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TRANSFORMATIONS AT HIGH LATITUDES: WHY DO RED KNOTS BRING BODY STORES TO THE BREEDING GROUNDS?

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Abstract. We examined changes in body composition of Red Knots (*Calidris canutus islandica*) following arrival on their High Arctic breeding grounds at Alert, Ellesmere Island, Canada. Knots arrived in late May and early June with large fat and muscle stores. In the next two weeks, fat and protein stores (pectoral muscles) declined, while increases occurred in gizzard, proventriculus, gut length, heart, liver, and possibly gonads. Most stores were used before egg laying occurred and were therefore not available for egg formation. Early development of ova in some females suggests that body stores may be incorporated into the earliest eggs. While stores may be used for survival when conditions are difficult after arrival, their rapid loss and the concomitant increase in other organs suggests that a major function may be to facilitate a transformation from a physiological state suitable for mi-

gration to one suitable, and possibly required, for successful breeding.

Key words: body stores, *Calidris canutus*, High Arctic, migration, phenotypic flexibility, Red Knot, shorebirds.

Transformaciones a Altas Latitudes: ¿Por qué *Calidris canutus islandica* Lleva Reservas Corporales a los Sitios de Nidificación?

Resumen. Examinamos los cambios en la condición corporal de individuos de *Calidris canutus islandica* luego de que éstos llegaron a sus territorios reproductivos a altas latitudes en el Ártico en Alert, isla Ellesmere, Canadá. Los individuos de *C. c. islandica* llegaron a fines de mayo y comienzos de junio con grandes reservas de grasa y músculo. Durante las dos semanas siguientes, las reservas de grasa y proteína (músculos pectorales) disminuyeron, mientras que la molleja, los proventriculos, el largo del intestino, el hígado y posiblemente las gónadas aumentaron de tamaño. La mayoría de las reservas fueron usadas antes

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del período de puesta de huevos, por lo que éstas no estuvieron disponibles para la formación de los huevos. En algunas hembras, el desarrollo temprano de los óvulos sugiere que las reservas corporales pueden ser incorporadas en los primeros huevos. Si bien las reservas pueden ser usadas para sobrevivir en el momento de la llegada cuando las condiciones son difíciles, su rápida pérdida y el aumento concomitante en otros órganos sugiere que una de las funciones principales de las reservas podría ser facilitar la transformación de un estado fisiológico apropiado para la migración a un estado apropiado y posiblemente requerido para la reproducción exitosa.

Shorebird species that migrate between High Arctic breeding grounds and more southerly temperate wintering areas undergo remarkable morphological changes during the course of their travels (Piersma 1998). These journeys may involve several long-distance flights, each of which involves cycles of fuel deposition and expenditure. Whereas it was once thought that all of the mass increase in birds before migration consisted of fat (Odum et al. 1964), more recent work has shown that changes in body composition are much more subtle and complicated, and may involve a suite of changes in the relative sizes of various organs and tissues which are highly adaptive in preparing the birds for the impending flight (Piersma 1990, Piersma and Gill 1998, Piersma et al. 1999). For shorebirds, typical morphological changes involve reduction in the size of "nutritional organs," such as the stomach and intestines, and increases in the "exercise organs," such as the pectoral muscles and heart, that power flight (Piersma and Gill 1998, Piersma et al. 1999). Calcium also appears to be accumulated by females (only) during the final stopover on northward migration (Piersma et al. 1996). During the flight, substantial reductions may occur in lean tissue mass in various organs, in addition to the loss of fat stores (Battley et al. 2000).

Red Knots (*Calidris canutus*) breeding in the High Arctic regions of the northeastern Canadian High Arctic and of Greenland belong to the race *islandica*, and migrate to European wintering quarters (Salomonsen 1951, Godfrey 1953, 1992, Morrison 1984, Davidson and Wilson 1992). In the spring, most pass northwards through Iceland where they undergo the morphological changes described above during a three-week stopover (Morrison and Wilson 1992, Wilson and Morrison 1992, Piersma et al. 1999). Knots departing Iceland are thus highly adapted for flight, but on arrival in the High Arctic are unlikely to be suitably adapted for breeding, especially considering the organ reductions that take place during such flights (Battley et al. 2000). Red Knots and Ruddy Turnstones (*Arenaria interpres*) arrive at Alert with substantial stores of fat and protein remaining (Morrison and Davidson 1990). These stores could serve several purposes, including: (1) providing energy stores for survival during severe weather or food shortages in the postarrival period, and (2) providing the nutritional resources needed for successful reproduction, including physical changes in the birds themselves and egg laying. For shorebirds at Alert, studies using stable isotopes have shown that body stores are not generally used directly in egg formation,

except possibly in the earliest-laid eggs (Morrison and Hobson 2004). The same appears to hold for shorebirds in other parts of the Canadian Arctic (Klaassen et al. 2001) further suggesting that body stores are used for survival or for facilitating morphological changes before breeding. In this paper we examined morphological changes in Red Knots following arrival at Alert to address these questions.

METHODS

STUDY AREA

We studied body condition of Red Knots at Alert (82°30'N, 62°20'W), on the northeast coast of Ellesmere Island, Nunavut, Canada. Much of the terrain consists of frost-shattered rock, gravel, and bare clay, with very low (<15%) vegetation cover; marshy ground may occur where moisture accumulates (Brugge and Calder 1953), but even here cover is rarely continuous.

The summer climate is severe, with mean temperatures for June, July, and August of -1.0°C , $+3.4^{\circ}\text{C}$, and $+1.0^{\circ}\text{C}$, respectively (1961–1990, Environment Canada 2003). These temperatures are colder than those recorded from the interior and west-central areas of Ellesmere Island owing to the cooling effects of persistent sea ice along the north and northeastern coasts (England et al. 1981). In the spring, snow cover is variable, but is usually extensive with scattered patches of open tundra, through the end of May. Temperatures generally reach the freezing point after the first week of June, and snow cover declines rapidly thereafter (Davidson and Morrison 1989).

Fieldwork involving capture and collection of specimens was carried out from 31 May to 13 June 1986, from 27 May to 10 June 1987 and from 31 May to 13 June 1990. Additional banding studies were carried out from late May to the end of June in 1999 and 2003.

SAMPLE COLLECTION

Birds were captured by rocket net on the garbage dump and near the sewage outfall stream near Alert. Data from all years were grouped into four periods: Period 1, 28–30 May; Period 2, 31 May–2 June; Period 3, 3–5 June; and Period 4, 6–9 June. Arrivals take place chiefly between late May and 3 June (MacDonald 1953, Morrison 1992), so that data from Periods 1 and 2 refer principally to newly arrived birds. Samples from Periods 3 and 4 in early June contain mostly birds in the postarrival phase, though some newly arrived individuals may also occur.

CONDITION ANALYSES

Following capture, birds were weighed (to nearest 1 g using a spring balance) and measured (wing chord: maximum flattened length to nearest mm; bill: exposed culmen to nearest 0.1 mm). Following collection in 1986, small samples of pectoralis muscle and liver were removed for ultrastructural studies (Evans et al. 1992). Sex was determined by gonadal inspection. Carcasses were sealed in plastic bags, frozen, and returned frozen to the laboratory.

After thawing, specimens were skinned, and the following parts dissected for separate analysis: pectoralis major and supracoracoideus muscles, liver, heart, giz-

zard, proventriculus, intestines, and gonads, plus the remaining parts consisting of other organs, skin, feathers, and skeleton. Intestinal length was measured to the nearest mm. All parts were weighed to the nearest 0.1 g and dried to constant mass at 60°C. The dried tissues were weighed to the nearest 0.1 g, packed in filter paper, and fat extracted in a Soxhlet apparatus, using petroleum ether (boiling point range 40–60°C). Body parts were again dried to constant mass and reweighed to obtain the lean (“fat-free”) dry mass. Fat loss was estimated as the loss of mass occurring during extraction.

STATISTICAL ANALYSES

In view of the small body size variation in the birds, mass values were not corrected for body size (van der Meer and Piersma 1994, Piersma et al. 1999). Statistical procedures were carried out using Statistica (Version 6, Statsoft, Inc. 2003). ANOVA and MANOVA were used to examine effects of sex, time period, and combinations of these on body composition measures. Independent two-tailed *t*-tests were used to compare measurements of populations. Values reported are means \pm SD.

RESULTS

ARRIVAL AND SEX RATIO

In 1986, four Red Knots were present on 31 May; numbers peaked at 43 on 3 June, and dropped steadily thereafter. In 1987, knots were first observed on 30 May; numbers increased to 35 on 5 June, and decreased rapidly thereafter. In 1990, 28 knots were present on 31 May; numbers peaked at 35 on 2 June, and decreased steadily during the next week. Many early arrivals remain and breed in the Alert area: of 95 knots captured and color-banded during late May and June in 1987–1990, 1999, and 2003, 67 (71%) were seen two days or more after banding or in subsequent years (varying from 57% in 2003 to 93% in 1999). We therefore treated the morphological patterns observed in sampled birds as reflecting those of locally breeding individuals.

Body composition analyses were carried out for 33 knots ($n = 3, 12, 8,$ and 10 in Periods 1, 2, 3, and 4, respectively). Knots collected in the immediate post-arrival period (Periods 1–2) contained more males (67%) than females, while later arrivals (Periods 3–4) contained more females (67%) than males.

MORPHOLOGICAL MEASUREMENTS

Wing length of males collected at Alert (171.8 ± 3.4 mm, $n = 16$) were similar ($t_{41} = 1.3, P = 0.20$) to those of males collected on migration in Iceland (Piersma et al. 1999; 170.4 ± 3.5 mm, $n = 27$); wing lengths of females in the two areas also did not differ significantly (Alert: 174.8 ± 5.2 mm, $n = 16$; Iceland: 173.0 ± 3.8 mm, $n = 32$; $t_{46} = 1.2, P = 0.18$). There were also no differences between the two areas in bill lengths of males (Alert: 32.1 ± 1.9 mm, $n = 16$; Iceland: 32.2 ± 1.4 mm, $n = 7$; $t_{21} = 0.3, P = 0.74$) or of females (Alert: 33.3 ± 1.8 mm, $n = 17$; Iceland: 33.8 ± 1.5 mm, $n = 32$; $t_{47} = 1.0, P = 0.30$). These results are consistent with the idea that the birds belong to the same population (Davidson and Wilson 1992).

At Alert, wing and bill measurements did not differ between years (1986 and 1987) for males and females (males: wing, $F_{1,14} = 0.2, P = 0.66$; bill, $F_{1,14} = 0.001, P = 0.97$; females: wing, $F_{1,14} = 4.6, P = 0.05$; bill, $F_{1,14} = 2.7, P = 0.12$), therefore we combined data from the two years (and the one bird from 1990). There were no significant differences between any of these measurements within each sex over the four periods following arrival (males: wing, $F_{3,12} = 0.8, P = 0.24$; bill, $F_{3,12} = 0.4, P = 0.75$; females: wing, $F_{3,12} = 1.6, P = 0.24$; bill, $F_{3,12} = 1.3, P = 0.33$), so that differences in other body components are not likely to have arisen from structural differences in size of the birds.

CHANGES IN BODY MASS

Mean mass of knots in each arrival period were very similar among years ($n = 153$ birds between 1974 and 2003, Fig. 1): mean masses of birds did not differ across years in Period 1 ($F_{1,4} = 0.5, P = 0.53$), Period 2 ($F_{4,28} = 1.0, P = 0.45$), or Period 4 ($F_{4,18} = 0.4, P = 0.81$). The significant variation across years in Period 3 ($F_{7,63} = 2.4, P = 0.03$) may have resulted from low masses in 1976 and 1999 compared to the long-term mean (Fig. 1); after removal of data from these years, there were no significant differences across years ($F_{5,53} = 0.8, P = 0.54$). Thus, we conclude that 1986, 1987, and 1990 were typical years in terms of mass changes after arrival on the breeding grounds.

After arrival, male and female Red Knots both lost overall body mass (Fig. 2). There were significant differences across sexes and periods (MANOVA: sex, $F_{1,28} = 9.9, P < 0.01$; period, $F_{3,28} = 5.0, P < 0.01$). Fat mass decreased significantly throughout the post-arrival period for both males ($F_{3,12} = 5.0, P = 0.02$) and females ($F_{3,13} = 8.1, P < 0.01$); there was no significant difference in fat content between the sexes ($F_{1,31} = 0.9, P = 0.34$). Total lean dry mass remained fairly constant over the postarrival period for both sexes, but was lower for males collected in Period 4 ($F_{3,12} = 4.7, P = 0.02$). Overall, total lean dry mass of females (42.9 ± 3.2 g, $n = 17$) was significantly greater than that of males (38.8 ± 2.8 g, $n = 16$; $F_{1,31} = 15.6, P < 0.01$).

ORGAN CHANGES

Nutritional organs. Three parts of the digestive system all showed similar patterns of increase during the post-arrival period (Fig. 3). Gizzard lean dry mass did not differ between the sexes ($F_{1,31} = 0.9, P = 0.34$), and increased significantly across periods for both sexes (males: $F_{3,25} = 5.0, P = 0.02$; females: $F_{3,13} = 8.1, P < 0.01$). Lean dry mass of the proventriculus was significantly higher in females than males ($F_{1,20} = 10.2, P < 0.01$). When the sexes were considered separately, there was no change in proventriculus lean dry mass among time periods (males: $F_{1,6} = 0.8, P = 0.55$; females: $F_{2,9} = 2.7, P = 0.12$); however, periods 1 and 3 were significantly different from each other ($F_{1,9} = 8.6, P = 0.02$) when sexes were combined, showing an increase in mass after arrival. Overall mean gut length of males was significantly shorter than that of females ($F_{1,21} = 5.74, P = 0.03$) and there was an increasing pattern over the postarrival period, similar to the other digestive organs, but which was not sta-

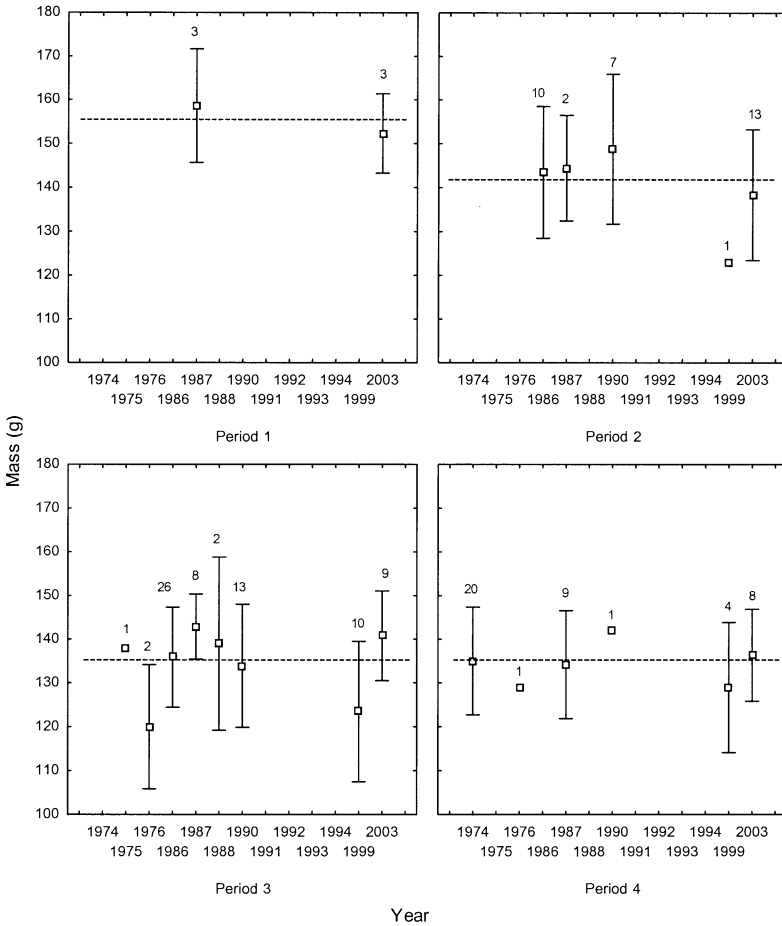


FIGURE 1. Mean masses of Red Knots captured or collected at Alert during post-arrival periods spanning 28 May–9 June 1974–2003. Period 1 = 28–30 May, Period 2 = 31 May–2 June, Period 3 = 3–5 June, and Period 4 = 6–9 June. Unfilled squares and whiskers indicate mean \pm SD and sample sizes are shown above the whiskers. Dashed lines indicate the overall means for each respective period.

tistically significant (males: $F_{3,6} = 1.3, P = 0.35$; females: $F_{2,10} = 0.3, P = 0.72$).

Mean dry liver mass of males and females did not differ ($F_{1,21} = 2.8, P = 0.11$) so we pooled data for both sexes. Both sexes showed mass increases after arrival ($F_{3,19} = 3.1, P = 0.05$), birds collected in later periods (Periods 3 and 4) having significantly heavier dry liver mass ($F_{1,21} = 5.2, P = 0.03$) than birds collected earlier in the season (Periods 1 and 2).

Exercise organs. During the post arrival period, lean dry pectoral muscle mass was significantly lower in males than females and tended to decrease across periods (Fig. 4, MANOVA: sexes: $F_{1,25} = 4.8, P = 0.04$; periods: $F_{3,25} = 2.6, P = 0.08$), with a significant decrease between periods 1 and 4 (sex: $F_{1,9} = 12.5, P < 0.01$; period: $F_{1,9} = 21.7, P < 0.01$). Pectoral muscle mass and fat mass were significantly correlated (males: $r = 0.70, P < 0.01$; females: $r = 0.53, P = 0.03$; both sexes: $r = 0.54, P < 0.01$). Heart lean dry mass of males and females did not differ ($F_{1,21} = 0.8, P =$

0.40); both increased, by factors of 2 and 2.7 times, respectively, between periods 1 and 4. Heart lean dry mass was significantly higher during Period 3 compared to the immediate postarrival period (Period 1, $F_{1,9} = 8.1, P = 0.02$). Lean dry mass of the remaining body components was, on average, lower in males than females ($F_{1,31} = 17.0, P < 0.01$) and for males there were significant changes among time periods ($F_{3,12} = 5.0, P = 0.02$).

Gonads. Male testis size showed little change during the postarrival period ($F_{3,12} = 0.3, P = 0.82$), with largest testis averaging 11.3 ± 2.5 mm ($n = 16$). Testis size ranged from 3.9–14.9 mm, with 13 of the 16 measurements falling between 10–15 mm, indicating that gonads were well developed (Nettleship 1974). Mean size of the largest ovum in females increased from 4.5 ± 1.2 mm ($n = 4$) in Period 2 to 7.6 ± 4.4 mm ($n = 6$) in Period 4, but differences across periods were not significant ($F_{3,13} = 0.9, P = 0.47$).

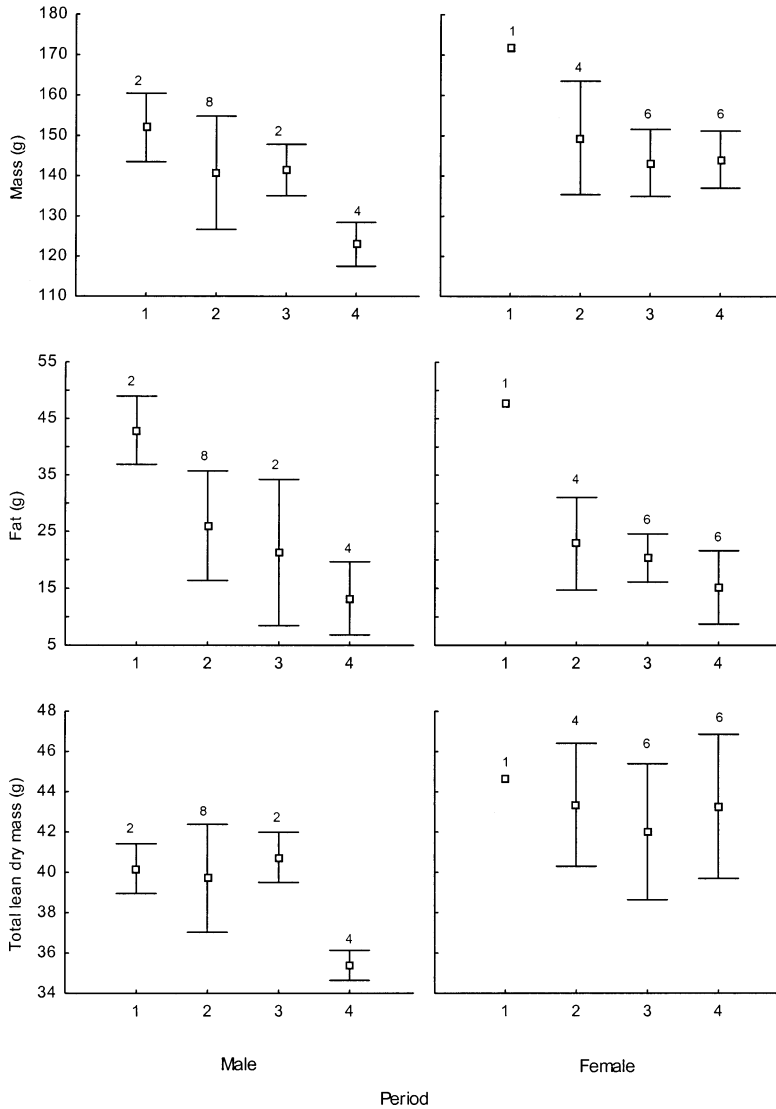


FIGURE 2. Changes in total body composition (mass, fat mass, lean dry mass) of male and female Red Knots after arrival at Alert. See Figure 1 for dates of each time period. Unfilled squares and whiskers indicate mean \pm SD and sample sizes are shown above the boxes.

DISCUSSION

We found many morphological changes in Red Knots after arrival at Alert. The earliest arrivals carried substantial stores of fat and protein; overall mass and fat content exceeded those of birds arriving on spring migration in Iceland (Piersma et al. 1999) and Norway (Davidson and Evans 1986), and of knots at the beginning and end of the wintering period in the United Kingdom (Morrison 1977). Pectoral muscle stores were similar to those on arrival in Iceland (Piersma et al. 1999), somewhat larger than those on spring migration in northern Norway, and clearly larger than

those of knots wintering in the United Kingdom (Davidson and Evans 1986, 1989).

Fat and protein stores were both lost rapidly after arrival at Alert. The consistent pattern of mass loss after arrival in different years suggests the changes are part of a pattern that occurs every year. Knots in captivity are known to have strong circannual rhythms in mass changes and basal metabolic rate similar to those of wild birds (Piersma et al. 1995, Cadée et al. 1996, Piersma 2002). Changes in pectoral muscle size are not dependent on power training, but are likely under the control of an endogenous circannual process: they tend

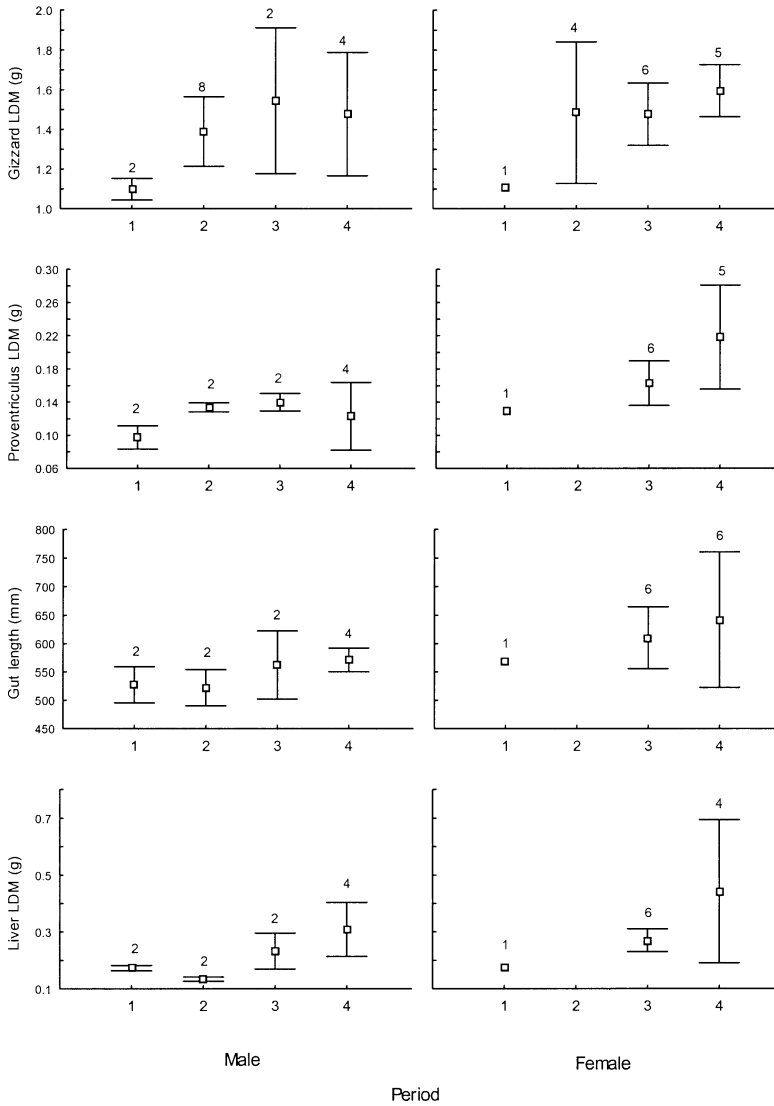


FIGURE 3. Changes in “nutritional organs” (gizzard lean dry mass [LDM], proventriculus LDM, gut length, and liver LDM) of male and female Red Knots after arrival at Alert. See Figure 1 for dates of each time period. Unfilled squares and whiskers indicate mean \pm SD and sample sizes are shown above the boxes.

to occur in parallel with changes in body mass (Dietz et al. 1999, Lindström et al. 2000).

Bringing endogenous stores to the breeding grounds presumably provides the birds with adaptive advantages that outweigh the cost of transporting such stores to the Arctic. Endogenous stores may provide nutritional resources for breeding, including egg formation: birds relying on endogenous stores have been termed “capital breeders,” while those relying on local food resources are referred to as “income breeders” (Drent and Daan 1980, Bonnet et al. 1998, Meijer and Drent 1999). Studies using stable isotopes have now shown that most Arctic-nesting shorebirds do not adopt a cap-

ital strategy but instead rely mostly on local food resources for egg formation (Klaassen et al. 2001, Morrison and Hobson 2004). At Alert, egg components reflected a local, terrestrial source of nutrients, with little indication of any contribution from body stores accumulated in marine habitats during migration or on wintering grounds (Morrison and Hobson 2004); eggs in some of the earliest-laid clutches, however, showed possible input of nutrients from marine sources. The rapid decline in fat and protein stores after arrival at Alert suggests that stored nutrients would not be available by the time most clutches are laid, even allowing for follicular development, which requires 5–6 days

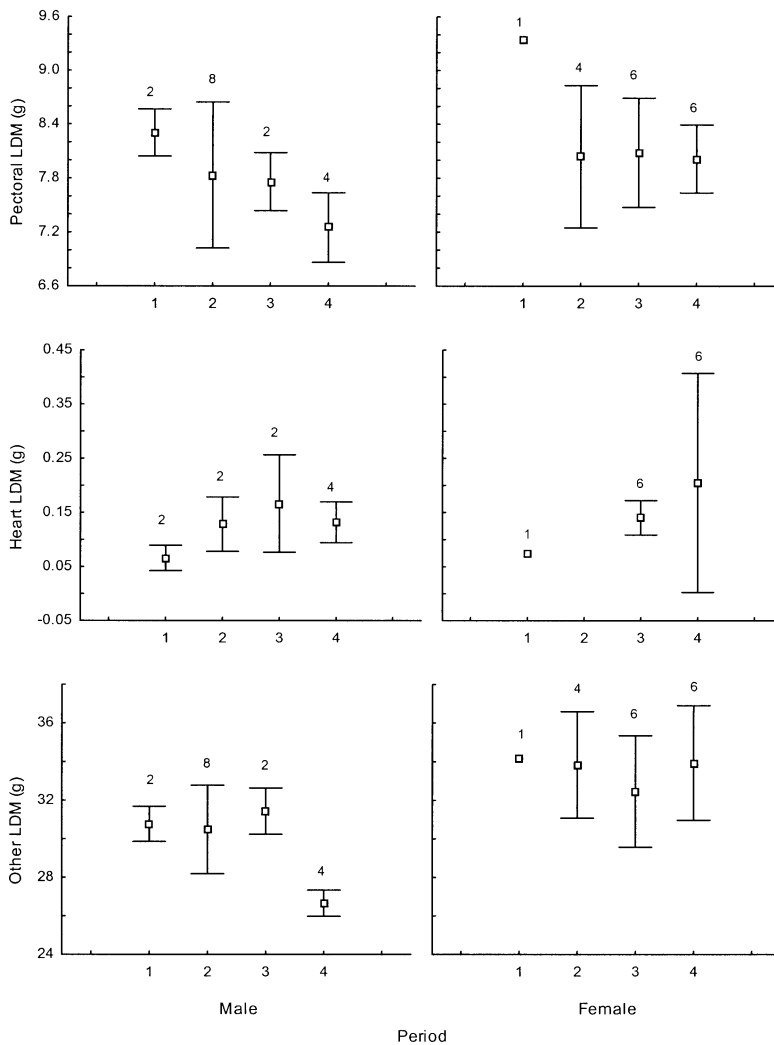


FIGURE 4. Changes in lean dry mass (LDM) of “exercise organs” (pectoral muscles, heart, and other body components) of male and female Red Knots after arrival at Alert. See Figure 1 for dates of each time period. Unfilled squares and whiskers indicate mean \pm SD and sample sizes are shown above the boxes.

before laying (Roudybush et al. 1979): the mean estimated clutch completion date for 19 Red Knot nests from 1974–1976 and 1986–1991 on northern Ellesmere Island was 20 June \pm 7 days (range 8–30 June, RIGM, unpubl. data). For clutches completed as early as 8 June, however, it is possible that some residual stores could be used for egg formation.

Fat and protein stores could provide energy or nutrients after arrival in years when the weather may be poor, or food resources are limited or unavailable. Birds leaving Iceland in better than average condition are more likely to survive severe summers (RIGM, NCD, and J. R. Wilson, unpubl. results); on the breeding grounds, starvation can occur during periods of prolonged bad weather (Morrison 1975). Knots of the *rufa* subspecies have been shown to experience reduced survival in

years when they were unable to acquire adequate stores at the final stopover site during spring migration (Baker et al. 2004). In 1999, postarrival masses of knots at Alert were lower than the long-term mean, and many shorebirds were unable to breed, or bred late, owing to extensive early season snow cover. The need to use stores for survival or supplementing lower-than-usual local food resources in that year may have contributed to delayed or failed breeding.

Another important function of body stores may be to provide the energy and nutrients needed for restoration of various tissues after losses during migration (Battley et al. 2000). Although knots leave their final staging grounds in Iceland well adapted for migration, their arrival condition at Alert is unlikely to be well adapted for successful breeding. After arrival, knots may need

to go through a "recovery" period in which they rebuild the organs that have been reduced prior to, or during, flight and which are needed for reproductive activities. Stores of fat and protein brought to the breeding grounds may enable these processes to start at a time when few feeding opportunities are available. Given the well-documented advantages that Arctic-breeding birds may acquire through nesting as early as possible, and the need to fit all phases of reproduction into the short season, the ability to arrive on the breeding grounds with stores of fat and protein may be an important aspect of shorebirds' ability to nest successfully in the High Arctic. The suite of morphological changes that takes place after arrival, including increases in heart, liver, gizzard, proventriculus, intestines, and possibly gonads, occurs at the same time as fat and protein stores are being lost. It therefore seems likely, if not inevitable, that metabolites from fat and protein stores will be used to enable these other body changes to take place. Stores acquired at staging areas remote from the nesting grounds may thus play a key role in enabling shorebirds to breed successfully in the Arctic.

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LIPID RESERVES OF MIGRANT SHOREBIRDS DURING SPRING IN PLAYAS OF THE SOUTHERN GREAT PLAINS

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Abstract. Inland-migrating shorebirds rely on wetlands as stopover sites to replenish nutrient reserves.

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Because wetlands are spatially and temporally dynamic, shorebirds may accumulate highly variable lipid reserves. We compared lipid reserves among four shorebird species (American Avocets [*Recurvirostra americana*], Long-billed Dowitchers [*Limnodromus scolopaceus*], Least Sandpipers [*Calidris minutilla*], and Western Sandpipers [*C. mauri*]) collected from playa wetlands in the southern Great Plains during spring 1993 and 1994. Because playas are ephemeral, we had