J Ornithol (2010) 151:123–131
DOI 10.1007/s10336-009-0434-y

ORIGINAL ARTICLE

# Carbon isotope turnover in blood as a measure of arrival time in migratory birds using isotopically distinct environments

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Received: 18 February 2009 / Revised: 9 June 2009 / Accepted: 12 June 2009 / Published online: 8 July 2009
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**Abstract** Arrival time on breeding or non-breeding areas is of interest in many ecological studies exploring fitness consequences of migratory schedules. However, in most field studies, it is difficult to precisely assess arrival time of individuals. Here, we use carbon isotope turnover in avian blood as a technique to estimate arrival time for birds switching from one habitat or environment to another. Stable carbon isotope ratios ($\delta^{13}$C) in blood assimilate to a new equilibrium following a diet switch according to an exponential decay function. This relationship can be used to determine the time a diet switch occurred if $\delta^{13}$C of both the old and new diet are known. We used published data of captive birds to validate that this approach provides reliable estimates of the time since a diet switch within 1–3 weeks after the diet switch. We then explored the utility of this technique for King Eiders (*Somateria spectabilis*) arriving on terrestrial breeding grounds after wintering and migration at sea. We estimated arrival time on breeding grounds in northern Alaska (95% CI) from red blood cell $\delta^{13}$C turnover to be 4–9 June. This estimate overlapped with arrival time of birds from the same study site tracked with satellite transmitters (5–12 June). Therefore, we conclude that this method provides a simple yet reliable way to assess arrival time of birds moving between isotopically distinct environments.

**Keywords** Arrival time · $\delta^{13}$C · Isotope turnover · *Somateria spectabilis* · Stable isotopes

Communicated by F. Bairlein.

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## Introduction

Arrival time on breeding, wintering, or staging areas can have fitness consequences for migratory birds, with earlier arrival dates often resulting in an individual's ability to secure higher quality resources (Kokko 1999; Baker et al. 2004; Gunnarsson et al. 2006). Determining the arrival time of individuals is thus of interest in many ornithological studies, either as a surrogate for individual quality (Siitari and Huhta 2002; Drent et al. 2003) or to relate to other measures of individual fitness (Møller 1994; Smith and Moore 2005; Kokko et al. 2006).

In most field situations, detectability of birds is not instantaneous, and the first observation date is not necessarily the arrival date of a bird. Assessing the arrival time of migratory birds to a breeding, wintering, or stopover site therefore poses a significant challenge in many ornithological studies. Here, we present a technique that uses stable carbon isotope ratios in blood to assess the arrival time of birds to a new habitat.

Stable carbon isotope ratios (denoted as $\delta^{13}$C) in consumer tissues reflect the isotope ratios of food sources (Hobson and Clark 1992a). When migratory birds switch habitat (e.g., by arriving at terrestrial breeding grounds after migrating or wintering in coastal or marine habitats), their new diet will have a different isotopic signature if the two habitats are isotopically distinct (Peterson and Fry 1987). This switch to a new diet causes the isotope ratios in

blood to change gradually over time until they reflect the isotope ratio of the new diet (Hobson and Clark 1992a; Evans Ogden et al. 2004; Morrison and Hobson 2004). The rate of change in $\delta^{13}$C is tissue dependent. For example, blood plasma generally assimilates to the stable isotope ratio of a new diet within a few days (Hobson and Clark 1992a; Pearson et al. 2003; Podlesak et al. 2005), whereas whole blood or the cellular fraction of blood (red blood cells, RBC) turn over within several weeks (Bearhop et al. 2002; Hobson and Bairlein 2003; Evans Ogden et al. 2004; Morrison and Hobson 2004). Several experimental studies have determined that isotopic turnover in blood closely follows an exponential decay function (Pearson et al. 2003; Evans Ogden et al. 2004; Carleton and Martinez del Rio 2005). This relationship can be used to determine the time an animal switched diets if the isotope ratios of the old and the new diet are known.

Phillips and Eldridge (2006) recognized the potential of this relationship to estimate the time since an animal switched its diet. They presented a method that utilized the differential turnover rate of two different tissues sampled simultaneously from the same animal to estimate the time that had elapsed after a diet switch (Phillips and Eldridge 2006). This method requires knowledge of turnover rates of both of the sampled tissues, and assumes that both tissues were at isotopic equilibrium prior to the diet switch. The latter assumption is potentially violated in many birds that use stopover areas for short time periods during migration, allowing some tissues (e.g., plasma, liver) to completely turn over whereas other tissues (e.g., muscle, RBC) would not equilibrate completely. We therefore extend the approach introduced by Phillips and Eldridge (2006) to estimate the time since diet switch using only a single tissue. We further overcome the problem that the turnover rate has not been experimentally determined in most bird species (Martínez del Rio et al. 2009) by utilizing a mass-dependent turnover rate constant (Carleton and Martinez del Rio 2005). We propose that this method can be used to estimate the arrival time of birds in a habitat with a different isotopic signature than the previous habitat.

We first describe the exponential turnover function of carbon isotope ratios in whole blood and RBC, and describe in detail what measurements are required in the field to successfully employ this technique. We validate the approach by using published data of a variety of bird species that were experimentally switched to an isotopically different diet at a known time. We then demonstrate the utility of this technique by estimating the arrival time of a sea duck species, the King Eider (*Somateria spectabilis*), on breeding grounds in northern Alaska. To corroborate the accuracy of this new method we present data from King Eiders equipped with satellite transmitters that allow for independent estimation of arrival dates in the study area.

## Methods

### Exponential turnover of carbon isotopes in blood

The carbon isotope turnover in avian blood approximately follows an exponential decay function (Hobson and Clark 1992a; Pearson et al. 2003; Carleton and Martinez del Rio 2005; Podlesak et al. 2005) of the form

$$y_{(t)} = y_{\text{new}} + a\mathrm{e}^{-kt} \quad (1)$$

where $y_{(t)} = \delta^{13}$C of blood at time $t$, $y_{\text{new}} = \delta^{13}$C of blood after equilibration to diet in the new environment, $y_{\text{old}} = \delta^{13}$C of blood in the old environment, $a$ = absolute difference in blood $\delta^{13}$C between old and new diet ($a = |y_{\text{old}} - y_{\text{new}}|$), $t$ = time since diet switch or arrival in the new environment, and $k$ = fractional rate of isotopic incorporation.

Parameter $k$ scales allometrically to body mass and can be calculated as

$$k = 10^{-0.52-(0.35\log(m))}$$

where $m$ is the body mass of the bird (Carleton and Martinez del Rio 2005).

Phillips and Eldridge (2006) proposed to solve the equation for $t$ based on the differential turnover of two tissues. While this approach does not require a measurement of tissues after equilibration to the new diet, it requires measurements of two tissues with substantially different turnover rates, and knowledge of the tissues' turnover rates $k$ (Phillips and Eldridge 2006). If, however, the isotope signatures of a tissue from both the old and new environment are known, and birds are captured at an unknown time $t$ after arrival, their blood $\delta^{13}$C can be used in Eq. 1 to solve for the time since arrival $t$:

$$t = (\ln(y_{(t)} - y_{\text{new}}) - \ln(y_{(t)} - y_{\text{old}}))/-k \quad (2)$$

Using this equation to estimate arrival time requires a blood sample of the bird, as well as knowledge of the isotopic composition of blood in both the new and old environment ($y_{\text{new}}$ and $y_{\text{old}}$). Ideally, both $y_{\text{new}}$ and $y_{\text{old}}$ would be measured directly by sampling diet items from both environments or by sampling blood from birds that are in equilibrium with either of the diets.

Isotopic turnover in tissues may not only be influenced by dietary sources, but may be affected by alternative sources such as body reserves. Incorporating multiple sources into studies of isotopic turnover can be accomplished using the reaction progress variable (Cerling et al. 2007; Martínez del Rio and Anderson-Sprecher 2008). A comparative experimental study demonstrated recently that isotopic turnover in red blood cells can be adequately described by a single-compartment model (i.e., the exponential decay function introduced above), whereas

**Table 1** List of bird species included in our validation of estimated time since diet switch based on an exponential turnover model

| Species | Scientific name | Mass (g) | Tissue | References |
|---|---|---|---|---|
| Japanese Quail | *Coturnix japonica* | 240 | Whole blood | Hobson and Clark (1992a, b) |
| American Crow | *Corvus brachyrhynchos* | 404 | RBC | Hobson and Clark (1993) |
| Canvasback | *Aythya valisineria* | 1,450 | Whole blood | Haramis et al. (2001) |
| Great Skua | *Catharacta skua* | 1,220 | Whole blood | Bearhop et al. (2002) |
| Dunlin | *Calidris alpina* | 59 | Whole blood | Evans Ogden et al. (2004) |
| Yellow-rumped Warbler | *Dendroica coronata* | 13 | RBC | Podlesak et al. (2005) |

Isotopic turnover in blood was determined experimentally by switching birds from one isotopically distinct diet to another differing by at least 3‰ in $\delta^{13}C$

turnover in plasma may be better described by a multi-compartment model (Carleton et al. 2008). Because plasma has a fairly rapid turnover, and several pools can potentially contribute to plasma turnover, whole blood and RBC with their respective half-lifes of several weeks (Hobson and Bairlein 2003; Pearson et al. 2003; Evans Ogden et al. 2004) are the most appropriate tissues for estimating arrival time.

We therefore used data from whole blood and RBC measured in captive experiments (Table 1) to validate the approach of estimating the time since a diet switch. In each experiment, birds were switched from one isotopically distinct diet to another differing by at least 3‰ in $\delta^{13}C$ (Hobson and Clark 1992a, 1993; Haramis et al. 2001; Bearhop et al. 2002; Evans Ogden et al. 2004; Podlesak et al. 2005). We calculated $t$ based on blood samples taken from birds between 1 and 85 days after the diet switch, and report the difference (prediction error $t_{err}$) between actual time since diet switch and model-estimated $t$ based on analysis of whole blood or RBC.

## Case study: arrival of King Eiders on breeding grounds in northern Alaska

We applied the technique described above to estimate the arrival time of individual King Eiders on breeding grounds in northern Alaska. King Eiders are large sea ducks (1,300–2,100 g) that migrate and winter in marine ecosystems where they forage on benthic invertebrates (Suydam 2000). Birds that breed in northern Alaska winter in the Bering Sea and migrate through the Chukchi and Beaufort Seas to arrive on breeding grounds in June (Phillips et al. 2007; Oppel et al. 2009a). King Eiders migrate as pairs during spring, but differ in their behavior on the breeding grounds after arrival. Female King Eiders forage for insect larvae in small freshwater ponds and lakes, whereas males forage very little after arrival on breeding grounds (Holcroft-Weerstra and Dickson 1997). During the time between arrival on breeding grounds and nest initiation, females need to accumulate body reserves for egg formation and incubation (Bentzen et al. 2008; Oppel 2008), while males focus on mate guarding to enhance their fitness (Hario and Hollmén 2004; Steele et al. 2007). We therefore included only female King Eiders in our analysis of arrival time, as males were not expected to show predictable isotope turnover in their blood due to their low incidence of foraging.

In 2006 and 2007, we captured 19 female King Eiders on breeding grounds in northern Alaska (70°26′N, 153°08′W) during the pre-nesting period (10–22 June) using mist-net arrays and decoys. We collected 1 ml of blood from each bird by jugular venipuncture. Blood samples were separated into blood plasma and RBC using a portable centrifuge and a precision syringe. We stored plasma and RBC samples frozen in liquid nitrogen until analysis.

We characterized the marine diet $\delta^{13}C$ ($y_{old}$) of King Eiders by sampling muscle tissue from birds shot by subsistence hunters during spring migration at Point Barrow, Alaska. This location is approximately 150 km west of our study area, and all King Eiders migrate past this point before arriving on terrestrial breeding areas. We characterized $\delta^{13}C$ of the diet consumed on breeding grounds ($y_{new}$) by collecting invertebrate prey items in ponds and lakes of the study areas where female King Eiders were observed foraging in June 2006. We kept all invertebrate samples frozen until analysis.

Diet–tissue discrimination varies among different tissues (Hobson and Clark 1992b; Bearhop et al. 2002; Cherel et al. 2005), and this variation needs to be considered when the origin and final equilibrium of a turnover model are not measured in the same tissue. Since we estimated turnover from RBC, but characterized the marine diet from muscle samples, we accounted for differential discrimination between muscle and RBC by subtracting 0.4‰ from muscle $\delta^{13}C$ (Evans Ogden et al. 2004). Similarly, we added +1.5‰ to $\delta^{13}C$ of invertebrate food sources to account for discrimination between diet and RBC (Evans Ogden et al. 2004; Carleton and Martinez del Rio 2005; Podlesak et al. 2005).

### Stable isotope analysis

We removed calcified exoskeletons from freshwater invertebrates, rinsed soft parts in de-ionized water, oven-dried them at 60°C for 24 h, and then ground them into powder using mortar and pestle. We freeze-dried muscle, plasma and RBC samples and homogenized them using mortar and pestle. We extracted lipids from muscle samples using a 2:1 chloroform:methanol rinse prior to analysis (Bligh and Dyer 1959). Invertebrate samples were too small for chemical lipid extraction, and we used an arithmetic correction to account for lipids in invertebrate carbon isotope ratios (Smyntek et al. 2007).

All dried and homogenized samples were analyzed for carbon isotope ratios at the Alaska Stable Isotope Facility (University of Alaska Fairbanks) using continuous flow stable isotope-ratio mass spectrometry with a Costech ECS4010 Elemental Analyzer (Costech Scientific, Valencia, CA) interfaced to a Finnigan Delta Plus XP isotope ratio mass spectrometer via the Conflo III interface (Thermo-Finnigan, Bremen, Germany). Results of isotope analyses are reported in delta ($\delta$) notation relative to an international standard (Vienna PeeDee Belemnite) according to the following equation: $\delta^{13}C = [(R_{sample}/R_{standard}) - 1] \times 1{,}000$, with $R$ representing the ratio of $^{13}C/^{12}C$. Using the standard deviation of replicate measurements of laboratory standards run concurrently with samples (peptone), the analytical error was estimated to be less than ±0.2‰. We report all isotope measurements as mean ± standard deviation.

### Satellite telemetry

To assess whether arrival times estimated with the blood isotope turnover model yielded reliable results, we used data from an extensive satellite telemetry project (Phillips et al. 2006; Oppel et al. 2008). Briefly, we trapped 27 adult female King Eiders on breeding grounds in northern Alaska from 2002 to 2007 and equipped each one with a satellite transmitter (PTT-100; Microwave Telemetry, Columbia, MD). Females returned to their breeding site in our study area the year after capture (Phillips and Powell 2006), and we were able to estimate arrival time based on locations provided by the satellite transmitter. The transmitter provided a location for each bird every 4–6 days during spring. We used the date of the first location recorded on land after spring migration as the latest arrival time in spring. We also considered the date of the previous location, when the bird was still recorded at sea, as the earliest arrival date on breeding grounds, as the bird may have conducted the short flight from offshore staging areas to its breeding site shortly after the transmission. We calculated 95% confidence intervals for both the earliest and latest possible arrival dates, and used the lower 95% boundary of the earliest arrival date and the upper 95% boundary of the latest arrival date to report arrival time confidence intervals.

We then compared the arrival time window estimated for female King Eiders equipped with satellite transmitters with the times estimated for female birds from which we collected blood samples. As we were not able to recapture females with satellite transmitters to collect blood samples, this comparison is at the population rather than at the individual level.

## Results

### Validation

Whole blood and RBC measured in captive birds could be used successfully to estimate the time since diet switch. Overall, there was a significant increase in $t_{err}$ over time (linear regression, $b = 0.49$, $P < 0.001$). The difference between model predicted and actual time since diet switch was on average 0.8 ± 2.8 days (range −6.1 to 4.2 days; Fig. 1) for the first 20 days after a diet switch, but increased dramatically after 3 weeks to a mean of 7.1 ± 21.4 days (range −27.6 to 50.8 days; Fig. 1). The increase in prediction error started much sooner for the smallest species analyzed: the isotope turnover model of Yellow-rumped Warbler (13 g) RBC was only reliable for 1 week after the diet switch (Fig. 1).

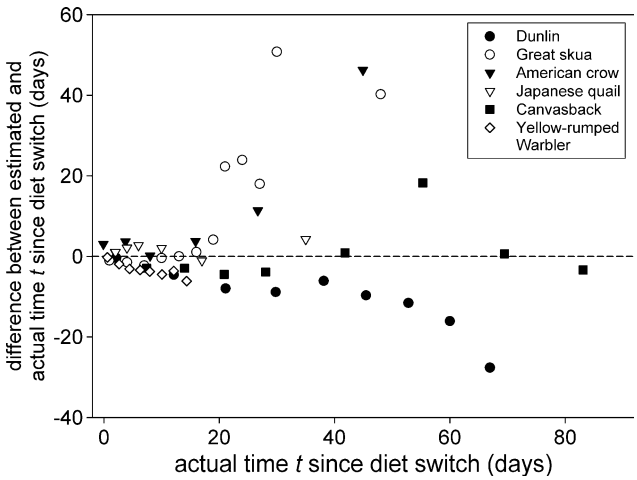


**Fig. 1** Difference between estimated and actual time $t$ since a diet switch calculated from carbon isotope turnover in whole blood (Dunlin, Great Skua, Japanese Quail, and Canvasback) or red blood cells (American Crow, Yellow-rumped Warbler), compared to actual time $t$ since diet switch for captive birds switched from an isotopically distinct diet to another. Data sources and scientific species names are listed in Table 1

## King Eider arrival time on breeding grounds

RBC $\delta^{13}$C of the 19 female King Eiders ranged from −20.7 to −18.1‰ (mean −19.3 ± 0.8‰; Fig. 2). Muscle $\delta^{13}$C sampled from birds prior to arrival on breeding grounds was slightly enriched compared to RBC ($\delta^{13}$C = −17.8 ± 0.5‰, $n = 8$). Freshwater invertebrate $\delta^{13}$C collected on the breeding grounds was on average depleted by 8.9‰ compared to muscle (mean lipid-corrected invertebrate $\delta^{13}$C = −26.6 ± 3.5‰, $n = 52$; Fig. 2). Plasma and eggshell membrane $\delta^{13}$C confirmed that King Eiders were consuming this diet on the breeding grounds (Oppel 2008). In one bird, plasma $\delta^{13}$C indicated consumption of more depleted food items ($\delta^{13}$C = −26.9‰), and we adjusted $y_{new}$ for that bird based on its plasma isotope signature. Another bird showed both RBC and plasma $\delta^{13}$C depleted compared to muscle $\delta^{13}$C, but the small difference (1.1‰) between RBC and plasma indicated that plasma had not completely turned over and arrival must have been fairly recent. We excluded that bird from analysis of arrival time as its $y_{old}$ presumably differed substantially from the endpoint we used in our model.

We estimated arrival time based on $\delta^{13}$C turnover in RBC to be 7 June (95% CI 4–9 June, range 29 May to 14 June; Table 2). Birds equipped with a satellite transmitter provided the first location on land from 5 to 25 June ($n = 27$). Three females had first terrestrial locations that were later in the season than the date of their capture on breeding grounds in the previous year. If we excluded these three birds, the average last location at sea was 6 June (95% CI 5–7 June, range 1–13 June, $n = 24$), and the average first terrestrial location was 10 June (95% CI 9–12 June, range 5–15 June, $n = 24$). The combined 95% confidence interval of potential arrival time for satellite-tracked birds spanned from 5 to 12 June and thus overlapped with the interval estimated from carbon isotope turnover in RBC (Fig. 3).

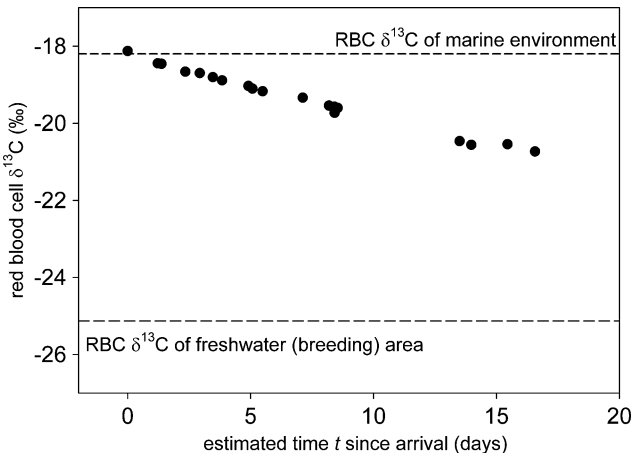


**Fig. 2** Red blood cell carbon isotope ratio ($\delta^{13}$C in ‰) of King Eiders (*Somateria specabilis*) captured shortly after arrival on breeding grounds in northern Alaska in relation to the estimated time since arrival. Arrival time was estimated based on each bird's body mass and $\delta^{13}$C of red blood cells. The isotopic signatures of red blood cells in marine and freshwater environments (*broken lines*) were characterized by sampling muscle from birds harvested prior to arrival on breeding grounds (marine) and freshwater food items, and corrected for discrimination

**Table 2** Estimated arrival date of 18 female King Eiders (*Somateria specabilis*) on breeding grounds in northern Alaska based on carbon isotope turnover of red blood cells (RBC)

| Band-number | Capture date | Mass (g) | *k* | Estimated arrival date |
|---|---|---|---|---|
| 1797-39583 | 14 Jun | 1,330 | 0.024 | 11 Jun |
| 1797-39584 | 15 Jun | 1,340 | 0.024 | 13 Jun |
| 1587-53486 | 22 Jun | 1,360 | 0.024 | 11 Jun |
| 1587-53498 | 14 Jun | 1,380 | 0.024 | 14 Jun |
| 1587-53445 | 22 Jun | 1,460 | 0.024 | 5 Jun |
| 1587-53422 | 13 Jun | 1,590 | 0.023 | 11 Jun |
| 1587-53460 | 12 Jun | 1,645 | 0.023 | 5 Jun |
| 1587-53458 | 13 Jun | 1,650 | 0.023 | 6 Jun |
| 1587-53449 | 12 Jun | 1,680 | 0.022 | 7 Jun |
| 1587-53474 | 14 Jun | 1,790 | 0.022 | 29 May |
| 1587-53468 | 14 Jun | 1,835 | 0.022 | 9 Jun |
| 1587-53444 | 20 Jun | 1,860 | 0.022 | 9 Jun |
| 1587-53463 | 14 Jun | 1,895 | 0.022 | 4 Jun |
| 1587-53459 | 12 Jun | 1,900 | 0.021 | 6 Jun |
| 1587-53446 | 20 Jun | 1,910 | 0.021 | 31 May |
| 1587-53452 | 10 Jun | 1,920 | 0.021 | 30 May |
| 1587-53452 | 12 Jun | 2,020 | 0.021 | 8 Jun |
| 1587-53453 | 10 Jun | 2,140 | 0.021 | 1 Jun |

The distribution of RBC carbon isotope ratios in relation to estimated time since arrival is shown in Fig. 2

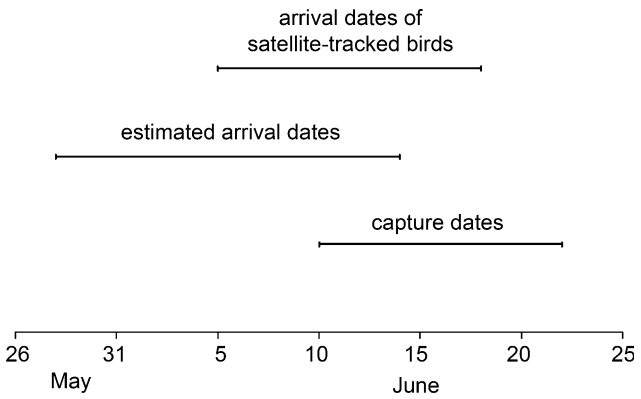


**Fig. 3** Range of capture and arrival dates of female King Eiders on breeding grounds in northern Alaska. Estimated arrival dates are based on carbon isotope ratio turnover of red blood cells ($n = 18$), arrival dates of satellite-tracked birds are based on females equipped with a satellite transmitter ($n = 24$)

## Discussion

Using carbon isotope turnover in blood provides an easy and inexpensive technique to estimate arrival time of birds in a new environment. A similar approach using differential turnover of two tissues has been validated previously (Phillips and Eldridge 2006). In this study, we demonstrated that it is possible to estimate the time since a diet switch for an individual bird by using only a single blood sample. This estimation was highly reliable for 3 weeks after an experimental diet switch in five different species, but we caution researchers that fairly small species may have more rapid turnover and a correspondingly shorter time span during which the model provides reliable estimates.

Both in the Yellow-rumped Warbler used in our validation, and another songbird species (Garden Warbler, *Sylvia borin*, 15 g) switched from a mixed controlled diet to elderberries or mealworms (Hobson and Bairlein 2003), the isotope turnover model provided reliable estimates only for about 1 week. The prediction errors in our study increased with the time that had elapsed since the experimental diet switch, and are most likely associated with the asymptotic portion of the turnover curve: a decrease in the steepness of the curve will lead to large errors in the estimated time since a diet switch even for small deviations in blood isotope ratios. As smaller species approach the asymptotic part of the curve more rapidly than larger birds, the time window during which the turnover model will yield reliable estimates is shorter for smaller birds. More experimental data on species weighing 30–300 g are required to determine the time window over which the turnover model will yield reliable results for species of that size range. In general, we do not recommend using this method more than 3 weeks after birds arrived at a new habitat.

Our case study of King Eiders demonstrates that this approach can be employed successfully in the field. Arrival time of King Eiders estimated from carbon isotope turnover in RBC conformed with field observations, traditional knowledge (Suydam 2000), and estimates from satellite telemetry (Phillips et al. 2007; Oppel et al. 2008). We excluded three females tracked with satellite transmitters due to their late arrival. These females were the only ones that had been captured at an earlier date during the previous season, so their late arrival in the tracking year indicates that their migration schedule may have been affected by the satellite transmitter. Satellite transmitters can affect the dive performance of sea ducks (Latty 2008), and their effects on migration are poorly understood. Potential effects include delays in the migration schedule (Bêty et al. 2003; Demers et al. 2003), or possibly a reduction in breeding propensity. Either of these two effects may cause birds to arrive later on the breeding grounds than unmarked birds.

Although the results of our isotope model overlap with results from satellite telemetry, there was a directional bias in that the isotope model estimated arrival time on average several days earlier. King Eiders stage in the Beaufort Sea after migrating past Barrow (Phillips et al. 2007), and the Beaufort Sea may provide food items depleted in $\delta^{13}$C compared to previous staging areas in the Chukchi Sea (Dunton et al. 1989; Schell et al. 1998). No information is available on isotope ratios of prey items consumed in the Beaufort Sea, but the ingestion of $\delta^{13}$C depleted food items in the Beaufort Sea could result in a bias in the estimate of arrival time on breeding grounds.

The technique introduced here holds potential for future applications where the arrival times of individual birds at breeding, staging, or wintering areas need to be estimated. However, we urge researchers to carefully consider the requirements and assumptions underlying this technique before using it for their research. The most important requirement for this technique to be applied successfully is that the two environments the birds use before and after arrival are sufficiently different in $\delta^{13}$C. Estimation errors in isotope models are highly sensitive to the isotopic difference between endpoints, and an isotopic difference $<2‰$ would result in very unreliable estimates (Phillips and Gregg 2001; Vander Zanden and Rasmussen 2001; Phillips and Eldridge 2006). Differences of $>2‰$ exist for most tundra-nesting species that use marine or coastal habitats during migration (e.g., many arctic-nesting shorebirds and waterfowl; see Morrison and Hobson 2004 for an example), but are unlikely in species that use similar environments during and after migration (e.g., many songbirds). If the two environments of the study system differ isotopically, it is important that the isotopic signatures of tissues in both environments are described accurately. In contrast to the approach described by Phillips and Eldridge (2006), our model requires samples of known diet items, or tissues known to reflect the diet, in each of the two environments.

The isotopic signature of each diet can be characterized by sampling blood from birds that have been feeding in either environment for several weeks, or by using tissues that are metabolically inert after growth. Feathers sampled from the bird captured at time $t$ may be useful to determine $\delta^{13}$C of the previous environment ($y_{old}$) if the molting strategy of the bird is sufficiently known and certain feathers are always grown in the previous environment. Plasma or RBC sampled from a bird captured at a later stage could be used to determine $y_{new}$ once birds have reached an equilibrium with the new diet (Morrison and Hobson 2004). For breeding grounds, eggshell membranes collected from hatched or depredated nests may provide a

simple way to characterize the diet of birds (Oppel et al. 2009b). All these samples can be collected non-destructively, which renders the method suitable for species of conservation concern. However, the potential incorporation of endogenous reserves in any of the tissues used to characterize a new diet should be considered (Cerling et al. 2007; Fox et al. 2009). Failure to adequately characterize the dietary endpoints for the isotopic turnover model will result in biased estimates of arrival time.

If the diet of either environment is characterized by an average measurement reflecting diet $\delta^{13}C$ for the whole population, an important assumption is that individuals use isotopically similar food sources and show little dietary specialization (Bolnick et al. 2003). King Eiders show individual variation in diet choice and behavior (Merkel et al. 2007; Oppel 2008), hence this assumption may have been violated in our case study. Nonetheless, our estimates of arrival time from RBC turnover were very similar to those derived from satellite telemetry (Fig. 3), indicating that the technique is robust towards some dietary variation among individuals. Individual variation may not only affect the isotopic signature of the diet but also the time that elapses between arrival and foraging in a new habitat. Another important assumption underlying our model is that this time period must be approximately equal among individuals. Many long-distance migrants reduce their intestines during long migratory flights (Piersma 1998), and the time required to restore digestive organs may vary among individuals. The model introduced here calculates the time since a diet switch occurred, and this will only reflect arrival time if the animal started foraging shortly after arrival. Further research is required to determine if individual differences in foraging delay may affect this assumption of the model.

In summary, we conclude that using isotope ratios of blood samples provides a simple, non-destructive, and accurate tool to estimate the arrival time of migratory birds in a new environment over a time window of approximately 3 weeks. It can thus be used in conjunction with other measures of fitness such as breeding success or survival to explore fitness consequences of individual migration strategies.

## Zusammenfassung

Berechnung der Ankunftszeit von Zugvögeln in einem isotopisch eindeutigen Habitat mittels des Umsatzes von Kohlenstoff-Isotopen im Blut

Ankunftszeit in Brut- oder Wintergebieten ist von Interesse in vielen ökologischen Untersuchungen die die Fitness Folgen von Zugstrategien untersuchen. In den meisten Felduntersuchungen ist es jedoch schwierig die genaue Ankunftszeit von Individuen zu bestimmen. Hier verwenden wir den Umsatz von Kohlenstoff-Isotopen in Vogelblut als eine Methode um die Ankunftszeit von Vögeln zu bestimmen, die von einem isotopisch eindeutigen Lebensraum in einen anderen wechseln. Das stabile Kohlenstoff-Isotopen-Verhältnis ($\delta^{13}C$) im Blut assimiliert zu einem neuen Gleichgewicht nach einem Nahrungswechsel entsprechend einer exponentiellen Funktion. Diese Beziehung kann benutzt werden, um die Zeit eines Nahrungswechsels zu bestimmen, wenn $\delta^{13}C$ von der alten und der neuen Nahrung bekannt sind. Wir benutzen veröffentlichte Daten von in Gefangenschaft gehaltenen Vögeln um zu bestätigen dass dieser Ansatz zuverlässige Schätzungen über den Zeitpunkt eines Nahrungswechsels innerhalb der ersten drei Wochen nach dem Nahrungswechsel ermöglicht. Wir untersuchen darüber hinaus wie nützlich dieser Ansatz für Prachteiderenten (*Somateria spectabilis*) ist, die nach dem Zug über das Meer in terrestrischen Brutgebieten ankommen. Wir berechneten die Ankunftszeit im Brutgebiet im nördlichen Alaska aus dem $\delta^{13}C$ Umsatz in roten Blutkörperchen auf den 4.–9. Juni (95% Konfidenz-Intervall). Diese Ankunftszeit deckt sich mit der Ankunftszeit von satellitentelemetrierten Individuen aus dem gleichen Untersuchungsgebiet, die im Zeitraum vom 5.–12. Juni ankamen. Wir folgern dass diese Methode eine einfache aber zuverlässige Möglichkeit bietet um die Ankunftszeit von Vögeln in einem isotopisch eindeutigen Habitat zu bestimmen.

**Acknowledgments** This study was funded by the Coastal Marine Institute (University of Alaska, Fairbanks), Minerals Management Service, and U.S. Geological Survey OCS Program. Further financial and technical support was provided by the U.S. Fish and Wildlife Service, North Slope Borough, ConocoPhillips Alaska, Inc., U.S. Geological Survey (Alaska Cooperative Fish and Wildlife Research Unit), and German Academic Exchange Service. We thank R. Bentzen, C. Latty, J. Rogalla, J. Heathcote, S. Sekine, and A. Patterson for assistance in the field. The manuscript benefited from thoughtful comments by D. O'Brien, J. Liebezeit, A. Taylor, T. Lee, C. van Hemert, S. Nash, J. Metzgar, and an anonymous reviewer. Mention of trade or product names is for descriptive purposes only and does not imply endorsement by the U.S. government.

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