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RESEARCH ARTICLE

Improved arrival-date estimates of Arctic-breeding Dunlin (*Calidris alpina arcticola*)

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ABSTRACT

The use of stable isotopes in animal ecology depends on accurate descriptions of isotope dynamics within individuals. The prevailing assumption that laboratory-derived isotopic parameters apply to free-living animals is largely untested. We used stable carbon isotopes ($\delta^{13}C$) in whole blood from migratory Dunlin (*Calidris alpina arcticola*) to estimate an in situ turnover rate and individual diet-switch dates. Our in situ results indicated that turnover rates were higher in free-living birds, in comparison to the results of an experimental study on captive Dunlin and estimates derived from a theoretical allometric model. Diet-switch dates from all 3 methods were then used to estimate arrival dates to the Arctic; arrival dates calculated with the in situ turnover rate were later than those with the other turnover-rate estimates, substantially so in some cases. These later arrival dates matched dates when local snow conditions would have allowed Dunlin to settle, and agreed with anticipated arrival dates of Dunlin tracked with light-level geolocators. Our study presents a novel method for accurately estimating arrival dates for individuals of migratory species in which return dates are difficult to document. This may be particularly appropriate for species in which extrinsic tracking devices cannot easily be employed because of cost, body size, or behavioral constraints, and in habitats that do not allow individuals to be detected easily upon first arrival. Thus, this isotopic method offers an exciting alternative approach to better understand how species may be altering their arrival dates in response to changing climatic conditions.

Keywords: blood, carbon, diet-switch, geolocator, migration, shorebird, stable isotope, turnover

Mejora en los estimados de la fecha de llegada migratoria de *Calidris alpina arcticola*

RESUMEN

El uso de isótopos estables en la ecología animal depende de descripciones precisas de la dinámica de los isótopos en los individuos. El supuesto generalizado de que los parámetros de los isótopos se aplican en los animales de vida libre aún no ha sido evaluado. Usamos isótopos estables de carbono ($\delta^{13}C$) en la sangre del ave migratoria *Calidris alpina arcticola* para estimar la tasa de recambio *in situ* y las fechas de cambio de dieta individual. Nuestros resultados *in situ* indicaron que las tasas de recambio fueron mayores en las aves de vida libre comparadas con un estudio experimental en *C. a. arcticola* en cautiverio y con estimados derivados de un modelo teórico de alometría. Las fechas de cambio de dieta calculadas con base en los tres métodos fueron usadas luego para estimar las tasas de llegada de *C. a. arcticola* al ártico; las fechas de llegada calculadas con la tasa de recambio *in situ* fueron posteriores a las estimadas con otras tasas de recambio, en algunos casos sustancialmente. Estas fechas posteriores de llegada coincidieron con las fechas en que las condiciones de nieve locales habrían permitido que *C. a. arcticola* se instalara, y estuvieron de acuerdo con las fechas anticipadas de llegada de *C. a. arcticola* que se calcularon mediante geolocalizadores. Este estudio presenta un método nuevo para estimar de manera precisa las fechas de llegada de individuos de especies migratorias cuando las fechas de regreso son difíciles de documentar. Esto podría ser particularmente apropiado para especies en las que no se pueden emplear fácilmente dispositivos externos de rastreo debido al costo, tamaño corporal o restricciones de comportamiento, o en hábitats que no permiten que los individuos sean fácilmente detectados luego de su primera llegada. Entonces, este método isotópico ofrece un método alternativo emocionante para entender mejor cómo las especies pueden alterar sus fechas de llegada en respuesta a condiciones climáticas cambiantes.

Palabras clave: aves playeras, cambio de dieta, carbono, geolocalizador, isótopos estables, migración, recambio, sangre

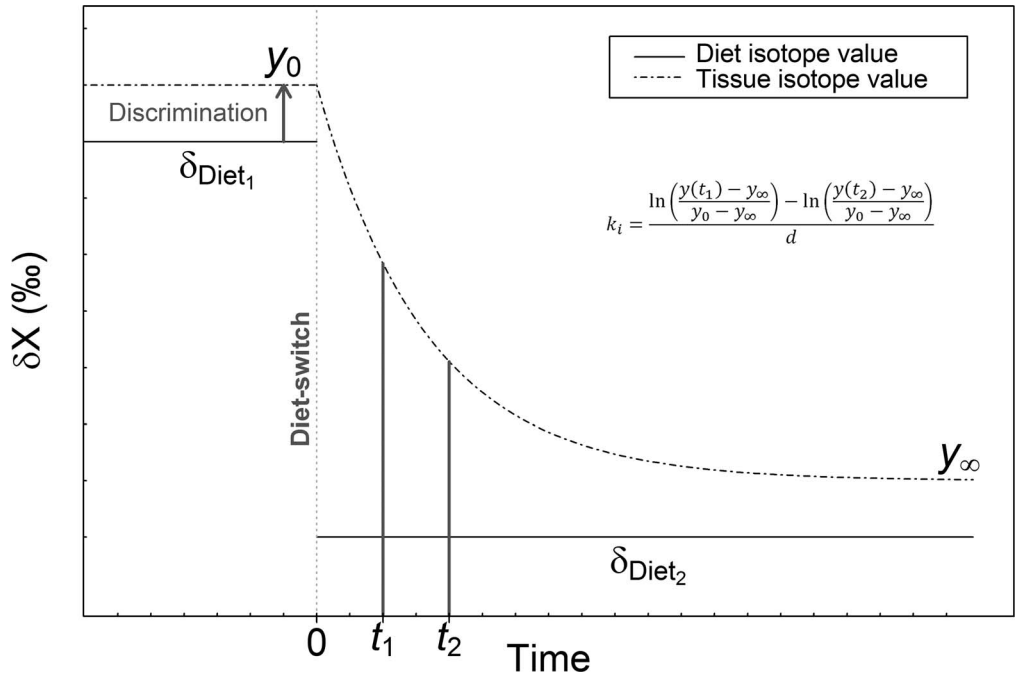

FIGURE 1. Example diagram of the isotopic transition that occurs in metabolically active tissue following an isotopic diet-switch. The rate of isotopic turnover (k_i) in an animal's tissue can be determined by measuring the δX (e.g., $\delta^{13}C$) values at times t_1 and t_2 and the isotopic endpoints (y_0 and y_∞).

INTRODUCTION

The analysis of naturally occurring stable isotopes in animal tissues has allowed ecologists to examine previously intractable aspects of population and community ecology, such as connectivity patterns in migratory species and trophic linkages within food webs (Chamberlain et al. 1997, Newsome et al. 2007). Much work has documented that stable isotope models can also be used to determine when animals switch from one diet to another (hereafter "diet-switch"), which often occurs when animals migrate between different habitats (Phillips and Eldridge 2006, Oppel and Powell 2010). These isotope techniques complement existing extrinsic-marking methods (GPS-equipped transmitters, light-level geolocators; Gauthreaux 1996) by providing arrival estimates for individuals that have not been captured previously, while circumventing constraints related to transmitter size requirements, behavior modification, and reduced inferential scope (Morales et al. 2010, Robinson et al. 2010, Bridge et al. 2011). However, isotope models require accurate species- and tissue-specific parameters to adequately infer movement patterns.

When animals switch between isotopically distinct diets, their metabolically active tissues transition to reflect the isotope values of the new diet (Figure 1). Tieszen et al. (1983) described this transition in a one-compartment, first-order kinetic model: $y(t) = y_\infty + (y_0 - y_\infty)e^{-kt}$. In this model, $y(t)$ is the isotope value of a tissue (e.g., blood) t days after a diet-switch; y_0 and y_∞ are isotope values of the tissue at isotopic equilibrium with the old and new diets, respectively. Isotopic equilibrium occurs when an animal has fed on an isotopically consistent diet long enough for the tissue to have completely regenerated. At equilibrium, the difference between tissue isotope values and dietary values is referred to as "isotopic discrimination" (Hobson and Clark 1992b); k represents the isotope turnover rate (day^{-1}), describing how quickly a tissue transitions to the new isotope value.

Isotope turnover rates are often determined in captive diet-switch experiments after an abrupt change in the isotopic composition of an animal's diet (Evans Ogden et al. 2004, Bauchinger and McWilliams 2009). The tissues sampled for isotopic analysis are usually highly proteinaceous. Because protein turnover rates scale predictably with body size (Houlihan et al. 1995), Carleton and Martínez del Rio (2005) proposed a simple allometric model for estimating isotope turnover rates of animal tissue. Oppel and Powell (2010) applied this allometric model with the isotopic transition model to estimate the timing of a diet-switch that occurs during the spring migration of King Eiders (*Somateria spectabilis*) between the marine wintering environment and terrestrial breeding grounds. Correlation between these estimates and arrival dates of individuals equipped with satellite transmitters support the use of these models. Although experimental

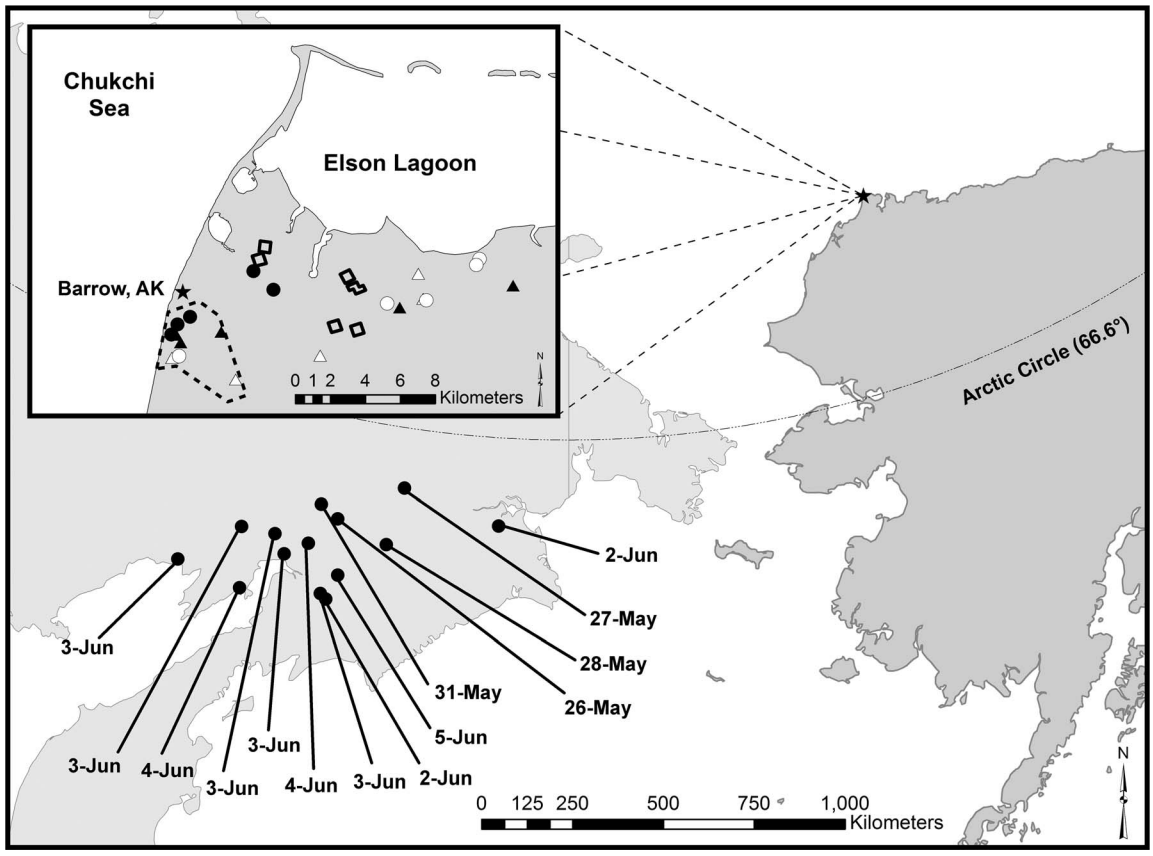

FIGURE 2. Map of Beringia, displaying the last known location and date when birds marked with light-level geolocators crossed northward into the Arctic. Inset: Study area around Barrow, Alaska, USA, and Dunlin sampling locations: solid-line polygons indicate the 6 long-term study plots; dashed-line polygon indicates the Fresh Water Lake study area; circles and triangles represent locations where Dunlin were collected in 2010 and 2011, respectively (black = prebreeding, white = postbreeding).

data and allometric models provide useful approximations of isotopic parameters, we know of no studies that have investigated whether turnover parameters adequately reflect isotopic transitions in wild populations. Therefore, we designed the present study to examine isotopic turnover in a wild population of migratory Dunlin (*Calidris alpina arcticola*; Figure 2).

Calidris alpina arcticola (hereafter "Dunlin") breeds in the tundra environment of northern Alaska, USA, and winters in coastal and estuarine areas in Southeast Asia (Warnock and Gill 1996, Lanctot et al. 2009). In the wintering areas and on coastal migration routes, individuals feed on marine organisms in intertidal areas along the East Asian–Australasian Flyway. By contrast, Dunlin breeding areas are inland, where birds consume terrestrial organisms on or near their nest sites (Holmes 1966b). Although marine foods may be available on the coastlines near the breeding grounds, we have no evidence of Dunlin feeding in these locations during the courting, egg-laying, or incubation stages. Marine-based stable carbon isotope values ($\delta^{13}C$) are ~7‰ greater than corresponding C_3 terrestrial-plant-based values (Peterson and Fry 1987) that are common to the tundra ecosystem. Therefore, we reasoned that upon arrival to the breeding grounds, Dunlin tissues will transition from relatively high marine isotope values to lower terrestrial values. Evans Ogden et al. (2004) exposed captive Dunlin to a similar diet-switch and quantified the rate of carbon turnover in whole blood. Considering the differences in environmental conditions (weather, resource availability) and behavioral stresses (molt, migration, reproduction) between the captive and natural settings, we predicted that wild Dunlin would exhibit a higher turnover rate.

Here, we describe a simple recapture approach to estimating the carbon turnover rate of whole blood in wild-caught Dunlin under natural breeding conditions. We estimated diet-switch dates using this in situ turnover rate and compared them to dates determined from using $\delta^{13}C$-based turnover rates derived from Evans Ogden et al.'s (2004) experimental trials and theoretical allometric models. Finally, assuming that diet-switch dates equate to arrival dates, we evaluated the accuracy of these 3 techniques by comparing the estimated arrival dates to local environmental conditions as well as to assumed

TABLE 1. Sample sizes of collected individuals (muscle) and captured individuals (blood) used to estimate isotope turnover rates and Arctic arrival dates of Dunlin. Numbers in each group that were captured a second time for estimation of turnover rates are in parentheses.

	Muscle samples		Blood samples		
Year	Prebreeding	Postbreeding	Male	Female	Total
2010	5	5	50 (18)	53 (15)	103 (33)
2011	5	5	57 (9)	63 (12)	120 (21)

Dunlin arrival dates based on independently derived light-level geolocation data (Clark et al. 2010). Understanding the appropriateness of experimentally derived turnover rates is important for evaluating previous efforts to track animal movements with stable isotopes and for interpreting laboratory-based isotope studies. The techniques described here demonstrate a simple and broadly applicable method for obtaining accurate arrival data for individuals migrating between isotopically distinct environments, rather than more commonly used first-sighting approaches that may be inaccurate and only provide population-level arrival estimates. This type of individual-level data is helpful for understanding complex demographic processes in migratory populations and for monitoring the ecological consequences of global climate change.

METHODS

Study Site

Blood and muscle samples from adult Dunlin were collected in June and July of 2010 and 2011 around the city of Barrow, Alaska, USA (71°17′44′′N, 156°45′59′′W; Figure 2). The habitat is primarily tundra consisting of grasses and sedges, with prostrate willows and flowering herbs occurring on the drier, elevated areas (MacLean and Pitelka 1971). Nesting Dunlin were sampled on six 600 × 600 m long-term study plots located near roads southeast of Barrow (Naves et al. 2008) and in the area around Fresh Water Lake, located southwest of the city.

Sample Collection

Each year, we obtained muscle tissue from the right pectoralis muscle of 10 adult Dunlin lethally collected with an air-powered pellet gun. Five ''prebreeding'' individuals were collected shortly after arrival to the breeding grounds (June 1–6), and 5 ''postbreeding'' individuals were collected at the end of the breeding season (July 20–24). We collected blood from 7 of the 10 birds in each group, using a nonheparinized capillary tube. We were unable to obtain sufficient quantities of blood for analysis from the remaining 6. Collected specimens were stored frozen prior to preparation and analysis and were subsequently deposited at the Denver Museum of Nature & Science, Denver, Colorado, USA.

We also captured live adult Dunlin at nests using bow nets (Bub 1995). Nests were located by systematically searching the study plots and nearby areas (Naves et al. 2008). We captured 103 and 120 adult Dunlin in 2010 and 2011, respectively (Table 1). Thirty-three and 21 of these individuals in 2010 and 2011, respectively, were captured a second time on their nests (1 individual was recaptured on a second clutch). Time between capture events ranged from 9 to 26 days. Adults were uniquely banded with U.S. Geological Survey (USGS) metal bands, color bands, and alpha-engraved flags. In 2010, we equipped 51 adults with light-level geolocators affixed to leg bands (Clark et al. 2010); 14 were subsequently retrieved in 2011. Whole blood samples (140–210 μL) were obtained from all captured adults by poking the brachial vein of the wing with a 27-gauge needle and collecting blood with a nonheparinized capillary tube; blood was then blown onto clean glass microscope slides, spread evenly, and allowed to air dry. The sample was later scraped into Eppendorf tubes, sealed, and stored at room temperature (S. D. Newsome personal communication). Adults were sexed using discriminant function equations derived for this subspecies or with conventional molecular techniques (Griffiths et al. 1998, Gates et al. 2013). Following each field season, we transported all samples to the University of Colorado Denver for storage and tissue preparation. Subsequent sample preparation and stable isotope analysis was conducted in the laboratories of USGS in Denver.

Isotopic Analysis

Muscle tissues were lyophilized and homogenized, followed by lipid extraction, prior to analysis of 1-mg aliquots (±0.05 mg) in tin capsules. Lipid extraction was performed in a Soxhlet apparatus with a heated azeotropic solvent solution of 2 parts chloroform to 1 part methanol (Stegall et al. 2008). Dried whole blood samples were used in their field-stored form and weighed in 1-mg aliquots (±0.05 mg) into tin capsules. To maintain a direct comparison with the results of Evans Ogden et al. (2004), lipids were not extracted from blood samples. Prepared samples were analyzed using a Carlo Erba elemental analyzer (CE Elantech, Lakewood, New Jersey, USA) interfaced to a Micromass Optima mass spectrometer (GV Instruments, Manchester, United Kingdom; Fry et al. 1992). Isotopic results are reported in per mil (‰) using standard δ notation (Sulzman 2007).

Isotopic data were normalized to V-PDB and to air using the primary standards USGS 40 (–26.24‰ and –4.52‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively) and USGS 41 (37.76‰ and 47.57‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively). Analytical error was assessed by replicate measures of primary standards (<0.2‰ for both isotopes across all analytical sequences),

and quality control was assessed using secondary standards analyzed within individual analytical sequences (<0.2‰). Accuracy was assessed using primary standards as unknowns and was within 0.2‰ for both isotopes. Sample reproducibility, determined via duplicate measurements, was generally better than 0.2‰.

Isotope Dynamics Modeling

Diet-switch endpoints. Muscle tissue generally has a slower turnover rate than blood components (Hobson and Clark 1992a, Bauchinger and McWilliams 2009). Thus, we assumed that muscle tissue from prebreeding birds would have turned over less since arrival than blood tissue and would therefore provide a better estimate of the marine isotope values characteristic of the diet during winter and during spring migration. We further assumed that muscle tissue of the postbreeding birds would have reached isotopic equilibrium with the terrestrial diet by the time of collection (~7 wk). For each year, we used the $\delta^{13}C$ mean and standard deviation of the muscle tissues sampled during the prebreeding and postbreeding periods to generate distributions of potential diet-switch endpoints (y_0 and y_∞, respectively) in whole blood. Evans Ogden et al. (2004) reported a difference in isotope discrimination from diet to muscle (1.9‰) and from diet to whole blood (1.3‰). Thus, prior to simulation, we subtracted 0.6 from each muscle $\delta^{13}C$ value to better represent "blood-like" isotope values (2010: $y_0 \sim N(-18.4, 1.4)$, $y_\infty \sim N(-26.4, 0.8)$; 2011: $y_0 \sim N(-19.5, 0.9)$; $y_\infty \sim N(-27.1, 1.2)$).

Isotopic turnover rates. To derive an experimental turnover rate (k_e) of $\delta^{13}C$ in Dunlin blood, we first bootstrapped the half-life of ^{13}C (11.2 ± 0.8 [SE] days) reported in Evans Ogden et al. (2004) and then converted these values into turnover rates, using the equation $k = \ln(2)/(\text{half-life})$. We determined the allometric turnover rate (k_a) using the mass of each captured individual (m_b) and the allometric model from Carleton and Martínez del Rio (2005): $\log_{10}(k_a) = -0.52$ to $0.35^{*}\log_{10}(m_b)$. Because we sampled only fully grown adults, we treated whole-blood turnover rates as proportions (ranging from 0 to 1) and, therefore, calculated mean turnover rates and 95% confidence intervals (CIs) using a beta distribution.

We estimated the in situ turnover rate (k_i) using blood $\delta^{13}C$ from 54 individuals sampled twice during the nest incubation period. The isotope values measured at each capture can be described by the equations

$$y(t_1) = y_\infty + (y_0 - y_\infty)e^{-k_i t_1} \quad (1)$$

$$y(t_2) = y_\infty + (y_0 - y_\infty)e^{-k_i t_2} \quad (2)$$

where t_1 and t_2 indicate the number of days since diet-switch to the first and second capture, respectively. Knowing that the number of days between capture events (d) is equal to the difference between t_2 and t_1, we combined Equations 1 and 2 and solved for the turnover rate (k_i; day^{-1}) as

$$k_i = \frac{\ln\left(\frac{y(t_1)-y_\infty}{y_0-y_\infty}\right) - \ln\left(\frac{y(t_2)-y_\infty}{y_0-y_\infty}\right)}{d} \quad (3)$$

For each individual, we randomly selected 5,000 bootstrapped endpoints constrained such that all y_0 values were higher than $y(t_1)$ and all y_∞ values were lower than $y(t_2)$. We fit these estimates of k_i to a beta distribution to determine a mean value for each bird. We then calculated a mean population turnover rate (k_i) by fitting these individual means to the beta distribution.

Diet-switch dates. For all captured individuals, we independently calculated individual diet-switch date estimates (T) using k_e, k_a, and k_i, respectively, by rearranging the decay function to

$$t = \frac{\ln\left(\frac{y_0-y_\infty}{y(t)-y_\infty}\right)}{k} \quad (4)$$

Subtracting t from the date of capture gave us the respective experimental (T_e), allometric (T_a), and in situ (T_i) diet-switch date estimates. As with our calculations of k_i, we selected 5,000 endpoint values from our simulated distributions of y_0 and y_∞ within an appropriate range for each individual. Because the resulting distribution of individual diet-switch date estimates were non-normal, we calculated a median diet-switch date estimate for each individual and report variability as median absolute deviation (MAD). For recaptured birds, we used only the isotope value from each individual's first capture because of the reported lack of reliability in diet-switch date estimates as the tissue approaches the asymptotic value (Oppel and Powell 2010).

Light-level Geolocation

Light-intensity data recorded by geolocators were used to generate migration track lines of 14 individuals originally tagged in 2010 and subsequently captured on the breeding grounds in 2011. We used sunrise and sunset times, indicated by the light-intensity data and the BASTrack program (http://www.biotrack.co.uk/software.php) to determine day length and solar midnight, which were then used to infer latitude and longitude, respectively. Because the sun does not set north of the Arctic Circle during the end of the spring migration period, we were unable to track individuals above ~66.6°N latitude. Thus, we used the date and location when birds crossed ~66.6°N moving northward to calculate an earliest possible arrival date in Barrow, assuming a nonstop flight, with an average flight speed of 75 km hr^{-1} (Warnock and Gill 1996). The error associated with geolocator estimates varies with several factors (Fudickar

et al. 2012). Using data from Dunlin at known locations of similar latitude and solar season, we estimated the 90th percentile of errors at ~190 km (S. Yezerinac personal observation), a negligible distance easily traveled by Dunlin in a matter of hours. Although some studies have suggested that geolocators may delay migration arrival times (e.g., Arlt et al. 2013), the devices used in the present study were below 2% of the bird's weight, and birds equipped with geolocators returned at higher rates than those equipped with bands and flags, which suggests that negative effects from geolocators were likely minimal.

Availability of Terrestrial Breeding Areas

Terrestrial breeding areas are suitable for Dunlin when snow recedes and birds gain access to invertebrates on the tundra. To evaluate when breeding areas might be suitable each year, we estimated the percent snow cover on the study plots every other day, using standardized protocols (Arctic Shorebird Demographic Network Protocol Subcommittee 2010), until only 10% of the study plots remained covered in snow. For days without direct observations, percent snow cover was computed by taking the mean of the immediately preceding and following days' values. We excluded data from a plot located at the Barrow landfill because snowmelt occurred earlier as a result of human activities (Saalfeld et al. 2013).

Evaluating Arrival Dates

We first evaluated the diet-switch date estimates (i.e. our proxy for arrival date) by comparing the average percentage of ground covered with snow with the cumulative number of captured birds present on the breeding grounds, using a Pearson's product-moment correlation test. We then compared diet-switch date estimates of the 14 birds equipped with light-level geolocators to the earliest possible arrival date as calculated from their last known location south of the Arctic Circle.

All analyses were conducted in the R statistical computing package, version 2.15.3 (R Development Core Team 2013; R code for these analyses is presented in Supplemental Material Appendix A). We used Welch's two-sample *t*-tests in all comparisons between datasets and estimates. Results are reported as means ± SD.

RESULTS

Muscle Isotope Values

The isotopic differences in the muscle tissue between the prebreeding and postbreeding periods showed a clear decrease in $\delta^{13}C$ (Figure 3). Lipid-extracted muscle samples from the prebreeding birds had mean $\delta^{13}C$ of –17.8 ± 1.4‰ (2010) and –18.9 ± 0.9‰ (2011). Those from the postbreeding Dunlin had mean $\delta^{13}C$ of –25.8 ± 0.8‰ (2010) and –26.5 ± 1.2‰ (2011). $\delta^{13}C$ for each group was not statistically different between years (prebreeding: $t_7 = 1.4$, $P = 0.2$; postbreeding: $t_7 = 1.1$, $P = 0.3$). Pooling both years, the prebreeding and postbreeding groups were significantly different ($t_{17} = 15.0$, $P < 0.001$).

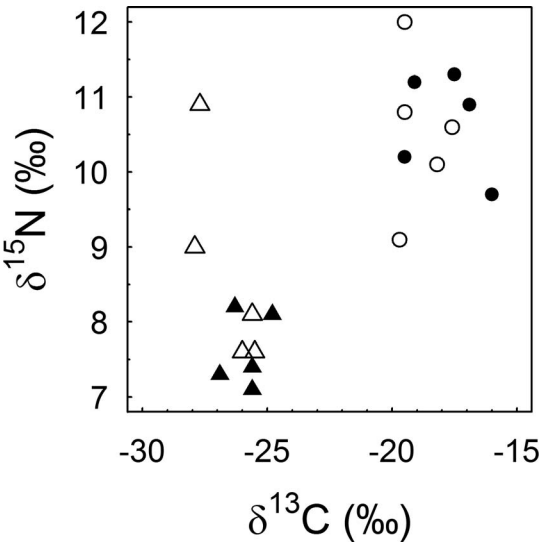

FIGURE 3. Muscle tissue $\delta^{13}C$ and $\delta^{15}N$ of prebreeding and postbreeding Dunlin. Solid symbols represent samples collected in 2010, and open symbols represent samples collected in 2011. Circles indicate prebreeding samples, and triangles indicate postbreeding samples.

Among individuals for which we had both blood and muscle samples, blood $\delta^{13}C$ was always lower. In prebreeding individuals, the mean difference in $\delta^{13}C$ between blood and muscle was 1.5 ± 1.7‰ ($t_6 = –2.2$, $P = 0.07$), which was similar to that in postbreeding individuals (1.2 ± 0.3‰; $t_6 = –11.7$, $P < 0.001$). This difference in $\delta^{13}C$ was twice the value of the muscle–blood isotopic difference derived from Evans Ogden et al. (2004). Because of the isotopic variability of dietary items consumed in the wild, we chose to use the experimental discrimination value in our model. In the captive experiment, discrimination factors were derived at equilibrium conditions (113 days). In the wild, natural variability in dietary isotope values over time would integrate into the 2 tissues differently, based on differences in turnover rates. Thus, discrimination values from recently migrated wild individuals would be suspect.

Distributions of simulated $\delta^{13}C$ initial endpoints (y_0) ranged from –24.7‰ to –13.3‰ in 2010 and from –23.0‰ to –16.1‰ in 2011. Distributions of $\delta^{13}C$ asymptotic endpoints (y_∞) ranged from –29.3‰ to –23.6‰ in 2010 and from –31.4‰ to –22.9‰ in 2011.

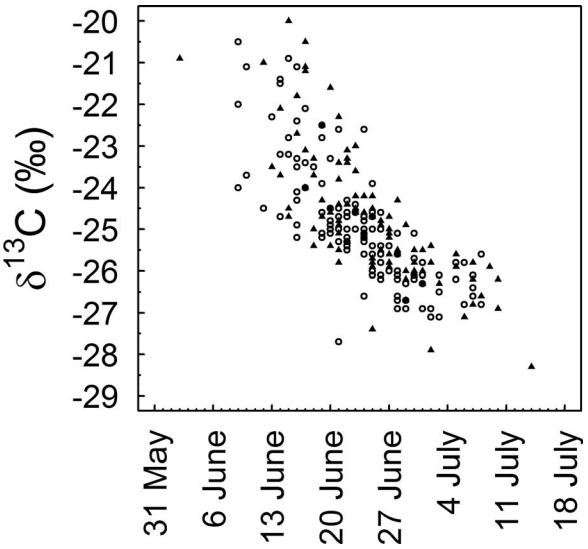

FIGURE 4. The $\delta^{13}C$ values of whole blood tissues sampled in 2010 (triangles) and in 2011 (circles) over time. For individuals captured twice in a season, only the isotope value from the first capture is included.

Blood Isotope Values

The blood $\delta^{13}C$ of captured birds decreased throughout the season in both years (Figure 4). For individuals captured twice in 2010, $\delta^{13}C$ ranged from –27.4‰ to –21.1‰ at first capture and from –28.0‰ to –25.1‰ at second capture (Figure 5). The mean difference between individuals' $\delta^{13}C$ at their first and second captures was 1.6 ± 1.1‰. In 2011, individual $\delta^{13}C$ values ranged from –25.6‰ to –21.1‰ at first capture and from –27.9‰ to –25.7‰ at second capture. The mean difference between individual $\delta^{13}C$ at the first and second captures was 2.5 ± 1.5‰.

For 1 individual in 2010, the difference in $\delta^{13}C$ measured between captures was 0.1‰, which was below measurement error. Such a small amount of change over 11 days between captures indicated that the individual was already at or near isotopic equilibrium with the terrestrial diet at the time of first capture. For this reason, we excluded this individual from our calculation of in situ turnover rate.

Isotopic Turnover Rate

The whole-blood $\delta^{13}C$ turnover rates determined experimentally and on the basis of allometric theory were lower than those determined in situ from our captured Dunlin (Table 2). The data simulated from the reported stable carbon half-life of 11.2 days (derived from Evans Ogden et al. 2004) indicated a beta mean of 0.0665 day^{-1} for k_e (95% CI: 0.0313–0.1137). Based on the masses of Dunlin captured in this study (mean = 58.6 g), the allometrically derived beta mean k_a was 0.0730 day^{-1} (95% CI: 0.0695–0.0766).

The beta mean in situ turnover rate of males ($k_{i.m}$ = 0.0878 day^{-1}; 95% CI: 0.0420–0.1480) was lower than that of females ($k_{i.f}$ = 0.1002 day^{-1}; 95% CI: 0.0528–0.1607). Although this difference was not statistically significant ($t_{50} = -1.6$, $P = 0.11$), it may be biologically relevant. Therefore, we chose to use sex-specific turnover rates ($k_{i.[m/f]}$) for calculating arrival dates with the in situ method.

Diet-switch Date Estimates

The in situ turnover rate consistently indicated a later arrival date than estimates made using either the experimental or the allometric turnover rate (Table 2 and Figure 6). Using k_e, the median T_e was May 30 (MAD = 7.4 days, $n = 103$) and June 4 (MAD = 4.4 days, n = 120) for 2010 and 2011, respectively. Using k_a, the median T_a was June 1 (MAD = 5.9 days, $n = 103$) and June 5 (MAD = 4.4 days, $n = 120$) for 2010 and 2011, respectively. Applying $k_{i.[m/f]}$, the median T_i was June 7 (MAD = 5.9 days, $n = 103$) and June 9 (MAD = 3.7 days, $n = 120$) for 2010 and 2011, respectively. Using our in situ method, the median arrival date of males was 4 days earlier than the female median arrival date in 2010 ($t_{99} = -3.2$, $P = 0.001$) and 2 days earlier in 2011 ($t_{116} = -3.0$, $P = 0.001$).

Evaluating Arrival Date Estimates

In 2010, melting on the study plots began after June 3; however, a late blizzard on June 7 contributed to delaying the snowmelt (Figure 6). The cumulative number of arrival estimates was negatively correlated with snowmelt in our study areas, and the strongest correlation resulted from the in situ method (for 2010 and 2011, respectively: T_e, $\rho = -0.66$ and –0.97; T_a, ρ = –0.72 and –0.98; T_i, ρ = –0.84 and –0.98). All correlations were significant ($P < 0.001$). Only 31% of in situ arrival dates in 2010 occurred before June 4, compared with 65% and 72% when estimated using the experimental and allometric methods, respectively (binomial tests: $P < 0.001$). In 2011, substantial melting had occurred prior to our field collections, and most arrival estimates (regardless of the method used) occurred after the tundra was open.

During the 2011 spring migration, last known locations of individuals with geolocators occurred in eastern Siberia (Figure 2) with individuals departing northward from May 26 to June 5. The remaining distance to Barrow ranged from 1,362 to 2,136 km. Under the assumption of nonstop flight, it would take ~1 day (range: 0.76–1.19 day) to cover these distances. Therefore, we added 1 day to the date of the last known location to determine the earliest possible date of arrival to the Barrow site.

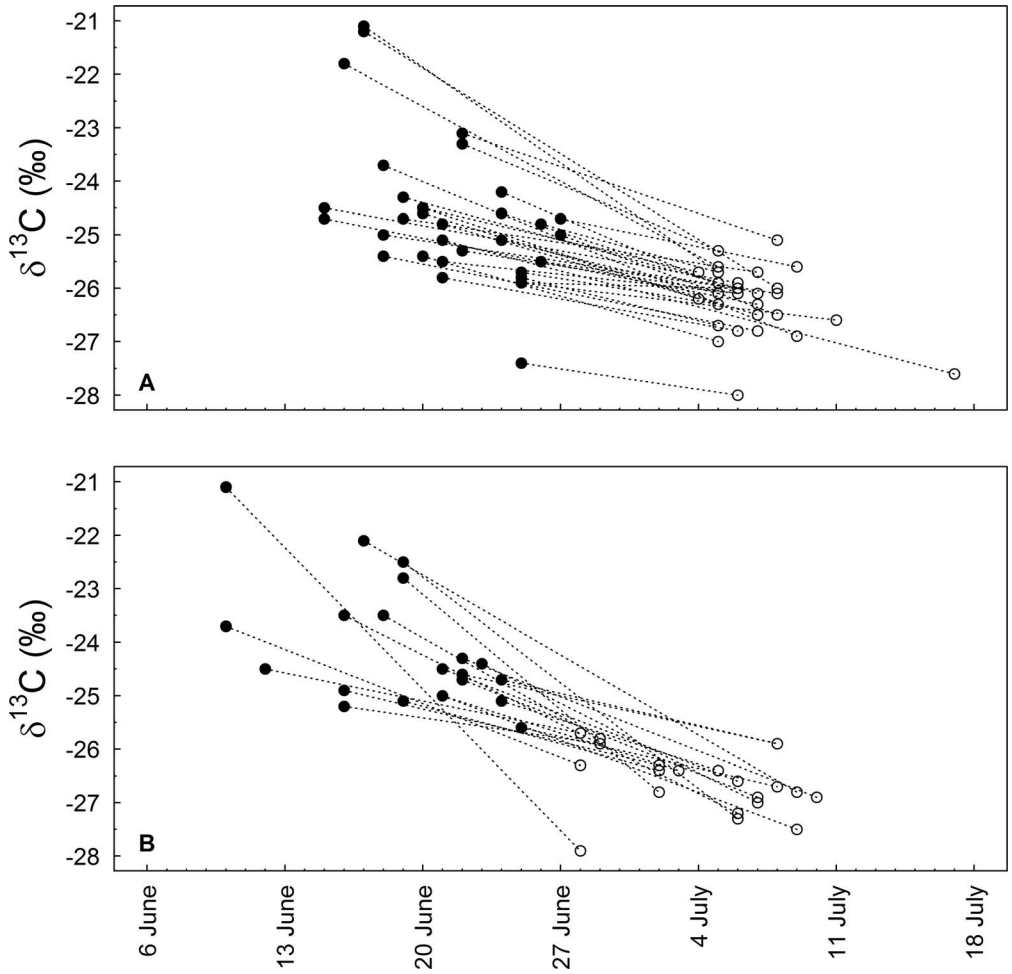

FIGURE 5. Whole blood $\delta^{13}C$ from recaptured Dunlin in 2010 (**A**) and 2011 (**B**) in relation to the date the blood sample was taken. Solid circles represent each individual's first capture; open circles represent second capture. Dotted lines connect sample points from the same individual.

Differences between the earliest possible arrival dates and arrival dates derived from the isotope data were 7.0 ± 3.5 days (positive numbers indicate that geolocator birds arrived prior to dates indicated by isotope data) for the in situ method, 1.2 ± 4.2 days for the experimental method, and 2.9 ± 3.9 days for the allometric method (one-way analysis of variance; $F_{2,39} = 8.8$, $P < 0.001$; Figure 7). In 4 and 3 instances, the experimental and allometric approaches, respectively, suggested that birds were on site before that was physically possible, based on the conservative extrapolations from the migration track lines. By contrast, none of the arrival date estimates from the in situ method indicated that birds were present before it was physically possible.

TABLE 2. Estimates of turnover rates in Dunlin determined using the experimental, allometric, and in situ methods, along with the median arrival-date estimates calculated from the respective turnover rates. Numbers in parentheses following turnover-rate estimates are 95% confidence intervals. Bracketed numbers following arrival-date estimates are median absolute deviation (MAD; units = days).

			Median arrival-date estimates			
Method	Turnover-rate estimates		2010		2011	
Experimental	$k_e = 0.0665$	(0.0313–0.1137)	T_e = May 30	[7.4]	T_e = June 4	[4.4]
Allometric	$k_a = 0.0730$	(0.0695–0.0766)	T_a = June 1	[5.9]	T_a = June 5	[4.4]
In situ (males, $n = 27$)	$k_{i.m} = 0.0878$	(0.0420–0.1480)	T_i = June 7	[5.9]	T_i = June 9	[3.7]
In situ (females, $n = 27$)	$k_{i.f} = 0.1002$	(0.0528–0.1607)				

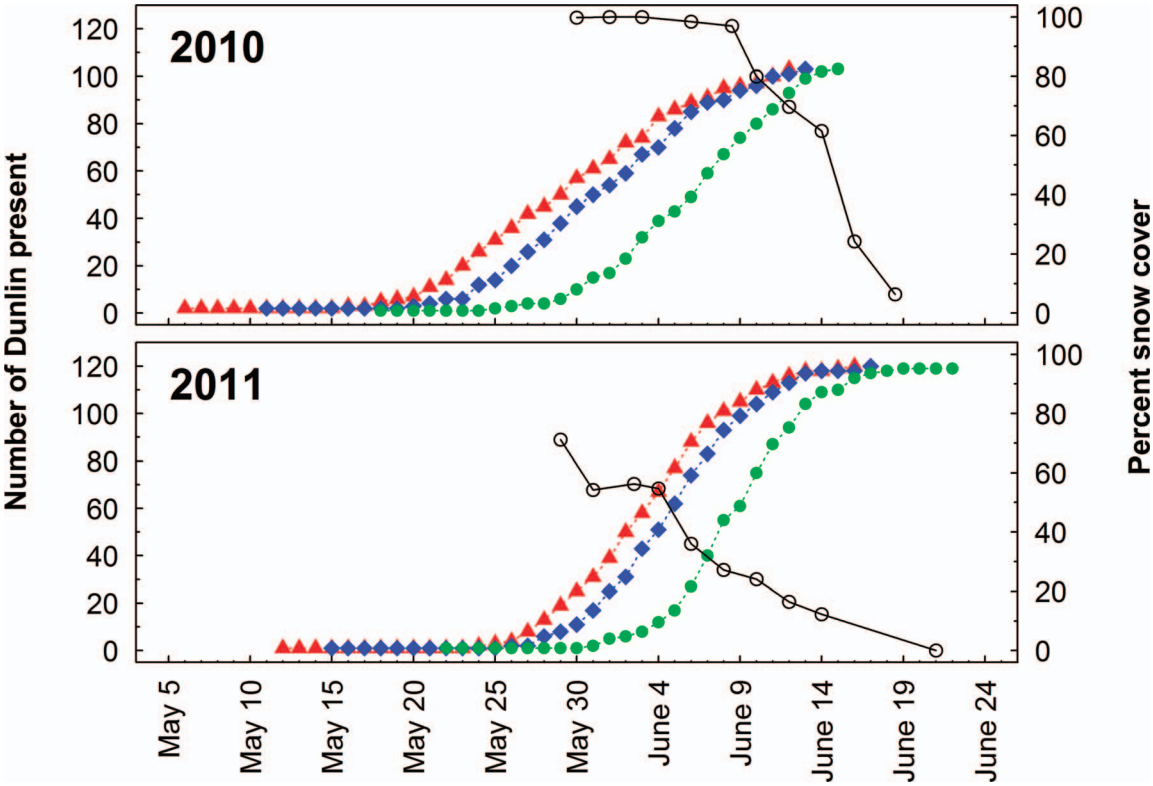

FIGURE 6. Progression of snowmelt and Dunlin arrival estimates for 2010 and 2011. Solid symbols represent the cumulative numbers of Dunlin estimated to be present as determined with the experimental (T_e; triangles), allometric (T_a; diamonds), and in situ (T_i; circles) methods. Open circles represent percent snow cover.

DISCUSSION

Our results demonstrate a simple and cost-effective method for determining real-world values of the isotopic parameters required for accurate assessments of the temporal movements of animals. By implementing a novel recapture method, we were able to corroborate and refine laboratory-based isotopic turnover rates under natural conditions. Including distributions of potential isotopic endpoint values allowed us to account for individual variability in dietary consumption. Determining turnover rates from field-based data provided a more plausible depiction of the isotope dynamics experienced by free-ranging Dunlin. Snowmelt and geolocator data supported the use of the in situ isotope turnover rates as a more conservative, if not more accurate, method of assessing arrival dates of individual birds.

The similarity between our in situ estimate of turnover rate and the experimentally determined and allometrically derived rates further validates the accuracy of each of these methods for making quantitative assessments of isotope turnover rates. In species for which recapture is unlikely or impossible, conducting captive feeding experiments may be the best way to determine a baseline turnover rate for the species. Where captive experiments are not viable, our results provide additional support for the allometric scaling of turnover rates. However, we believe that, whenever possible, in-the-field validation is the best way to account for complicating factors such as interindividual variability in diet, physiology, and behavior that occur in the natural environment. Furthermore, although sampling muscle tissue may not be appropriate for all species (e.g., the critically endangered), it was the most practical option under the constraints of our study and it allowed us to estimate isotopic endpoints while avoiding the possibility of inaccurate diet characterizations from prey sampling.

Stable nitrogen isotopes values ($\delta^{15}N$) were also measured with the intention of duplicating these procedures to validate our findings. However, $\delta^{15}N$ did not systematically decrease over time in the recaptured individuals, as found with $\delta^{13}C$. It is possible that sufficient overlap in the marine and terrestrial $\delta^{15}N$ sources existed such that increasing $\delta^{15}N$ values simply represent the real diet-switch, though in a different direction than assumed. It is also possible, perhaps even probable, that the physiology of nitrogen integration during this postmigration reproductive and molting period differs between individuals according to postmigration energy store and

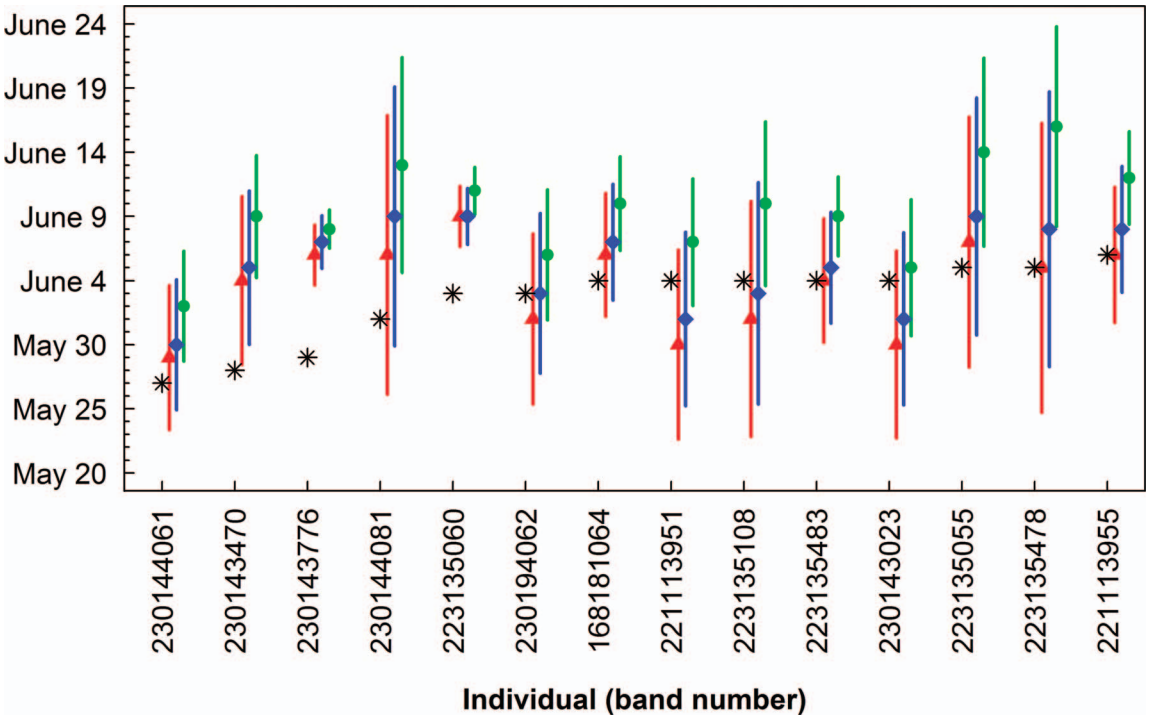

FIGURE 7. Earliest possible arrival dates (asterisks) of birds fitted with geolocators as determined from the date of their last known location during northward migration in 2011. Symbols represent the median arrival-date estimates determined with the experimental (T_e; triangles), allometric (T_a; diamonds), and in situ (T_i; circles) methods. Error bars represent the median absolute deviation in arrival estimates.

body condition. Regardless of the cause, the considerable variability in $\delta^{15}N$ of Dunlin blood prevented us from using nitrogen as an informative intrinsic marker for determining turnover rates or estimating arrival times. Future studies may benefit from a more thorough investigation of the apparent decoupling of carbon and nitrogen isotope dynamics in these Dunlin or in migratory animals in general.

Turnover Rate Estimation

Although the allometric and the experimental turnover rates were remarkably similar to the rate we measured in the field, small differences can be amplified when used to derive arrival dates. The in situ $\delta^{13}C$ turnover rate in whole blood equates to a half-life of 7.4 days (sexes pooled), which is ~4 days shorter than the 11.2-day half-life reported in Evans Ogden et al. (2004) and >2 days shorter than a 9.6-day half-life derived from k_a. Given that after 4 half-lives the blood will have transitioned to >90% of the asymptotic value, k_i will shorten the dietary-equilibration time by about 9–15 days in comparison to k_a and k_e, respectively. Although the 95% confidence intervals surrounding these rate estimates overlap considerably, the in situ rate estimates clearly tend toward higher values. Studies that use experimentally determined or allometrically derived isotope turnover rates to assess temporal movements likely overestimate the amount of time since a recent diet-switch, which would bias estimates of arrival dates early and, by association, bias correlations between arrival times and other life history events (e.g., nest initiation).

The difference between turnover-rate estimates generated from wild versus captive Dunlin is likely due to differences in catabolic and anabolic requirements. In Evans Ogden et al.'s (2004) experimental study, birds were maintained in captivity for 3 months to attain isotopic equilibrium before they were subjected to a diet switch. By contrast, the birds sampled in Barrow had recently completed an intense migration of thousands of kilometers. The captive birds were at stable mass and were healthy, well fed, and sheltered when the experiment began. The wild birds were dealing with postmigration tissue reorganization (Landys-Ciannelli et al. 2003), feather molt (Warnock and Gill 1996), uncertain food supplies (Danks 2004, Tulp and Schekkerman 2008), stress from potential predation (Scheuerlein et al. 2001, Lima 2009), severe weather conditions (Piersma and Morrison 1994, Piersma et al. 2003), and exposure to a 24-hr light cycle permitting a higher daily activity level (Steiger et al. 2013). In addition, the wild birds were able to run and fly to a greater extent than the captive animals, resulting in higher metabolic rates (Nagy 1987), although Hobson and

Yohannes (2007) suggested that exercise may have little impact on erythrocyte turnover rates. Although the captive birds likely experienced elevated stress levels due to their captivity, such stress quickly diminishes with acclimation (Dickens et al. 2009).

Another important difference between Evans Ogden et al.'s (2004) study and our in situ study was the season in which each was conducted. The captive experiment took place in early February, when the birds' reproductive system is dormant. The majority of wild individuals in our study were captured in June, during the peak of reproductive activities. These birds were investing significantly greater resources and energy into gonad development, courting, and nesting activities (Vézina and Salvante 2010) than the captive birds.

These environmental and biological factors require significant increases in metabolic activity and are, therefore, likely responsible for the observed difference in turnover rates between captive and wild Dunlin. Similar factors must be considered on a per species basis when making decisions about the suitability of turnover parameters for use in analyzing stable isotope data.

Reliability of Diet-switch Date Estimates

Applying sex-specific turnover rates, rather than a single population mean, resulted in male arrival dates that were earlier than female arrival dates. This finding supports the long-held assumption that male Dunlin typically arrive before the females to establish territories (Holmes 1966a).

The 2010 median in situ diet-switch date estimate (T_i), indicative of Dunlin arrival dates on the breeding grounds, was 4 days later than the median T_a and 7 days later than the median T_e. This difference was smaller in 2011, with a 3- and 4-day difference from the median T_a and median T_e, respectively. Differences between T_i and T_e in any individual ranged from 1 to 19 days. Differences of this magnitude are significant in Arctic environments and would substantially alter the biological interpretations made from these data. For example, if we wanted to determine whether individuals were able to adjust their arrival so that laying and hatching occur at suitable times, given recent phenological shifts resulting from climate change (see Dunn and Winkler 2010), to misrepresent the lag-time between arrival and laying would downplay the importance of incremental changes occurring in the environment and obscure the subtle relationship between arrival and reproduction.

Because snowmelt is closely tied to food availability (i.e. invertebrate emergence) for Dunlin (Høye and Forchhammer 2008), we initially evaluated arrival estimates in comparison to the timing of snowmelt at our site. Snowmelt data were particularly useful in 2010 because the spring thaw occurred very late that year (Figure 2). In fact, many birds appeared to arrive before the snow began melting that year, regardless of which turnover rate was used. One explanation could be that some Dunlin began feeding at a more southerly terrestrial location while waiting for conditions to improve; however, we lack any evidence to support this theory. Another possibility is that Dunlin were using the few snow-free areas in the city of Barrow and along the nearby road system, where lower snow levels and wind-blown dust cause early melting. Casual observations of Dunlin indicated that some birds arrived as early as May 26 (R. B. Lanctot personal observation); thus, the fact that the snow-covered study plots were not open for foraging would not preclude some Dunlin arriving and feeding elsewhere. However, in relation to the population as a whole, the number of Dunlin present at this time was likely quite low, given the limited available habitat. Although the experimental and allometric methods resulted in relatively high proportions of arrival dates preceding the onset of snowmelt, our in situ method produced a more moderate result. Holmes (1966a) reported that the first wave of Dunlin typically arrive in late May, but arrival of the majority of the population varies from year to year and is commonly delayed in years with unfavorable conditions. Our in situ method of estimating turnover rates yielded arrival-date estimates that were more consistent with this observation.

Like the snowmelt data in 2010, migration tracks from light-level geolocation supported the estimated arrival dates generated from the in situ method. Perhaps most important is our finding that both the experimental and allometric turnover rates resulted in arrival dates that were not possible, given the last known locations in Siberia. By contrast, all arrival-date estimates made with the in situ turnover rate occurred within a plausible time frame for the tagged Dunlin. Lag-times between the date of last known location and T_i suggest that these geolocator-equipped Dunlin staged at stopover sites for 2–13 days during the last stretch through the Arctic. Although stopover data at High Arctic refueling sites are unavailable for Dunlin, Piersma et al. (2005) indicated a 28-day stopover for Red Knots (*Calidris canutus*) refueling at similar latitudes in Iceland before completing their migration to breeding grounds in Greenland. The energy reserves obtained at these final stopover sites may be vital for the physiological changes from migratory to breeding condition that occur upon arrival (see Skagen 2006).

Although interindividual variation in turnover rate is certain to introduce inaccuracies when population mean values are applied at an individual level, our results indicate that the field-based, sex-specific turnover rates more accurately describe the isotope dynamics of free-living individuals than the experimentally or theoretically determined rates.

Conclusions

The methods presented here provide accurate individual-level arrival data without the need for previous handling of the animals or attachment of extrinsic monitoring devices. The present study is also novel in that we were able to estimate the necessary parameters in a natural setting. Because migration arrival dates can have notable effects on both individual survival and reproductive success (Both and Visser 2001, Newton 2006), inclusion of individual-level data in population-dynamics models will improve our understanding of the factors that drive fluctuations in abundance and demographics. With global climate change and widespread habitat destruction causing dramatic ecological changes that affect species at both the individual and population scales, individual-level data will be essential for developing effective monitoring and conservation strategies to protect the biodiversity of this planet.

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Ethics statement: All trapping, handling, and collection procedures were carried out in accordance with the University of Colorado Denver Institutional Animal Care and Use Committee protocols 92010(05)1C and 92010(05)1E and under U.S. Fish and Wildlife Service (MB085371-14), State of Alaska Department of Fish and Game (10–044, 10–130, 11–018, 11–131), and North Slope Borough Planning and Community Services (10–310, 11–347) permits. The use of any trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service, U.S. Geological Survey, University of Colorado Denver, or Mount Allison University.

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