As part of a general study on redstart breeding ecology, nests were found and monitored every 2–3 days. Once nestlings were greater than 4 days old, we climbed up to the nest using a ladder and extracted 5–6 body feathers from each individual (n = 9 individuals from 9 different nests).

Isotope analysis

Frozen blood samples were freeze-dried (24 hrs) and powdered (Hobson et al. 1997). Feather samples were cleaned by soaking them a 2:1 chloroform:methanol solution for 24 hours and left to air-dry for an additional 72 hours. For both tissue types, a small (0.150–0.400 μg) amount was loaded into a tin capsule and combusted in a NCS 2500 Elemental Analyzer, then introduced on-line to a Finnigan MAT 252 Isotope Ratio Mass Spectrometer. One in-house standard was run for every five unknowns. Repeated measures of individuals (n = 40) indicated samples were replicable to within 0.2‰. Stable-carbon isotope ratios ($^{13}C/^{12}C = R$) are expressed in δ units where $\delta = [(R_{sample}/R_{standard}) - 1] \times 1000$. $R_{standard}$ is the international standard Pee Dee belemnite.

Statistical analysis

We used paired t-tests to compare $\delta^{13}C_{PL}$ and $\delta^{13}C_{RECAP}$ with $\delta^{13}C_{RBC}$. To examine if there were differences between summer and winter values, we used a one-way ANOVA and examined differences between means using Tukey's post-hoc multiple comparison test. Because some birds that were sampled for $\delta^{13}C_{RBC}$ were also sampled for $\delta^{13}C_{PL}$ (n = 17) and $\delta^{13}C_{RECAP}$ (n = 11), including these individuals in the $\delta^{13}C_{RBC}$ sample would violate the assumption of independence in the ANOVA (Zar 1996). Therefore, we removed these individuals from the $\delta^{13}C_{RBC}$ sample. Regardless of whether those individuals were removed or not, results of the ANOVA were the same. We present the results from the independent sample. Means are presented ± SE and $\alpha = 0.05$ for all statistical tests.

Results

Overall, winter $\delta^{13}C$ values were significantly different from breeding samples (ANOVA, $F_{5,98} = 35.23$, $P < 0.001$; Fig. 1). Tukey's post-hoc test revealed no significant differences between breeding ground values ($\delta^{13}C_{PL}$, $\delta^{13}C_{RECAP}$, $\delta^{13}C_{NEST}$; all $P > 0.05$; Fig. 1). However, these values were all significantly different from wintering ground signatures and $\delta^{13}C_{RBC}$ ($P < 0.05$). $\delta^{13}C_{RBC}$ was similar to $\delta^{13}C_{MANG}$ but not $\delta^{13}C_{SCRUB}$.

As predicted, $\delta^{13}C_{PL}$ (-24.93 ± 0.22) was more depleted than $\delta^{13}C_{RBC}$ (-23.14 ± 0.15; paired t-test: $t = -8.07$, $n = 17$, $P < 0.0001$). Results were the same when sexes were analyzed separately (Fig. 2; males: mean $\delta^{13}C_{RBC}$: -23.43 ± 0.13, mean $\delta^{13}C_{PL}$: -24.97 ± 0.32, $t = -4.75$, $n = 9$, $P < 0.005$; females: mean $\delta^{13}C_{RBC}$: -22.80 ± 0.23, mean $\delta^{13}C_{PL}$: -24.92 ± 0.31, $t = -4.75$, $n = 8$, $P < 0.005$). We found no relationship between $\delta^{13}C_{RBC}$ or $\delta^{13}C_{PL}$ with the number of days between arrival and capture ($\delta^{13}C_{RBC}$: $r^2 = 0.01$, $F_{1,64} = 0.65$, $P = 0.42$; $\delta^{13}C_{PL}$: $r^2 = 0.01$, $F_{1,15} = 0.17$, $P = 0.70$).

If $\delta^{13}C_{RBC}$ contained a signature from the wintering grounds, we predicted that red-blood cell values would be significantly different due to sex-biased habitat use in the tropics. In addition, if $\delta^{13}C_{PL}$ represented breeding ground values, plasma should be similar between sexes. Consistent with both predictions, $\delta^{13}C_{RBC}$ was significantly more depleted in males than females ($t = 2.50$, $df = 15$, $P = 0.02$) but $\delta^{13}C_{PL}$ was similar between sexes ($t = 0.06$, $df = 15$, $P = 0.949$; Fig. 2). We suspected that a single outlier in females could have driven the difference in $\delta^{13}C_{RBC}$ between sexes (Fig. 2). However, when

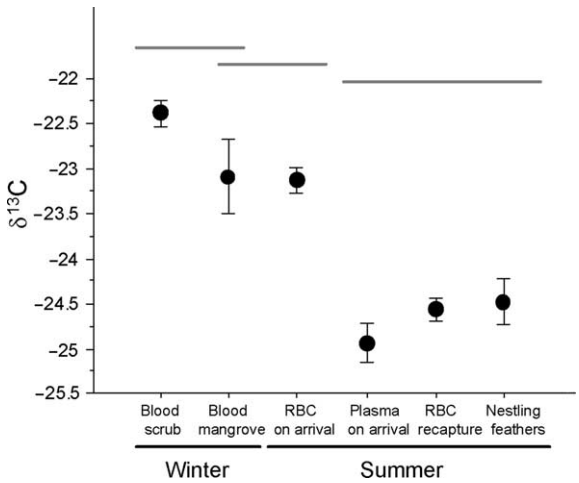

Fig. 1. Mean $\delta^{13}C$ values (±1 SE) of American redstarts sampled from the breeding and wintering grounds. Detailed descriptions of each of the samples are given in methods. Overall, differences between values were significant (ANOVA, $P < 0.001$). Grey lines above plots show samples that are not significantly different (Tukey's post-hoc test, $P > 0.05$). Numbers at the top of the graph indicate sample sizes.

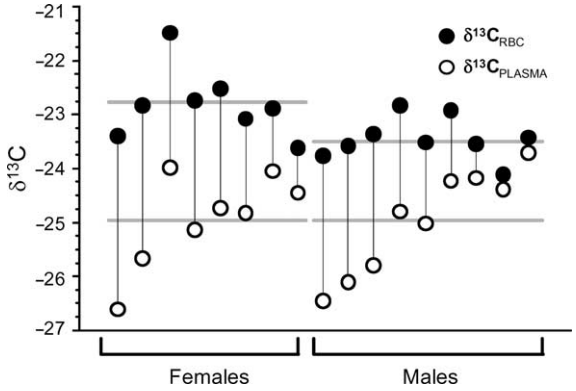

Fig. 2. Differences between $\delta^{13}C$ values sampled from red-blood cells ($\delta^{13}C_{RBC}$) and plasma ($\delta^{13}C_{PL}$) of female (n = 8) and male (n = 9) American redstarts upon arrival to the breeding grounds. In all cases, $\delta^{13}C_{PL}$ was more negative than $\delta^{13}C_{RBC}$, indicating that plasma turned over quickly after arrival to the breeding grounds. The order of individuals presented is not related to time of capture. Grey lines denote means of values $\delta^{13}C_{RBC}$ and $\delta^{13}C_{PL}$ for each sex. $\delta^{13}C_{RBC}$ was significantly different between sexes ($P < 0.001$).

we removed the outlier, results remained significant ($t = 2.28$, $df = 14$, $P = 0.04$). The difference in $\delta^{13}C_{RBC}$ between sexes was also evident among the larger sample of all individuals caught in 2002 (male mean: -23.20 ± 0.07; female mean: -22.88 ± 0.13; $t = 2.14$, $df = 64$, $P = 0.04$).

Individuals recaptured later in the breeding season had significantly more depleted $\delta^{13}C$ values (mean $\delta^{13}C_{RECAP}$: -24.56 ± 0.11) compared to arrival (mean $\delta^{13}C_{RBC}$: -23.12 ± 0.12; paired t-test: $t = -8.38$, $df = 10$, $P < 0.001$). We predicted that magnitude of the difference between $\delta^{13}C_{RBC}$ and $\delta^{13}C_{RECAP}$ would increase as the amount of time between initial capture and recapture increased. However, we found no significant relationship between the two variables ($r^2 = 0.18$, $F_{1,9} = 1.98$, $P = 0.19$).

Discussion

Our results provide evidence that $\delta^{13}C$ in red-blood cells ($\delta^{13}C_{RBC}$) of American redstarts represents an isotopic signal that was acquired before arrival to the breeding grounds. $\delta^{13}C_{RBC}$ was significantly less depleted compared to all $\delta^{13}C$ values representative of the breeding grounds (Fig. 1). These included stable-carbon isotopes in red-blood cells of known birds recaptured later in the breeding season ($\delta^{13}C_{RECAP}$), and nestling feathers grown at the same breeding site ($\delta^{13}C_{NTL}$). $\delta^{13}C_{RBC}$ was also less depleted than $\delta^{13}C$ in plasma ($\delta^{13}C_{PL}$) from the same individuals captured upon arrival (Fig. 2). This finding supports previous results from an experimental study on American crows, which found that the $\delta^{13}C$ half-life in plasma was significantly shorter than in cellular blood (Hobson and Clark 1993), as well as a diet-switching experiment on a similar sized passerine as the redstart, the yellow-rumped warbler *Dendroica coronata*, that found that the half-life of $\delta^{13}C$ in plasma was 0.4 to 0.7 d (Pearson et al. 2003). In our study, individuals were captured within 7 days of arrival, suggesting that a week or less is enough time to integrate local foodweb signatures into the plasma component of blood.

Results reported here may be partially attributed to different fractionation rates between diet and sample tissue. For example, $\delta^{13}C$ in feathers have been shown to be anywhere from 0.2 to 2‰ heavier than whole blood from the same organism (Hobson and Clark 1992a, Bearhop et al. 2002, Pearson et al. 2003). We did find $\delta^{13}C$ values in nestling feathers to be slightly, but non-significantly, heavier than the $\delta^{13}C$ values in other tissues ($\delta^{13}C_{RECAP}$: red blood cells, $\delta^{13}C_{PL}$: plasma; Fig. 1) we have proposed to be representative of the breeding grounds. Our intention with using nestling feathers was to provide an approximate benchmark of breeding ground values. The appropriate comparison is between $\delta^{13}C$ values from the same tissue and we found significant differences in red-blood cells within the same individual ($\delta^{13}C_{RBC}$ and $\delta^{13}C_{RECAP}$).

Changes in $\delta^{13}C_{RBC}$ from early to late in the breeding season could also be due to shifts in the carbon isotope signatures of plants and/or insects in the local foodweb. This would account for the difference observed between $\delta^{13\,C}_{RBC}$ (sampled early in the season) and $\delta^{13\,C}_{RECAP}$ and $\delta^{13\,C}_{NTL}$ (sampled in the latter half of the season). However, we found that $\delta^{13}C_{PL}$ (also sampled early in the season) was significantly more depleted than $\delta^{13}C_{RBC}$ but similar to δ^{13}_{RECAP}, supporting the notion of minimal temporal change in basal $\delta^{13}C$ values of local foodwebs during the breeding period.

Higher metabolic rates in smaller organisms may increase elemental turnover rate in tissues (Theizen et al. 1983, Bearhop et al. 2002). For example, dunlin *Calidris alpina pacifica* (55 g body weight) have faster turnover rates in blood (Evans-Ogden et al. 2004) compared to canvasbacks *Aythya valisineria* (1200 g; Haramis et al. 2001) and great skuas *Catharacta skua* (1220 g; Bearhop et al. 2002). The only experimental study to examine the turnover rate in the cellular portion of blood found a half-life of 30 d in American crows (Hobson and Clark 1993). Among small-bodied passerines, Pearson et al. (2003) sampled whole blood in yellow-rumped warblers and found a $\delta^{13}C$ half-life between 3.9 to 6.1 d (one treatment group was 33 d). They acknowledged that $\delta^{13}C$ may not have equilibrated on the last day before diet-switching, suggesting that the time for complete turnover was longer than the acclimation period of 21 d. This latter finding would be in agreement with our results, which suggest that $\delta^{13}C$ in red-blood cells take longer than a week for complete

elemental turnover. In correspondence with their final estimate of 3.9 to 6.1 d, however, Hobson and Bairlein (2003) found a half-life of 5 to 5.7 d in whole blood for another small-bodied passerine, the garden warbler *Sylvia borin*.

Experimental studies are needed to determine if higher metabolic rates not only increase the turnover rates in plasma and whole blood but cellular fractions as well. Slower turnover rates observed in redstarts may be due to birds fasting for extended periods during migration, reducing the rate of elemental turnover in cellular blood. As Hobson and Bairlein (2003) suggested, long-distance migrants do not have access to ad libitum food and likely use a significant portion of lipid and protein reserves during the migration period. During spring migration, Morris and Glasgow (2001) found that most redstarts spent less than a day and did not gain significant mass at a stopover site in Maine. In addition, a recent study on migratory shorebirds found evidence that isotopic signatures in the red-blood cells of individuals arriving on their high arctic breeding grounds were indicative of wintering ground foodwebs (Morrison and Hobson 2004), supporting the contention that migratory birds may have slower turnover rates compared to captive birds.

We believe that redstarts likely take less than a month to migrate from the wintering grounds to the breeding grounds. Using banding recoveries from passerines on migration, Fransson (1995) found that the average spring migration speed of four passerines breeding in two regions (Great Britain and Scandinavia) was 150 kilometers per day (including stopover time). Using this value and assuming an average distance of 3000 km (Jamaica to southern Ontario), we calculated redstarts would take approximately 20 days to migrate from the wintering grounds to our study site. This is a conservative estimate given that anywhere from 10–40% of migration may be over water where individuals must fly non-stop. Consistent with estimates of migration speed from band recoveries of European passerines (Fransson 1995), evidence also indicates that redstarts migrate faster during spring than fall. During migration in Maine, the frequency of recaptured individuals was significantly higher during fall migration (Morris and Glasgow 2001). In the spring, only 3% percent of all birds initially banded were recaptured, suggesting that most individuals did not spend multiple days at the site.

Differences in observed between sexes also supports our contention that $\delta^{13}C$ in red-blood cells contain a wintering ground signature. Wintering populations of redstarts show strong sexual habitat segregation (Parrish and Sherry 1994), where males occupy primarily high quality habitat with depleted ^{13}C compared to females, who primarily occupy low quality habitat that is enriched with ^{13}C (Marra et al. 1998, Marra 2000). We found that males arriving on the breeding grounds had significantly more negative $\delta^{13}C$ values compared to females, implying that winter signatures were present in cellular blood upon arrival to the breeding grounds.

Redstarts may be incorporating isotopic signatures solely from the migration period rather than from the wintering grounds. Considering our finding that $\delta^{13}C_{RBC}$ differed between sexes, redstarts would have to meet one of two criteria to support this hypothesis: 1) females and males exhibit sexual habitat segregation at migratory stopover sites. Although this phenomenon is known to occur on the wintering grounds (Marra 2000), sexual habitat segregation has not been observed during migration (Woodrey and Chandler 1997, Morris and Glasgow 2001). 2) males and females consume different prey items during migration, leading to differences in $\delta^{13}C$ values. We believe this is unlikely considering the similarities in foraging habits between sexes on both the wintering and breeding grounds (Holmes 1986, Sherry and Holmes 1997). Given lack of experimental studies (e.g. removal experiments to test habitat segregation) and foraging data at stopover sites, we cannot rule out these possibilities completely. In general, however, redstarts migrating between our study site in Ontario and the tropics will primarily travel through mixed hardwood forests of eastern North America. $\delta^{13}C$ values from plants across this eco-region, which include our study site, are generally more negative than those observed on the wintering grounds (Lowdon and Dyck 1974, Kelly 2000). Therefore, if redstarts incorporate $\delta^{13}C$ signatures primarily from migratory stopover sites, we would expect $\delta^{13}C_{RBC}$ to be similar to values recorded at our study site ($\approx -25‰$) rather than the tropical wintering grounds ($\approx -23‰$).

An alternative explanation is that $\delta^{13}C_{RBC}$ shows some isotopic mixing between the over-wintering and migration periods. Our data support this hypothesis: when $\delta^{13}C$ values from both winter habitats are combined, they are significantly more positive than $\delta^{13}C_{RBC}$ ($\delta^{13}C_{WINTER}$ mean: -22.30 ± 0.09; $\delta^{13}C_{RBC}$ mean: -23.13 ± 0.10; $t = -6.085$, $df = 138$, $P < 0.001$). This suggests that $\delta^{13}C$ values become more negative as individuals migrate through the eastern USA. The integration of $\delta^{13}C$ from migratory stopover sites, however, does not affect the potential to use $\delta^{13}C_{RBC}$ as an indicator of winter habitat quality if one is primarily concerned with the relative differences in winter signatures of individuals arriving on the breeding grounds (e.g. comparing early arriving versus later arriving individuals). The key assumption here is that most individuals spend a similar amount of time on the migration route. In our case, however, even if this assumption is invalid, we would expect that individuals arriving later on the breeding grounds (i.e. lower quality) would take longer to migrate from the tropical wintering

grounds. These individuals would incorporate more negative $\delta^{13}C$ signatures relative to their original winter habitat, making observed differences between early and late arriving individuals on the breeding grounds (Norris et al. 2004) more conservative.

In conjunction with elemental turnover rates, we emphasize two additional points that should be considered when using cellular blood (or other tissues) as an isotopic marker of winter habitat. First, individuals must be sampled within a few days of arrival to properly obtain isotopic signatures indicative of the previous season. Study areas should also be monitored daily to accurately record the arrival of new individuals. For redstarts, we found no relationship between the number of days between arrival and capture and $\delta^{13}C$, likely because birds most birds were sampled less than 4 days after arrival (maximum: 7 days). If the sampling window between arrival and capture was extended, we expect that individuals would quickly incorporate signatures representative of the breeding grounds, as seen in red knots *Calidris canutus* and turnstones *Arenaria interpres* in the high arctic (Morrison and Hobson 2004), and colonial waterbirds at Great Slave Lake (Hobson and Wassenaar 1997).

Second, isotopic differences in foodwebs between the wintering and breeding grounds must be large enough to detect wintering signatures in birds upon arrival. In our case, the mean difference between winter habitats in Jamaica and Ontario was approximately 2‰, significantly greater than the measurement error for $\delta^{13}C$ analysis (0.2‰) or the standard error of any of the tissues measured (Fig. 1). Smaller differences between wintering and breeding foodwebs (e.g. 1‰ or less) and/or large variances within winter habitats may not provide an adequate ecological system for detecting isotopic signatures in migratory birds from the previous season.

The use of red-blood cells provides a potentially powerful tool to investigate how events during different seasons of the annual cycle interact to influence individual success (see also Morrison and Hobson 2004). The primary advantage is that individuals can be sampled and followed for the remainder of the season/and or their lives. Other tissues that can be non-invasively sampled may also provide long-term information. For example, Bearhop et al. (2003) recently presented evidence that avian claws could be used as dietary indicators over a period of several months. This tissue may be particularly useful because it is metabolically inert after growth and has a systematic growth rate. Non-invasive isotopic markers will allow researchers to determine the ecological consequences of events that occur in the previous season (Webster et al. 2002), a critical aspect of migratory population dynamics that has been difficult to examine using conventional techniques.

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