USE OF BODY STORES IN SHOREBIRDS AFTER ARRIVAL ON HIGH-ARCTIC BREEDING GROUNDS

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Abstract.—Stable-isotope analyses of egg components can illuminate the contributions of endogenous and exogenous nutrients to egg formation in cases where birds move from one isotopic biome to another just before egg-laying, as in Red Knots (*Calidris canutus islandica*) and Ruddy Turnstones (*Arenaria interpres interpres*) nesting in the northeastern Canadian High Arctic. Those populations use inshore marine habitats during the winter and northward migration periods, but switch to feeding and breeding in terrestrial C-3 habitats in the Arctic. Upon the birds' arrival at Alert, Nunavut, Canada, stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope values for their red blood cells were consistent with those expected from an inshore marine diet. After the birds switched to a terrestrial diet, those values decayed in a negative exponential fashion until they reached asymptotic values consistent with a local terrestrial C-3 diet. Components of eggs laid later in the season, including lipid-free yolk, albumen, yolk lipid, and albumen lipid, generally showed isotope values consistent with routing from exogenous (i.e. local) nutrient sources, which supports the notion that High Arctic shorebirds are primarily income and not capital breeders. However, eggs in earliest clutches were enriched in ^{13}C and ^{15}N, which suggests that some residual marine nutrients were available for reproduction. The extent to which endogenous stores are transferred to eggs in High Arctic shorebirds may depend on year and climatic conditions. *Received 20 March 2003, accepted 3 December 2003.*

Resumen.—Los análisis de isótopos estables de los componentes del huevo pueden dar luz sobre la contribución de nutrientes endógenos y exógenos a la formación del huevo en casos en que las aves se mueven de un bioma isotópico a otro justo antes de la puesta, como en las poblaciones de *Calidris canutus islandica* y *Arenaria interpres interpres* que nidifican en el Ártico alto del noreste de Canadá. Estas poblaciones utilizan ambientes marinos ubicados cerca de la costa durante los períodos de invierno y migración hacia el norte, pero cambian a alimentarse y reproducirse en ambientes terrestres C-3 en el Ártico. Al arrivar a Alert, Nunavut, Canadá, los valores de los isótopos estables de carbono (δ^{13}C) y nitrógeno (δ^{15}N) de los glóbulos rojos de las aves fueron consistentes con los esperados con base en una dieta marina costera. Luego de que las aves cambiaron a una dieta terrestre, estos valores decayeron de forma exponencial negativa hasta alcanzar valores asintóticos consistentes con una dieta local C-3. Los componentes de los huevos puestos más adelante, incluyendo la yema sin lípidos, el albumen, los lípidos de la yema y los lípidos del albumen, generalmente mostraron valores isotópicos consistentes con la incorporación de nutrientes exógenos (i.e. locales), lo que sugiere que las aves playeras del Ártico alto son reproductoras principalmente de ingreso y no de capital. Sin embargo, los huevos de las nidadas más tempranas estuvieron enriquecidos en ^{13}C y ^{15}N, lo que sugiere que algunos nutrientes marinos residuales estaban disponibles para la reproducción. El grado al que las reservas endógenas se transfieren a los huevos en las aves playeras del Ártico alto podría depender del año y de las condiciones climáticas.

Nutritional resources used for breeding by migratory birds may be acquired locally on the breeding grounds or accumulated elsewhere and brought to the breeding grounds in the form of body stores. Birds adopting those two strategies have been referred to as "income" breeders and "capital" breeders, respectively (Drent and Daan 1980). Early considerations of income and capital strategies examined investment of nutrients in just the eggs (clutch). More recently, the terms have been taken to include requirements of both the eggs and the female during formation, laying, and incubation of

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eggs, and to represent extremes on a continuous scale (Bonnet et al. 1998, Meijer and Drent 1999). Birds breeding in the Arctic appear to use strategies ranging from income to capital. In a recent re-examination, using published data, of the extent to which capital and income breeding occur in birds, Meijer and Drent (1999) found that only 3 of 12 well-studied species showed substantial reliance on a capital strategy. All three nested in cold regions; their dependence on endogenous stores ranged from 100% in the Common Eider (*Sommateria mollissima*), which arrives on the breeding grounds with large stores and fasts throughout laying and incubation (a true capital breeder), to about half in the Lesser Snow Goose (*Chen caerulescens caerulescens*). Whereas early studies of Arctic geese indicated that a number of species appeared to rely only on stores accumulated prior to arrival on the breeding grounds, subsequent work has shown that feeding resources on the breeding grounds also play an important role in reproduction (see references reviewed in Tombre et al. 1996, Gladher 1999, Gauthier et al. 2003). Species whose strategies appear to be more income-based include shorebirds (Klaassen et al. 2001) and subfamily Tetraoninae, once considered possibly extreme income breeders (Thomas 1982, 1988), but which may be able to use endogenous reserves of energy and protein for clutch formation (Meijer and Drent 1999). In a range of other species that breed in warmer climates, >90% of total energy and protein required for breeding came from direct food intake (Meijer and Drent 1999).

Many birds migrate long distances to reach Arctic breeding grounds. Klaassen (2003) has pointed out that the composition of stores required for migration are likely to differ from those required for breeding—involving emphasis on energy (fat) and protein, respectively. Thus, it is important to distinguish between protein and energy stores and to differentiate their possible uses for reproduction. Shorebirds breeding in the Arctic undertake long migrations between wintering and nesting areas, during which they undergo substantial body changes involving fuel and nutrient storage and physiological adaptations for migration (Piersma 1998, Piersma and Gill 1998, Piersma et al. 1999, Battley et al. 2000). In shorebirds breeding on northern Ellesmere Island, stores of protein and fat accumulated at stopover

areas appear to be larger than required for the flight to the breeding grounds (Davidson and Evans 1988), and early spring arrivals have been shown to have substantial stores of both fat and protein remaining (Morrison and Davidson 1990, Davidson and Morrison 1992) in at least some years (Reneerkens et al. 2002). Until recently, it has been extremely difficult to quantify direct use of such stores in egg formation. Measurement of naturally occurring stable isotopes in eggs and tissues of laying females, however, may provide an effective method in cases where birds store nutrients in one habitat and subsequently breed and feed in another (Hobson 1995; Hobson et al. 1997a, 2000). This approach is based on the fact that foodwebs in different habitats (e.g. inshore marine vs. terrestrial) often differ in their isotopic compositions, which will be reflected in the tissue composition of animals feeding in those habitats.

Stable isotopes of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) are useful for distinguishing whether tissues were formed from marine—in the case of shorebirds, inshore marine as opposed to pelagic or "offshore"—or terrestrial foodwebs, because the heavier stable isotope of those elements is typically more abundant in marine systems (Hobson et al. 1997a). In shorebirds spending the winter and migration periods in coastal habitats, stores derived from a diet of inshore marine invertebrates should differ in stable-isotope ratios from tissues formed of terrestrial C-3 food sources obtained on the tundra (Schell and Ziemann 1988, Tieszen and Boutton 1988) after arrival on the breeding grounds. Examination of stable-isotope ratios in egg components should reflect the source of nutrients used for egg formation and show whether (1) stores laid down during migration or (2) local terrestrial food resources were the main source. Examination of stable-isotope ratios in blood samples from captured birds should reflect metabolic turnover in that component, as reflected by the change from an inshore marine to a terrestrial diet, during the postarrival–prebreeding period (Hobson and Clark 1993).

Recently, Klaassen et al. (2001) used stable-carbon isotope analysis of shorebird feathers and egg material from birds breeding in the Canadian Arctic to conclude that there was little evidence for a capital strategy and suggested that all such shorebirds are income strategists.

Further clarification of the extent to which their conclusions may be universal is required, for several reasons. First, use of neonate feathers to trace marine (endogenous) inputs to reproduction puts focus solely on use of protein components of stores, leaving potential routing of lipid stores to eggs still to be investigated. Second, increased sample sizes of egg components are needed to assess within- or among-year variation in the extent to which protein or lipid stores may be transferred to eggs. Third, broader spatial and temporal sampling of shorebird species is desirable, because individuals of some of the species described (e.g. White-rumped Sandpipers [*Calidris fuscicollis*]; Parmelee 1992) may have taken an interior migration route through North America to the breeding grounds and thus would likely already have accumulated stores with terrestrial signatures.

Here, using the stable-isotope approach, we assess use of nutrient stores on the breeding grounds in populations of Red Knots (*Calidris canutus islandica*) and Ruddy Turnstones (*Arenaria interpres interpres*) that breed in the High Arctic regions of northeastern Canada and Greenland and migrate to wintering areas on the European seaboard, where they feed on marine intertidal invertebrates (Salomonsen 1951; Godfrey 1953, 1986; Morrison 1975, 1977, 1984; Davidson and Wilson 1992). In spring, the majority of these birds pass northward through Iceland, where they stop for about three weeks to refuel (Morrison 1977, 1992a; Morrison and Wilson 1992). During that period, they again feed principally on marine intertidal invertebrates (Alerstam et al. 1992, Gudmundsson and Gardarsson 1993) and accumulate substantial stores of both fat and protein (Morrison 1977, Wilson and Morrison 1992, Piersma et al. 1999), much of which is required to power their flight across the Greenland icecap (Alerstam et al. 1990) into the High Arctic regions of northwestern Greenland and Canada. Part of the populations passes through staging areas in northern Norway, where similar stores are accumulated (Davidson et al. 1986, Davidson and Wilson 1992, Davidson and Evans unpubl. report). After arrival at Alert and other points on Ellesmere Island, both species switch to a diet of terrestrial invertebrates (Parmelee and MacDonald 1960; Nettleship 1973, 1974; R. I. G. Morrison pers. obs.). Sanderlings (*Calidris alba*) are also thought to migrate to European wintering

quarters (Morrison 1992b) and occupy inshore marine habitats during the migration and wintering periods. Given that background, we tested the assumption that birds arrived with endogenous stores with isotope signatures typical of an inshore marine, rather than terrestrial, origin and evaluated whether egg components were subsequently derived from local foods or from those endogenous stores.

Study Area and Methods

To determine if body stores were being used in egg formation, three types of data were examined. First, stable-isotope ratios were measured in samples of albumen and yolk collected from shorebird eggs. Ruddy Turnstones provided the largest sample sizes; smaller numbers of eggs were sampled for Red Knots and Sanderlings (see below). These three are the most common shorebird species breeding in the Alert area (R. I. G. Morrison pers. obs.). Second, starting in the immediate postarrival period, blood samples were collected from Red Knots and Ruddy Turnstones to determine whether shorebirds did indeed arrive with "marine" stable-isotope signatures in their tissues and to examine the dynamics of change in stable-isotope signatures as birds switched from an inshore marine to a terrestrial C-3 diet. Third, stable isotope ratios were measured in samples of potential food items taken from inshore marine habitats on the wintering grounds in Europe and from inshore marine and terrestrial habitats on the breeding grounds at Alert, to compare them with ratios measured in eggs and body tissues.

Study area.—Studies were carried out in the vicinity of Alert (82°30′N, 62°20′W), situated on the northeast coast of Ellesmere Island, Nunavut, Canada, during the summers of 1998 (18 June–9 July), 1999 (27 May–16 September), and 2000 (15 June–21 July). The local terrain is barren, consisting of frost-shattered rock, gravel, and bare clay, with low vegetation cover (generally <15%; MacDonald 1953). The summer climate is cold, with a mean July temperature of 3.4°C (Environment Canada 1998). In spring, snow cover is variable though usually extensive through the end of May; temperatures generally reach the freezing point after the first week of June; snow cover declines rapidly thereafter.

Collection of albumen and yolk samples from eggs.—Nests of Ruddy Turnstones and Sanderlings were located by searching suitable habitat for territorial birds and following individuals back to their nests. The single Red Knot nest found in 1999 was located by tracking a radiotagged bird. Eggs were sampled for yolk and albumen by making a small hole in the side of the egg using a sterile needle, inserting a hypodermic needle attached to infusion tubing to a suitable depth in the egg, and gently withdrawing ~0.1 mL of

yolk or albumen (Schwabl 1993). Samples were transferred to microcentrifuge tubes and kept on ice until frozen at approximately –20°C. The puncture site was sealed with Nuskin liquid bandage and allowed to dry, and the egg was returned to the nest.

In 1998, all eggs were sampled in four-egg clutches from six turnstone nests found between 20 and 29 June. Collection dates for samples in 1999 were 7 July for the Red Knot (estimated clutch completion 4 July), and 6 July for Sanderling (clutch completion date unknown). No turnstone nests were found in 1999, apparently because of very high predation pressure from Arctic foxes (*Alopex lagopus*). In 2000, a total of 36 eggs (up to two eggs per four-egg clutch) were randomly selected for sampling from 19 Ruddy Turnstone nests found between 16 and 26 June; day of incubation of each egg was estimated from measurements and mass of the egg by using a regression equation derived from eggs of known incubation stage obtained at Alert during the period 1974–1994 (Fig. 1). That enabled, in turn, estimation of the date on which eggs were laid. Three Sanderling nests were sampled (up to two eggs per four-egg clutch) in 2000; nests were found during the period 16–22 June, and dates of laying of first eggs in two of the clutches were 15 and 18 June.

Collection of blood samples from shorebirds.—Birds were captured from their arrival in early June throughout the summer of 1999 to assess isotope ratios of blood components. Immediately following capture, blood was collected from the brachial vein in heparinized micro-hematocrit capillary tubes and the samples returned to the laboratory at Alert and centrifuged at

FIG. 1. Relationship between the density index ($m/l \times b^2$, where m = mass in grams, l = length in millimeters, and b = breadth in millimeters) and day of incubation (i.e. day since start of incubation) for 28 Ruddy Turnstone eggs of known age measured at Alert during the period 1974–1994. The regression equation can be used to estimate the stage of incubation of eggs of unknown age, from which a predicted laying date can be calculated.

13,200 × g for 15 min. Red blood cells and plasma were separated and stored frozen at approximately –20°C. Birds were individually color-banded, weighed, examined for molt and abdominal profile (Wiersma and Piersma 1995), and measured before release.

Food resources.—Samples of both inshore marine and terrestrial invertebrates potentially used as food items by shorebirds were collected for stable-isotope analysis. Samples of the bivalves *Macoma balthica* and *Cerastoderma edule*, both of which are major food items taken by knots on their European wintering grounds, were obtained from the Wadden Sea in The Netherlands. Amphipods were collected from tidal pools along the gravel shoreline of Cape Belknap at Alert. Terrestrial invertebrates were selected at random from specimens collected in pitfall traps in various habitats in the Alert area and preserved in 70% ethanol, and samples of the following major groups were analyzed for stable isotopes: spiders (Araneae), chironomids (Chironomidae), fungus gnats (Mycetophilidae), crane flies (Tipulidae), and springtails (Collembola). Preservation and storage of samples in ethanol does not affect subsequent stable-isotope analyses (Hobson et al. 1997b). Reported isotope ratios were based on duplicate analyses of pooled samples of each food item or group.

Stable-isotope analyses.—All samples were thawed or removed from ethanol at the laboratory, rinsed in distilled water, and dried in a drying oven (60°C) or a freeze drier. Lipids were removed from invertebrates and from yolk and albumen samples using a 2:1 chloroform:methanol rinse and then dried under a fumehood. All samples were powdered using a dental amalgam mill prior to loading for stable-isotope analysis.

Mass spectrometric analyses for carbon and nitrogen isotope assays were performed on 1-mg samples of dried tissues and lipids at the stable-isotope facility of the Department of Soil Science, University of Saskatchewan, using a continuous-flow Europa 20:20 isotope-ratio mass spectrometer (CFIRMS) interfaced with a Robo Prep elemental analyzer. On the basis of several hundred replicate measurements of a laboratory albumen standard, measurement error was estimated to be ±0.1‰ and ±0.3‰ for stable carbon and nitrogen isotope ratios, respectively. All samples were weighed into tin cups and combusted at 1,800°C in an elemental analyzer prior to isotopic measurement. All isotope values are expressed in delta (δ) notation, where $\delta X = [(R_{sample}/R_{standard}) - 1] \times 1{,}000$ where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Standards used for carbon and nitrogen were PeeDee Belemnite (PDB) and atmospheric air, respectively (see Hobson 1995).

Statistical analyses.—Statistical analyses were carried out using STATISTICA software (StatSoft 2001). Negative exponential curves were fitted to data on isotope ratios in blood samples following the birds' arrival at Alert, using nonlinear–exponential growth
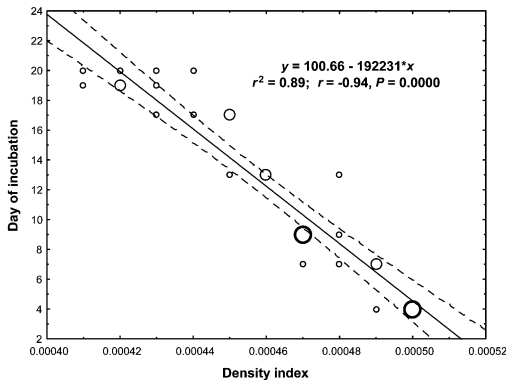
Body Stores in Arctic Shorebirds

procedures with Quasi-Newton or Simplex methods or a combination (StatSoft 2001). Differences between groups of samples were evaluated using ANOVA and *post-hoc* Tukey tests.

<div align="center">Results</div>

Stable-isotope ratios in food resources.—The $\delta^{13}C$ signatures in inshore marine invertebrates from European wintering areas and from Alert were clearly different from those in terrestrial invertebrates collected from tundra habitats at Alert (Table 1; ANOVA, $F = 257.8$, df = 1 and 12, $P = 0.0000$); differences within each group were not significant (ANOVA, marine $F = 0.53$, df = 2 and 2, $P = 0.53$; terrestrial $F = 0.56$, df = 4 and 4, $P = 0.71$). The $\delta^{13}C$ values for inshore marine invertebrates were similar to those reported from other temperate and arctic localities (Hobson and Welch 1992, Hobson et al. 2002). Values for $\delta^{15}N$ were more variable within each group: there was significant variation within the marine group though not within the terrestrial group (ANOVA, marine $F = 341.7$, df = 2 and 2, $P = 0.003$; terrestrial $F = 3.40$, df = 4 and 4, $P = 0.13$). That resulted in there being no significant difference in $\delta^{15}N$ values between inshore marine and terrestrial foods (ANOVA, $F = 1.75$, df = 1 and 12, $P = 0.21$), though values ranged lower in the terrestrial species.

Table 1. Stable-isotope values (mean ± SD [n]) for marine and terrestrial food resources available to shorebirds on wintering and breeding grounds, respectively. All material collected at Alert, Ellesmere Island, Canada, except for *Macoma balthica* and *Cerastoderma edule*, which were collected in the Wadden Sea, The Netherlands. Analyses were carried out on pooled samples of organisms.

Organism[a]	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)
Marine		
Amphipods	9.4 ± 0.1 (2)	−16.0 ± 1.7 (2)
Cockle	11.6 (1)	−17.5 (1)
Bivalve	13.4 ± 0.2 (2)	−17.3 ± 0.2 (2)
All marine groups	**11.4 ± 2.0 (5)**	**−16.8 ± 1.1 (5)**
Terrestrial		
Spiders	12.2 ± 5.1 (2)	−26.1 ± 0.07 (2)
Midges	6.7 ± 0.2 (2)	−26.9 ± 0.2 (2)
Fungus gnats	10.1 ± 0.4 (2)	−26.2 ± 0.2 (2)
Crane flies	13.7 (1)	−25.5 (1)
Springtails	4.1 ± 2.2 (2)	−25.4 ± 2.2 (2)
All terrestrial groups	**8.9 ± 4.1 (9)**	**−26.1 ± 1.0 (9)**

[a]Scientific names: cockle *Cerastoderma edule*, bivalve *Macoma balthica*, spiders Araneae, midges Chironomidae, fungus gnats Mycetophilidae, crane flies Tipulidae, springtails Collembola.

Stable-isotope ratios in egg components (carbon-13).—The $\delta^{13}C$ values of lipid-extracted yolk and albumen were similar in eggs of the three shorebird species (Table 2; ANOVA, $F = 0.180$, df = 4 and 127, $P = 0.95$). However, as expected (e.g. DeNiro and Epstein 1978, Tieszen et al. 1983, Hobson 1995), the lipids themselves in Ruddy Turnstone egg yolk and albumen had significantly lower $\delta^{13}C$ values than the lipid-extracted yolk and albumen, respectively, either from Ruddy Turnstones themselves or from Sanderlings ($P = 0.00002$ in all cases, *post-hoc* Tukey test), or from Red Knot egg yolk ($P = 0.02$ vs. yolk and $P = 0.06$ vs. albumen, *post-hoc* Tukey test).

In general, mean $\delta^{13}C$ values for all egg components of turnstones, knots, and Sanderlings were consistent with derivation from terrestrial invertebrates from the local C-3 tundra biome (Table 1) but not from inshore marine invertebrates, after application of isotopic fractionation factors determined by Hobson (1995) between egg components and diet (*post-hoc* comparisons, Tukey test: no significant differences compared to terrestrial invertebrates, $P \gg 0.05$ [range 0.84 to 1.00] in all cases; all differences significant compared to marine invertebrates, $P \ll 0.05$ [range 0.02 to 0.00003] in all cases).

Stable-isotope ratios in egg components (Nitrogen-15).—Stable-nitrogen isotope ratios were obtained for proteinaceous, lipid-extracted components of egg yolk and albumen, but could not readily be obtained from lipid components themselves, because the latter contain primarily carbon and hydrogen. Although $\delta^{15}N$ values of turnstone yolk and albumen differed from one another (Tukey *post-hoc* test, $P = 0.007$), there were no other significant differences in $\delta^{15}N$ values for egg components among knots, turnstones, and Sanderlings (Table 2; Tukey *post-hoc* tests, P range from 0.47 to 1.00). Theoretical mean $\delta^{15}N$ dietary values that would result in our observed albumen and lipid-free yolk $\delta^{15}N$ values can be estimated using previously derived diet–egg isotopic fractionation factors (Hobson 1995): those dietary values ranged from 1.2‰ to 3.0‰ and were generally less enriched in ^{15}N than both inshore marine and terrestrial foods measured in our study. In fact, dietary values differed from those of most of the marine and terrestrial invertebrates measured (Tukey *post-hoc* test, significantly different, P range from 0.01 to 0.00002), with the exception

Table 2. Stable-isotope analysis (mean ± SD [n]) of (A) egg components and (B) red blood cells of shorebirds and reference species, and inferences of corresponding diet isotope values based on Hobson (1995) and Evans Ogden et al. (2004).

		$\delta^{15}N$ (‰)	Predicted mean dietary $\delta^{15}N$ (‰) value[a]	$\delta^{13}C$ (‰)	Predicted mean dietary $\delta^{13}C$ (‰) value[a]
(A) Egg components					
Species	*Component*				
Ruddy Turnstone	yolk	6.4 ± 1.0 (59)	3.0	−25.3 ± 1.7 (59)	−25.3
	albumen	5.4 ± 1.6 (56)	2.0	−25.4 ± 1.3 (56)	−26.3
	yolk lipid	NA	NA	−30.4 ± 1.9 (20)	−27.0
	albumen lipid	NA	NA	−30.8 ± 1.5 (19)	−27.4
Red Knot	yolk	5.1 ± 0.2 (2)	1.7	−25.6 ± 0.08 (2)	−25.6
Sanderling	yolk	6.1 ± 0.8 (8)	2.7	−25.4 ± 0.2 (8)	−25.4
	albumen	4.6 ± 0.7 (7)	1.2	−25.7 ± 0.3 (7)	−26.6
(B) Red blood cells					
Species	*Date of collection*				
Red Knot	1–10 June	11.5 ± 1.1 (18)	8.5	−16.6 ± 1.4 (18)	−15.1
	11–20 June	9.1 ± 1.7 (8)	6.1	−19.0 ± 1.9 (8)	−17.5
	21–30 June	7.0 ± 0.9 (6)	4.0	−21.6 ± 1.3 (6)	−20.1
	July–August	5.1 ± 0.5 (7)	2.1	−24.7 ± 0.6 (7)	−23.2
Ruddy Turnstone	1–10 June	10.4 ± 1.7 (6)	7.4	−18.1 ± 2.3 (6)	−16.6
	21–30 June	7.6 ± 0.06 (2)	4.6	−20.9 ± 0.5 (2)	−19.4
	July–August	4.4 ± 1.7 (32)	1.4	−24.1 ± 1.3 (32)	−22.6

[a] Represents the predicted lipid-free values of diet items that would produce the observed values in egg or blood components after appropriate fractionation between diet and tissues; see text for details. SD and n for predicted values are the same as those for tissues.

of Collembola (not significantly different from all components, P range 0.68 to 1.00) and chironomids (not significantly different for yolk components from turnstones [P = 0.23] and Sanderlings [P = 0.16]), both of which may be important in shorebird diets during the early part of the season (R. I. G. Morrison pers. obs.).

Seasonal variation in isotope values of eggs.—Plots of mean stable-isotope values of egg components in clutches of Ruddy Turnstones indicated that $\delta^{13}C$ values were highest in the earliest-laid clutches and fell with increasing laying date (Fig. 2). Correlations between $\delta^{13}C$ values and laying date were significant in both albumen and yolk (for statistics see Fig. 2), and a similar phenomenon was evident in lipids extracted from albumen and yolk, though there the correlation was significant only for yolk components. No significant correlations were found between mean $\delta^{15}N$ values and laying date.

Turnover of stable isotopes in blood.—Red Knots and Ruddy Turnstones arrived at Alert with blood isotope values closely conforming to those that would be expected from the inshore marine diet used by birds during the previous winter and northward migration periods. Thus, $\delta^{13}C$ values in red blood cells of the earliest-arriving

(earliest caught) Red Knots (1–4 June 1999, −15.8 ± 1.2‰ SD, n = 9) or Ruddy Turnstones (1–3 June 1999, −16.6 ± 1.7‰ SD, n = 3) were very similar to the mean value expected from a diet of the three inshore marine food resources measured after applying the expected diet–tissue isotopic fractionation factor of about +1.5‰ (Evans Ogden et al. 2004; i.e. −16.8 + 1.5 = −15.3 ± 1.1‰ SD, n = 5; ANOVA, F = 1.05, df = 2 and 14, P = 0.37). Values for inshore marine foods measured here are similar to those expected from diets of benthic marine invertebrates from other locations (Hobson and Welch 1992).

Following arrival, $\delta^{13}C$ values in red blood cells of both Red Knots and Ruddy Turnstones fell throughout June and into July–August (see Fig. 3 and Table 2). We anticipated a negative exponential decay model for turnover of both stable isotopes following the diet switch from inshore marine to terrestrial C-3 foods (i.e. following spring arrival at Alert) and so fitted our data to equations of the form $\delta X = \delta X_0 + ae^{bt}$, where X is the isotope in question, δX_0 the final asymptotic value, a the magnitude of the diet switch, b the turnover rate, and t the time. The negative exponential model fit the data well for both isotopes (being significant in all
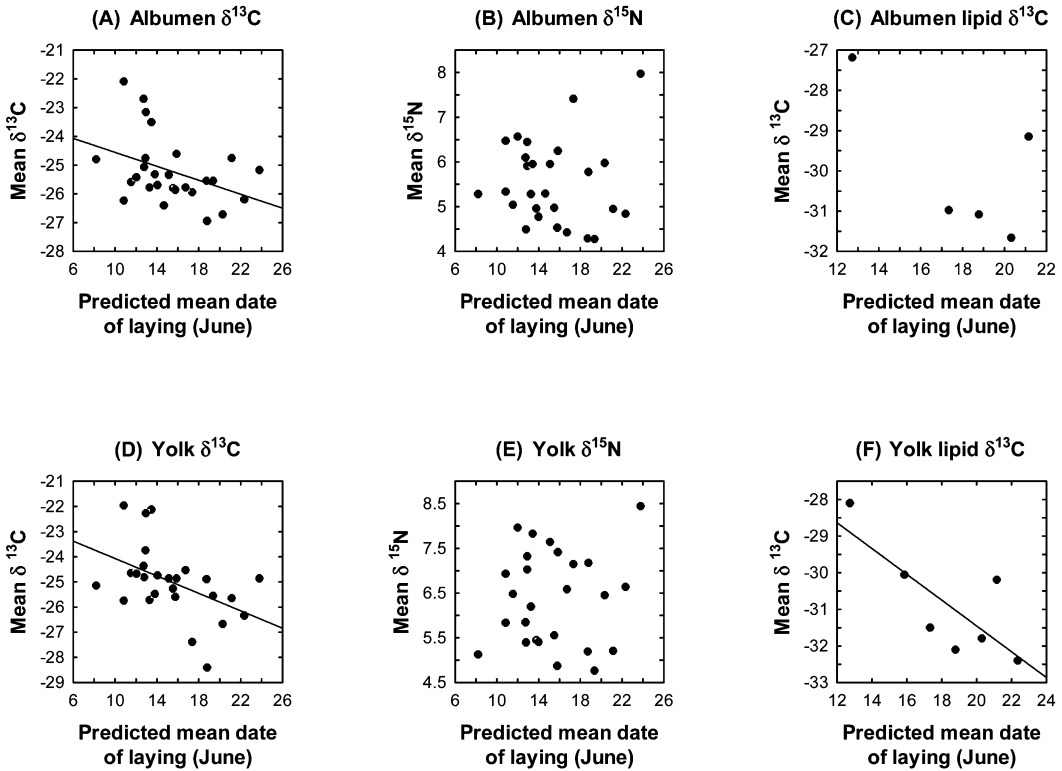
Fig. 2. Changes in mean isotope values of egg components in clutches of Ruddy Turnstones at Alert with mean laying date. Data from 1998 and 2000. Results of regression analyses are as follows: (A) Albumen δ^{13}C: $y = -23.34 - (0.12 \times x)$; $r^2 = 0.16$; $r = -0.40$, $P = 0.04$; (B) Albumen δ^{15}N: $y = 5.35 + (0.01 \times x)$; $r^2 = 0.0026$; $r = 0.0509$, $P = 0.80$; (C) Albumen lipid δ^{13}C: $y = -23.35 - (0.37 \times x)$; $r^2 = 0.44$; $r = -0.66$, $P = 0.22$; (D) Yolk δ^{13}C: $y = -22.34 - (0.17 \times x)$; $r^2 = 0.22$; $r = -0.47$, $P = 0.02$; (E) Yolk δ^{15}N: $y = 5.98 + (0.03 \times x)$; $r^2 = 0.0095$; $r = 0.0976$, $P = 0.64$; (F) Yolk lipid δ^{13}C: $y = -24.40 - (0.35 \times x)$; $r^2 = 0.59$; $r = -0.77$, $P = 0.04$.

cases except δ^{15}N of Ruddy Turnstone red blood cells, where $P = 0.07$; for statistics, see Fig. 3). Half-life estimates for decay curves for the two isotopes ranged from 11 to 21 days (see Fig. 3). The asymptotic values reached by July–August for δ^{13}C (–27.3‰ for knots and –24.3‰ for turnstones) corresponded well to the range expected from a diet of terrestrial invertebrates collected at Alert (i.e. +1.5‰ fractionation applied to values for terrestrial invertebrates in Table 1: range –23.9‰ to –25.4‰, overall mean –24.6 ± 1.0‰ SD).

A decrease similar to that observed for δ^{13}C values was found in mean δ^{15}N values of red blood cells during the postarrival period, with δ^{15}N values for Red Knots falling from 11.5 ± 1.1‰ SD to 5.1 ± 0.5‰ SD between 1–10 June and July–August, and from 10.4 ± 1.7‰ SD to

4.4 ± 1.7‰ SD for Ruddy Turnstones over the same period (Table 2). Applying a δ^{15}N diet–tissue fractionation factor of 3.0‰ for red blood cells (derived by Evans Ogden et al. 2004 for Dunlin [*Calidris alpina pacifica*]) to our data predicts a marine-diet δ^{15}N value for arriving knots and turnstones of 8.5‰ and 7.4‰, respectively. Stable-nitrogen isotope values for marine and terrestrial food resources were more variable than those for δ^{13}C values, ranging between 9.4‰ and 13.4‰ (mean 11.5 ± 2.0‰ SD) for marine, and between 4.1‰ and 13.7‰ (mean 8.9 ± 4.1‰ SD) for terrestrial invertebrates (Table 1). The late-summer asymptotic δ^{15}N values in red blood cells of knots (3.1‰) and turnstones (2.9‰) (Fig. 2) were generally lower than those for the terrestrial or inshore marine invertebrates measured here.
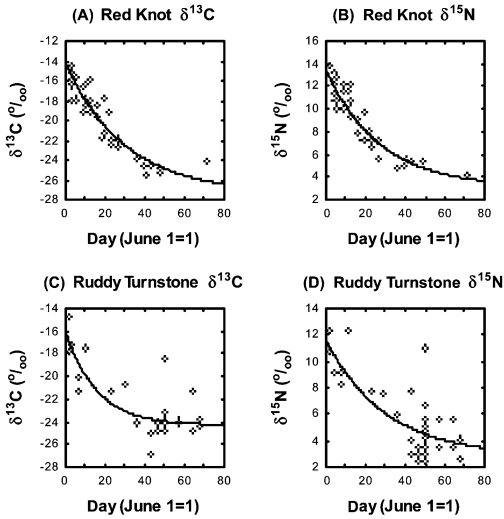
Fig. 3. Change in δ^{15}N and δ^{13}C values of Red Knot and Ruddy Turnstone red blood cells following arrival at Alert, Nunavut, Canada, and results of an exponential decay curve fit for each species and isotope. All data from 1999; Day 1 = 1 June. Negative exponential regression equations are as follows: (A) Red Knot: δ^{13}C = −27.303 + exp(2.573 + [−0.034 × day]); r^2 = 0.87, P = 0.0002; half life = 20.6 days; (B) Red Knot: δ^{15}N = 3.136 + exp(2.335 + [−0.037 × day]); r^2 = 0.88, P = 0.000; half life = 18.6 days; (C) Ruddy Turnstone: δ^{13}C = −24.305 + exp(2.111 + [−0.063 × day]); r^2 = 0.69, P = 0.000, half life = 11.0 days; (D) Ruddy Turnstone: δ^{15}N = 2.869 + exp(2.170 + [−0.034 × day]); r^2 = 0.62, P = 0.07, half life = 20.6 days.

Discussion

Dynamics of stable-isotope composition of red blood cells of shorebirds after arrival at Alert.—We found that measurement of δ^{13}C values in blood and food resources of shorebirds provided a useful means of tracking the fate of endogenous stores as birds moved from inshore marine to terrestrial habitats. Thus, δ^{13}C values in red blood cells of knots and turnstones caught immediately after arrival at Alert showed stable-isotope signatures that were completely compatible with derivation from their marine prey and clearly distinguishable from those of potential local terrestrial C-3 food items. By implication, other body components and nutrient stores of the birds, including fat and protein accumulated during the winter and on migration, would also be expected to have inshore marine signatures. After arrival and the switch to a terrestrial diet, δ^{13}C values in the blood fell

exponentially, reaching asymptotic values in July and August that were completely compatible with values expected from their terrestrial prey. Although turnover rates differ in different tissues, our results indicate that blood δ^{13}C values equilibrated with the new terrestrial diet by early July.

The δ^{15}N values also generally reflected the change from a more ^{15}N-enriched marine to a more depleted terrestrial diet, but in a less clearcut fashion. The δ^{15}N values in blood of arriving birds was compatible with derivation from inshore marine sources, though the high variability in δ^{15}N values of potential marine and terrestrial food items did not allow a clear distinction of dietary origin with this isotope. The δ^{15}N values after arrival again fell in a negative exponential fashion, and the low asymptotic values reached by midsummer suggest that a number of the terrestrial invertebrates we measured with high δ^{15}N values—especially crane flies, fungus gnats, and spiders—are unlikely to feature in shorebird diets. Those insects with the lowest δ^{15}N values—midges (chironomids) and Collembola—are thought to be prominent in the diets of knots and turnstones on Ellesmere Island (Nettleship 1973, 1974; R. I. G. Morrison pers. obs.), and that would be consistent with our isotopic equilibration results.

Estimated half-lives of 19–21 days for δ^{15}N values in blood of knots and turnstones and δ^{13}C values in blood of Red Knots were similar to values presented by Haramis et al. (2001) for wintering Canvasback (*Aythya valisinaria*) and by Hobson and Clark (1992) for captive Japanese Quail (*Coturnix japonica*), whereas the value of 11 days for δ^{13}C in turnstones more closely matches an estimate of ~10 days for both isotopes in whole blood in captive Dunlin (Evans Ogden et al. 2004). Reasons for those differences are not presently understood and could be a reflection of metabolic rates, diet, or other factors. For example, in addition to invertebrates, the diet of turnstones and knots during the early postarrival period often includes some vegetation, especially in Red Knots (Nettleship 1973, 1974). Pearson et al. (2003) recently showed that elemental turnover rate can vary according to the nitrogen composition of diets, with high-N foods (e.g. invertebrates) having faster turnover than lower-N foods (e.g. fruits and plant material). Our discovery of relatively low turnover in knots as compared with

turnstones is consistent with those findings if plant material makes up a substantial proportion of the knot diets.

In summary, shorebirds arriving at Alert had enriched $\delta^{13}C$ and $\delta^{15}N$ blood values that reflected their previous diet of inshore marine invertebrates and that gradually became depleted as birds came into equilibrium with the local, predominantly terrestrial C-3 foodweb, involving a diet that likely consisted of lower-trophic-level invertebrates and some early vegetation—providing a convenient, natural tracing experiment that allowed us to investigate endogenous inputs into eggs.

Origin of nutrients used in egg formation.—Hobson (1995) provided a model relating the stable-isotope signatures in bird diets to their egg components for both herbivorous and carnivorous birds that represent income strategists. That study provided fractionation values of isotopes between food and eggs that allow the prediction of dietary isotope values from those in eggs, or vice versa. Major departures between predicted values and actual measured values can provide evidence for incorporation of stored endogenous nutrients where they may differ from local dietary endpoints (Hobson et al. 1997a, 2000).

That approach, using the carnivore model and relying only on mean $\delta^{13}C$ values of egg components, suggests that marine-derived endogenous nutrients made up a relatively small contribution to eggs. Considering the close correspondence of egg components and terrestrial food resources in the shorebird species, and the compatibility between those values in terms of the generally small and positive fractionation factors observed for $\delta^{13}C$ values (Hobson 1995), it would appear that terrestrial food items were the main proteinaceous nutrient source for egg components in our study and that, in those years, body stores imported from wintering or migration areas did not make substantial contributions. However, eggs in the earliest-laid clutches of Ruddy Turnstones were comparatively enriched in ^{13}C in albumen, yolk, and lipids, which indicates that marine-derived endogenous components, including lipids, may be used in formation of the earliest-laid eggs. We might expect stored lipids to be influenced by nutrient storage dynamics, because follicular development requires 5–6 days prior to laying and lipid reserves are labile (Roudybush et al. 1979).

Our ability to distinguish between marine and terrestrial reserve inputs to shorebird eggs was less clear using $\delta^{15}N$ analyses because of large variability in $\delta^{15}N$ signatures of potential prey items and because $\delta^{15}N$ values are determined also by trophic level within marine and terrestrial biomes. Nonetheless, the relatively low $\delta^{15}N$ values of egg proteinaceous components supports use of terrestrially derived protein nutrients (from lower-trophic-level organisms) for egg production in shorebirds.

Our results, therefore, suggest that although local food resources may be used to produce much of the protein and lipid components of eggs, endogenous stores of both protein and lipid may be used in formation of the earliest eggs. That finding underlines the need to consider macromolecular routing in questions of isotopic tracing of nutrients to eggs (Hobson 1995). The present work generally supports and extends the conclusion of Klaassen et al. (2001) that High Arctic shorebirds show income rather than capital breeding strategies, though it raises the likelihood that stores not used in the immediate postarrival period may find their way into eggs laid early in the season. Further study is needed to assess interyear variation in contribution of endogenous stores to eggs.

Other considerations support the conclusion that shorebirds breeding in the Arctic are unlikely to depend heavily on nutrient stores for egg formation. At Alert, most of the stores carried by early arrivals are lost before egg-laying begins (Morrison and Davidson 1990, R. I. G. Morrison et al. unpubl. data). For instance, mean masses of Red Knots fell some 15–20 g, from ~150 to ~135 g, during the first week after arrival (Morrison and Davidson 1990); with a clutch of four eggs weighing approximately 72 g (4×18 g), it is clear that knots do not have adequate stores for substantial direct contribution to egg formation. The situation is even clearer in small species of shorebirds, such as the Semipalmated Sandpiper (*Calidris pusilla*), where the female lays a clutch weighing as much as herself over a period of 4–5 days (Gratto-Trevor 1992). Similar considerations apply to calcium stores, which are built up by female knots in Iceland, but not to an extent that would enable production of a four-egg clutch (Piersma et al. 1996).

What are the purposes of stores, if they are not used for egg formation? Knots and turnstones arrive at Alert in late May through early June,

when the weather is cold and unpredictable and food resources scarce. Nutrient stores may potentially provide a source of energy for survival in years when conditions are difficult. They are also likely to reflect strategic storage of a nutritional requirement that may be in short supply (Piersma and Jukema 2002). Another important possibility that warrants further investigation is that stores may contribute nutrients required for physiological changes occurring after arrival and in preparation for breeding. Red Knots undergo remarkable physiological changes during their stopover in Iceland, involving increases in "exercise organs" and fuel used in long-distance flight and decreases in muscles and organs that are less needed during their flight to the breeding grounds (Piersma et al. 1999). That physiological reorganization leaves them exquisitely adapted for migration, but not physiologically prepared for breeding. After arrival at Alert, the birds undergo a further series of physiological changes in preparation for breeding, including increases in masses of liver, gonads, and intestines (R. I. G. Morrison et al. unpubl. data). A potentially important additional function of stores brought to the breeding grounds may therefore be to enable the physiological changes required for breeding to take place successfully at a time when food resources are scarce. Stores brought to the breeding grounds thus offer a number of potential benefits that appear to outweigh the fitness costs of transportation (Witter and Cuthill 1993).

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