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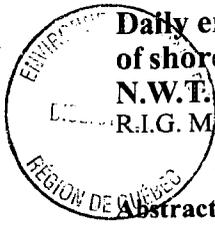
Daily energy expenditure and water turnover of shorebirds at Alert, Ellesmere Island, N.W.T.

R.I.G. Morrison,[a] N.C. Davidson,[b] and Theunis Piersma[c]

Abstract

Shorebirds have adapted to their energetically demanding lifestyles through metabolic, organ-level adjustments reflected by a high basal metabolic rate (BMR). BMRs may vary during the year, increasing, for instance, during the energy-demanding period associated with buildup of mass before migration. For birds inhabiting apparently extreme environments, such as those found in the most northern part of the Canadian High Arctic, estimates of energetic costs of existence during the breeding season are of particular interest. Few studies have been carried out to measure field metabolic rates directly. This note reports preliminary results of such studies at Alert, on the north coast of Ellesmere Island, for two long-distance migratory shorebirds, the Ruddy Turnstone *Arenaria interpres* and Red Knot *Calidris canutus*. Studies undertaken in 1990 and 1994 show that the birds have high field metabolic rates, indicating a high energy demand; these rates, however, are comparable to or less than those experienced in other parts of the Canadian Arctic, in the Siberian Arctic, or on the European wintering grounds to which the species migrate.

Introduction

Shorebirds breeding along the northern shores of Ellesmere Island inhabit some of the most northerly land in the world. Reaching and utilizing these areas involve a considerable energetic investment for the birds, as northern Ellesmere Island not only is geographically remote from the birds' wintering areas (Morrison 1975, 1977; Godfrey 1986) but also experiences one of the coldest summer climates in the Canadian Arctic (Environment Canada 1982). In addition, plants and invertebrates are scarce in comparison with more southerly locations (Danks 1981; Rannie 1986), suggesting a likely paucity of potential breeding habitats and food sources. The question of how birds are able to survive and reproduce successfully under such energetically demanding conditions is therefore of considerable interest.

Shorebirds appear to have adapted metabolically to the energetic demands of their lifestyle, in that they have higher basal metabolic rates (BMRs) in relation to body mass than initially predicted (Aschoff and Pohl 1970); these lead to an enhanced ability to metabolize energy during periods of high demand (Kersten and Piersma 1987). Little information is available, however, from Arctic breeding grounds with which to assess the birds' energetic performance at this time of the year. Compilation of time–activity budgets indicates that shorebirds' daily energy expenditures (DEEs) may reach between 3.7 and 5.5 times their predicted BMR in Alaska and at Alert (Ashkenazie and Safriel 1979; Davidson and Morrison 1992). The few empirical studies reported to date involve work on Ruddy Turnstones *Arenaria interpres*, Purple Sandpipers *Calidris maritima*, and Red Knots *Calidris canutus* in the Canadian Arctic, on Spitsbergen, and in the Siberian Arctic, respectively; in these studies, DEEs ranged from 3.5 to 4 times the predicted BMR (Pierce 1989; Drent and Piersma 1990; Piersma and Morrison 1994; Lindstrom and Piersma 1995). For turnstones breeding on Rowley Island in the Canadian Arctic, the energetic costs of activity (above maintenance) averaged 1.8 W, leaving about 2.7 W for maintenance costs (basal metabolism and thermoregulation), if a maximum sustainable level of energy expenditure, or metabolic ceiling, of about 4.5 W is assumed (Drent and Daan 1980). This level of maintenance costs was exceeded on about 15% of days over the 33-year period 1958–1990 and on over 30% of days in seven of those years, suggesting that conditions were indeed energetically costly on a regular basis for turnstones in the Foxe Basin (Piersma and Morrison 1994). Similar levels of maintenance costs were found for Red Knots during the early part of the breeding season at Alert, as determined by heated taxidermic mounts (Piersma et al. 1991).

This Progress Note presents the results of the first empirical measurements of DEEs of shorebirds during the breeding season at Alert, using the doubly labelled water (DLW) technique. Measurements of water turnover rates are also presented.

Study area and methods

Studies were carried out in the vicinity of Alert (82°30′N, 62°20′W), on the northeast coast of Ellesmere Island, N.W.T., Canada. Much of the terrain is barren, consisting mostly of frost-shattered rock, gravel, and bare clay, with very low vegetative cover. More heavily vegetated patches of marshy or mossy ground occur in areas where moisture accumulates or persists (Bruggeman and Calder 1953); even in these situations, however, cover is rarely

[a] Canadian Wildlife Service, National Wildlife Research Centre, Environment Canada, 100 Gamelin Boulevard, Hull, Quebec, Canada K1A 0H3.

[b] International Wader Study Group, c/o Joint Nature Conservation Committee, Monkstone House, City Road, Peterborough PE1 1JY, U.K.

Netherlands Institute for Sea Research, Postbus 59, 1790 AB Den Burg, Texel, The Netherlands, and Zoological Laboratory, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands.

continuous. The summer climate is colder than in other areas of Ellesmere Island and most other parts of the Canadian Arctic, with 30-year normals for June, July, and August mean temperatures of −1.0°C, 3.6°C, and 0.9°C, respectively (Table 1; Environment Canada 1982). Coastal areas in northeastern Ellesmere Island are influenced by the cooling effects of persistent sea ice, which are particularly severe along the north coast (England et al. 1981). To the east of Alert, towards the Sheridan River, the terrain rises fairly gently to a plateau at elevations of some 150–200 m; to the west, steep coastlines surround Colan Bay and Black Cliffs Bay, and the terrain is hillier. Steep ravines, ponds, and rivers are found throughout the area.

Birds nest in very low densities around Alert, and areas with nesting shorebirds were located and reached using all-terrain vehicles. Experimental work was conducted in the vicinity of Alert itself and at sites within a radius of approximately 10 km of Alert. In 1990, Red Knots were captured during the postarrival period with a rocket net on dry, snow-free slopes near the sewage outfall stream at Alert. In 1994, Ruddy Turnstones and Red Knots were captured during the incubation and brood-rearing phases of the breeding cycle. Nests were located by following territorial birds returning to their eggs. Turnstones were captured using walk-in traps, banded with combinations of metal alloy and plastic colour bands, and in some cases fitted with radiotransmitters (Kenward 1987). Transmitters (Model BD-2G, Holohill Systems Ltd., Carp, Ontario; weight 1.5 g) were attached to the lower back area with Superglue, using techniques described by Warnock and Warnock (1993). Birds were sexed on the basis of plumage, measurements were taken using rulers (wing, to nearest 1 mm) and vernier calipers (bill, to nearest 0.1 mm), and birds and eggs were weighed (to nearest 0.1 g) using Pesola spring balances. Although the low densities and renowned difficulties in finding Red Knot nests precluded capturing knots regularly on nests in the Alert area, it was possible to trap both knots and turnstones attending young chicks less than about one week old by placing the chicks in large drop-door traps and capturing the adults when they entered the traps to brood the young. Older chicks were not brooded regularly by the adults, so adults could not be caught at this stage using this method.

Doubly labelled water protocol

After capture, adult turnstones selected for DLW measurements were banded, weighed, and measured. Samples of blood were then taken for measuring background levels of the stable isotopes. A small puncture was made either in the brachial vein in the wing or in a vein in the leg, and a small sample (approx. 25 µL) of the resulting blood was drawn into a 50-µL glass capillary tube, after which the tube was immediately sealed by melting its open ends. Approximately six capillary tubes of blood were collected during the sampling procedure. In 1990, knots captured during the postarrival period were given a subcutaneous injection of 2.4 mL doubly labelled water, consisting of 67% by weight of 90.10 atom percent of $H_2^{18}O$ and 33% by weight of 99.84 atom percent of ^2H_2O

Table 1
A comparison of mean climatic conditions at Alert (Ellesmere Island) and Hall Beach (Foxe Basin), 1951–1980 (from Environment Canada 1982)

Month	Station	Temperature (°C ± SD)	Wind speed (km/h) and direction	Global solar radiation (MJ/m²)
June	Alert	−1.0 ± 1.3	10.5 (NE)	24.57 ± 1.86
	Hall Beach	0.0 ± 2.0	18.7 (NW)	23.87 ± 1.40
July	Alert	3.6 ± 1.4	12.2 (NE)	18.78 ± 1.76
	Hall Beach	5.4 ± 1.4	16.9 (N)	18.95 ± 2.09
August	Alert	0.9 ± 1.2	10.5 (NE)	10.66 ± 1.66
	Hall Beach	4.6 ± 1.1	18.9 (N)	13.11 ± 1.21

(deuterium oxide) in physiological saline (0.9% NaCl). In 1994, birds were given a subcutaneous injection in the ventral region of 0.75–0.95 mL doubly labelled water (dose based on the body mass of the bird = 0.2 mL plus 0.1 mL for each 20 g body mass), consisting of 67% by weight of 90.94 atom percent of $H_2^{18}O$ and 33% by weight of 99.9 atom percent of ^2H_2O. The isotope mixture was warmed by body heat as much as possible prior to injection to reduce stress to the bird. The bird was then kept in an aerated dark space (a cloth bag in a box, to reduce activity and to keep the bird calm) for approximately two hours (mean = 117 minutes, range = 98–138 minutes, all birds 1990 and 1994, n = 11) to allow equilibration of the doubly labelled water throughout the body. Another set ("initial") of blood samples was taken, and the bird was weighed and released. Nesting birds appeared to resume incubation activities within a few hours (if their partner had not already taken over incubation), and birds attending young rejoined their offspring immediately. In one case, an injected turnstone was returned to the nest trap/cage, where it continued to incubate its eggs during equilibration. Attempts were made to recapture injected birds at an interval of approximately one day, either at the nest or while attending young. Two birds were captured twice after initial injection. In 1990, one injected knot was collected near the sewage outfall to obtain a final blood sample for the postarrival phase.

Blood samples were stored in a refrigerator until sent for analysis (within six months) to the Laboratory for Isotope Physics, University of Groningen, Groningen, The Netherlands. Calculations on water turnover and energy expenditure were made using the D20NEW software supplied by the laboratory. Percentage of body water was calculated by back-extrapolation of the $H_2^{18}O$ enrichment above the background concentration after equilibration without extrapolation to the point of injection. Background values were measured and used for individual birds where possible: average values (Ruddy Turnstone: 0.1967 atom percent for $H_2^{18}O$ and 0.01274 atom percent for ^2H_2O, n = 3; Red Knot: 0.1991 and 0.01364, n = 9, respectively) were used when the measurement was not available for the individual. Water turnover values were calculated as the average of the influx and efflux. The DEE was calculated from the estimated rate of CO_2 production, based on

equation 35 in Lifson and McClintock (1966), using an RQ value of 0.72 and an energy equivalent of 27.1 kJ/L CO_2, as recommended by Gessaman and Nagy (1988). This estimate of DEE is considered to be robust and not sensitive to small deviations in RQ and energy-equivalent values (Gessaman and Nagy 1988), and we have therefore used it for the conditions and activities of the birds during the measurement period.

Estimating maintenance metabolism

Maintenance metabolism ("thermostatic costs"; see Piersma et al. 1991) is defined as the net energy expenditure required to maintain a core body temperature of approximately 41°C, excluding costs of synthesis and activity. In this case, it is the sum of the BMR plus the thermoregulatory cost associated with maintaining core body temperature below the lower critical temperature. Maintenance metabolism was estimated in two ways: (a) using equations developed in Wiersma and Piersma (1994) and Piersma and Morrison (1994) for knots and turnstones, respectively, based on studies using heated taxidermic mounts; and (b) using equations developed from biophysical first principles by Cartar and Morrison (1997). Both methods use three standard weather variables—temperature, wind speed, and global solar radiation—as recorded at the Alert Weather Station, operated by Environment Canada.

Results

Estimates of DEE and water turnover were made for three individual turnstones (two females and one male): the two females were both caught twice after initial injection, so estimates of DEE were obtained for five separate measurement periods for this species (Table 2). Mean overall DEE for the three individual turnstones was 3.89 ± 0.63 W (n = 3) or, when the five measurement periods were considered separately, 3.75 ± 0.64 W (n = 5). The two females both had lower DEE estimates (mean 3.55 ± 0.35 W, n = 2) than that obtained for the male (4.55 W). The estimated maintenance metabolism of the three individual turnstones (over the five measurement periods) was calculated from the formula of Piersma and Morrison (1994) using hourly weather records from the Alert Weather Station and averaged 1.92 ± 0.08 W, or 51% of the overall DEE. The Red Knot captured during the postarrival period in June 1990 had an estimated DEE of 2.84 W (Table 3); during the period between release and recapture, the estimated maintenance metabolism using the "behind hillock" formula of Wiersma and Piersma (1994) was 2.309 ± 0.514 W (81% of DEE), calculated from the three-hourly weather records from the weather station at Alert. The DEE of the knot attending young chicks in early July 1994 was 2.98 W (Table 3); its estimated maintenance metabolism was 1.39 W (47% of DEE).

Mean water content of the three turnstones was 63.6 ± 1.6% and of the eight knots captured during 1990 and 1994 was 66.6 ± 7.2%. For the seven knots captured during the postarrival period in 1990, water content averaged 68.4 ± 5.4% and was negatively related to the initial mass at capture (Fig. 1; % body water = 104.611 − 0.255*initial mass, n = 7, R^2 = 0.89, p < 0.01). If the single knot caught attending young in July 1994 was included, the correlation was not significant. The three turnstones trapped during the incubation phase also showed a negative relationship between body water content (average 63.6 ± 1.6%) and mass, although the relationship was not significant (presumably because of the small sample sizes and small range of values).

For the turnstones captured during incubation and early brood attendance, average water flux was positively related to the mass change during the measurement period (Fig. 2; average water flux = 67.25 + 3.20*daily mass change, n = 5, R^2 = 0.79, p < 0.05). In all cases, rates of water influx were less than rates of water efflux, although the difference in means was not statistically significant (mean influx 40.32 ± 25.71 g/day, mean efflux 45.20 ± 22.00 g/day, n = 5, t = −2.58, p = 0.06). Mean rate of loss of mass of the captured birds (7.64 ± 5.34 g/day) was somewhat larger than the difference in rates of water influx and efflux.

Discussion
Comparison with estimates from other localities

The few empirical estimates of DEE (using the DLW technique) available from Arctic breeding grounds have indicated that shorebirds have a high daily energy output (Pierce 1989; Drent and Piersma 1990; Piersma and Morrison 1994; Lindstrom and Piersma 1995), in keeping with their "energetically expensive way of life" (Kersten and Piersma 1987). DEEs of turnstones measured at Alert were generally somewhat lower than those of turnstones from the Foxe Basin, some 1600 km to the south (overall, 3.89 ± 0.63 W vs. 4.21 ± 0.72 W; Piersma and Morrison 1994). In each case, females had lower DEE estimates (3.55 W and 3.86 W for Alert and Rowley Island, respectively) than males (4.55 W and 5.07 W). Estimates for the male turnstone at Alert, in particular, imply a high energy demand: Ruddy Turnstones are thought to have a BMR of about 0.99 W (Kersten and Piersma 1987), so the males were at or exceeding the implied metabolic ceiling of approximately 4.5 times the BMR postulated by Drent and Daan (1980). Weather conditions during the period of measurement were not especially cold, and estimated thermostatic costs, or maintenance metabolism, made up approximately half (51% for the turnstone, 47% for the knot) of the energy output measured by the DLW technique. Thermostatic costs as a proportion of DEE were thus similar to, or slightly less than, those experienced by incubating turnstones on Rowley Island in the Foxe Basin (56%; Piersma and Morrison 1994).

Relating energy expenditure to BMR, however, requires an estimate of BMR during the period under consideration. BMRs of shorebirds can vary considerably during the year (Piersma 1994; Piersma et al. 1995, 1996; Weber and Piersma 1996), and elevated levels occur in spring prior to and during the period of northward migration to the breeding grounds. Changes in body composition, rather than a change in the metabolic activity of specific tissues, are thought to be responsible for the observed changes in

Table 2
Results of DLW measurements on individual Ruddy Turnstones captured at Alert, Ellesmere Island, 1994

No.[a]	Experiment	Sex[b]	Initial mass (g)	Recapture Date	Recapture Time	Time between captures (days)	Mass change between captures (g)	Rate of mass change (g/day)	% body water content	Water influx (g/day)	Water efflux (g/day)	Average water flux (g/day)	DEE kJ/day	W
1f1	94lt02	f	107.5	3/7/94	17:00	0.87	−13	14.94	65.1	16.2	25.9	21.1	279.9	3.240
2f2	94lt02	f	94.5	4/7/94	13:47	1.46	−2	1.37	65.1	53.3	54.2	53.7	288.9	3.344
3f1	94lt03	m	119.5	4/7/94	20:50	0.91	−3	3.30	64.0	73.8	75.9	74.8	393.5	4.554
4f1	94lt05	f	121.5	5/7/94	22:04	0.96	−14	14.58	62.0	13.0	22.1	17.5	374.1	4.330
5f2	94lt05	f	107.5	6/7/94	21:00	1.00	−4	4.00	62.0	45.4	47.9	46.6	284.2	3.289
		Mean	110.1			1.04	−7,2	7.64	63.6	40.3	45.2	42.8	324.1	3.751
		SD	10.9			0.24	5,8	5.34	1.6	25.7	22.0	23.8	55.0	0.636

Note: All birds were adults.
[a] f1 = first "final" blood sample; f2 = second "final" blood sample.
[b] f = female; m = male.

Table 3
Results of DLW measurements on individual Red Knots captured at Alert, Ellesmere Island

No.[a]	Experiment	Sex[b]	Initiale mass (g)	Recapture Date	Recapture Time	Time between capture (days)	Mass change between captures (g)	Rate of mass change (g/day)	% body water content	Water influx (g/day)	Water efflux (g/day)	Average water flux (g/day)	DEE kJ/day	W
1i	90lt01	u	127	3/6/90	1:25				74.6					
2i	90lt02	u	134	3/6/90	1:31				67.9					
3i	90lt03	u	167	3/6/90	1:38				61.2					
4i	90lt04	u	144	3/6/90	1:43				66.3					
5f1	90lt05	f	171	3/6/90	1:48	3.84	−22	5.73	62.8	42.8	46.6	44.7	245.5	2.841
6i	90lt06	u	119	6/6/90	1:38				75.0					
7i	90lt07	u	130	6/6/90	1:45				71.2					
8f1	94lt06	m	132	7/7/94	0:43	0.98	−9	9.18	54.0	17.4	22.5	19.9	257.2	2.977
		Mean	140.5			2.41	15.5	7.46	66.6	30.1	34.5	32.3	251.4	2.909
		SD	18.9			2.02	9.2	2.44	7.2	18.0	17.0	17.5	8.3	0.10

Note: All birds were adults.
[a] i = indicates "initial" blood sample; f1 = "final" blood sample.
[b] u = unknown; f = female; m = male.

Figure 1
Relationship between body water content and initial mass of Red Knots at Alert during the postarrival period, June 1990. Linear regression line and 95% confidence intervals are shown. % body water = 104.611 − 0.255*initial mass.
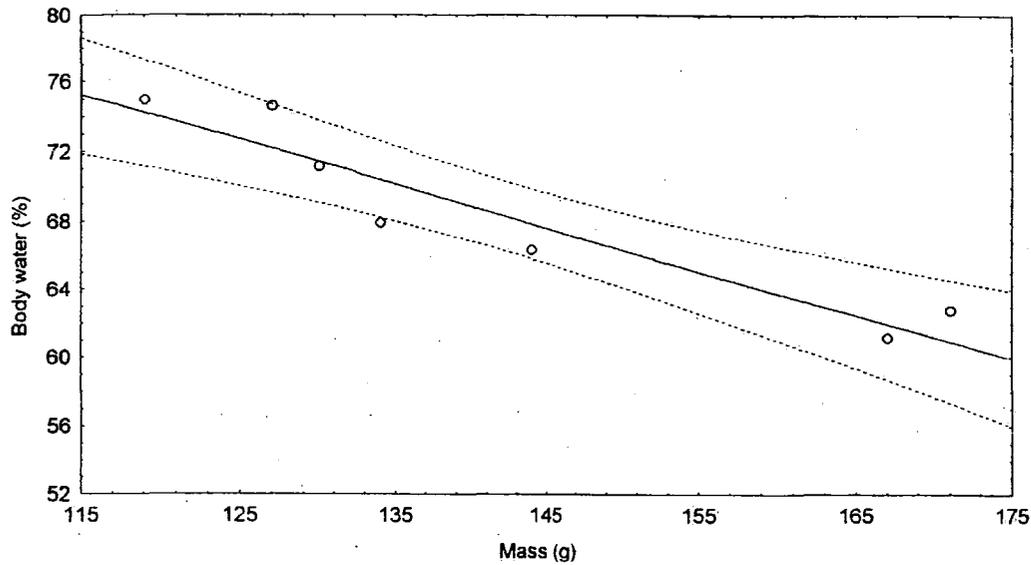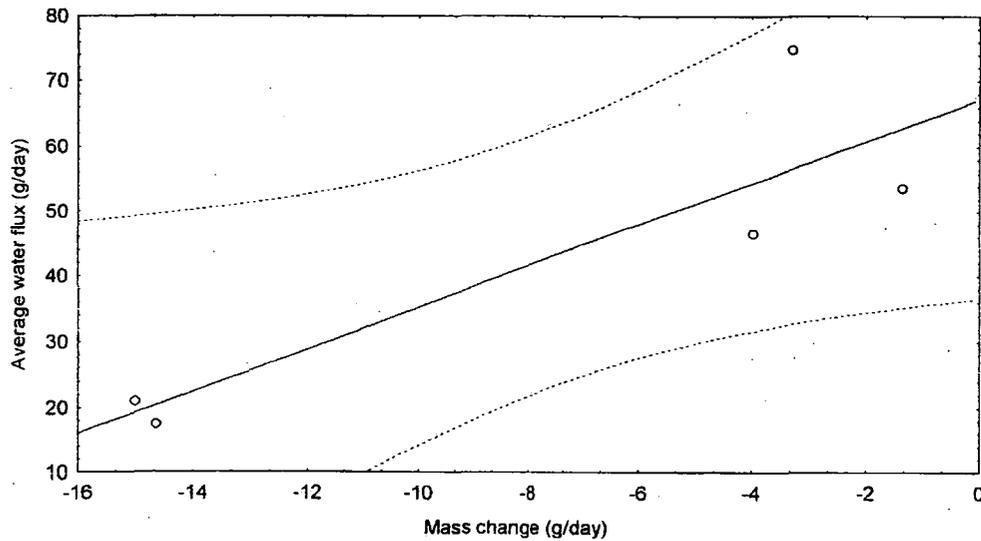

Figure 2
Relationship between average daily water flux and daily mass change of Ruddy Turnstones during DLW experiments at Alert, July 1994. Linear regression line and 95% confidence limits are shown. Average water flux = 67.25 + 3.20*daily mass change.

BMR (Piersma et al. 1996; Weber and Piersma 1996). In addition to putting on large amounts of (metabolically inactive) fat, needed as fuel during long migratory flights, shorebirds also build up muscle mass and mass of organs associated with energy mobilization, particularly the liver and heart; at the same time, they decrease body components, such as gizzard and gut, that will not be needed during the flight (Piersma 1994; T. Piersma, G.A. Gudmundsson, and K. Lillienthal, unpubl. data). On arrival at Alert, knots tend to lose excess fat stores while retaining protein stores (females) and building up gizzard and gut again (unpubl. data). How these physiological adjustments, and any associated with the breeding effort, affect the BMR on the breeding grounds is not known at present, so the validity of scaling DEE as a product of BMR remains uncertain. Further work on body composition and on

5

developing methods for assessing body composition in a nondestructive manner is needed, as are empirical measurements of BMR during the breeding period.

Two of the turnstones captured for the DLW experiments, both females, lost a considerable amount of mass between the initial capture and the first recapture approximately one day later (13 and 14 g). Both birds were recaptured a second time after a further interval of approximately one day and had lost considerably less mass during this second period (2 and 4 g, respectively). For the first female, the DEE estimates for the two periods were fairly similar (3.24 and 3.34 W), although the average water flux was considerably less during the first period than during the second (21.1 vs. 53.7 g/day). The female spent the first period after injection resting and feeding, while the male incubated, and she was recaptured on each of the following days while incubating again. The second female was first captured on the nest, incubating heavily starred eggs, which were in the process of hatching when she was first recaptured the following day; she was captured again attending small young one day later. This female showed a similar pattern of water flux, low (17.5 g/day) the first day and higher the second (46.6 g/day), with consecutive DEE estimates of 4.33 W during the egg-hatching phase and 3.29 W during the first day of attending chicks. The average water flux was significantly related to the rate of change of daily mass. The low water fluxes during the first recapture period suggested that both females fed little during this period.

The DEE estimates for knots are the first available from the Canadian Arctic and suggest a high, but not exceptionally high, energetic demand at Alert. The estimates (2.84 W for a postarrival female undergoing egg formation in 1990, 2.98 W for a male attending chicks in 1994) both approached three times the BMR, if a BMR of approximately 1 W is assumed (Kersten and Piersma 1987; Wiersma and Piersma 1994). These levels are considerably lower than those obtained for incubating knots (of the subspecies C. c. canutus) in the Siberian Arctic: DEEs there averaged 4.6 W, the data indicating a strong weather effect and suggesting that foraging birds incurred higher energy costs than those incubating eggs (Lindstrom and Piersma 1995), as might be expected if foraging involved occupation of more exposed microhabitats. The two measurements of DEE for knots at Alert are also lower than estimates of field metabolic rates for knots wintering in the Wadden Sea in The Netherlands (Piersma et al. 1996).

DEE estimates for the turnstones at Alert averaged 3.75 ± 0.64 W, compared with 4.21 ± 0.72 W for eight turnstones captured on Rowley Island in the Foxe Basin (Piersma and Morrison 1994): the birds at each locality were of similar mean body mass (110.1 ± 10.9 g at Alert vs. 109.0 ± 6.2 g on Rowley Island), although of different subspecies (A. i. interpres vs. A. i. morinella). These observations suggest that the climatic conditions at Alert, although severe by comparison with other parts of the Canadian Arctic, do not stress the birds beyond levels experienced either during the winter or during worse weather conditions at other Canadian Arctic localities. In fact, mean July temperatures over the Canadian Arctic islands range only between <5°C

on the north coast of Ellesmere Island and around 8–10°C along the mainland coast (Maxwell 1980). An analysis of seasonal metabolic conditions at Alert (1970–1990) indicates that maintenance metabolism exceeded 2.7 times the BMR (limit inferred by Piersma and Morrison 1994) on an average of only 2.5% and 3.6% of days during the months of June and July for Red Knots and Ruddy Turnstones, respectively; in comparison, this limit was exceeded on an average of 15.3% of days during the shorter period of 21 June to 20 July for Ruddy Turnstones in the Foxe Basin (1958–1990; Piersma and Morrison 1994). A comparison of the 30-year climate normals for Alert and Hall Beach (Foxe Basin) indicates that although Alert is slightly colder than Hall Beach, with mean temperatures about 1–2°C colder at Alert in June and July, Hall Beach is considerably windier, with mean wind speeds 1.4–1.8 times those at Alert during the same months: global solar radiation at the two stations did not differ greatly (Table 1). Standard deviation in mean temperature was also slightly higher at Hall Beach than at Alert during June. It would thus appear that although the Foxe Basin is a slightly warmer location than Alert, the windier and more variable conditions there combine to make it metabolically less predictable and perhaps more stressful than Alert for a medium-sized shorebird such as a knot or turnstone.

The water contents and turnover rates for the small sample of turnstones at Alert were considerably lower than those obtained for Ruddy Turnstones on Rowley Island in the Foxe Basin. The low water turnover rates may have been related to the possibility that the birds involved had not fed a great deal during the period of DLW measurements. For knots, the negative relationship between water content and mass noted for the sample of birds caught during the immediate postarrival period, when they are all likely to be in a similar nutritional condition, probably reflects the larger amounts of fat carried by the heavier birds. This relationship became nonsignificant when the data point from the male caught later in the season while attending young was included: changes in body composition that may occur during the breeding effort may preclude any simple relationship between water content and fat content over the entire period.

For the small samples available, males of both knots and turnstones showed higher DEE estimates than females. Similar results were found for turnstones in the Foxe Basin (Piersma and Morrison 1994); this may result from males spending more time in exposed habitats and in energetically expensive activities, such as territorial defence.

The results from Alert indicate that the area is energetically quite expensive for knots and turnstones but is comparable to or possibly less energetically expensive than other Arctic regions or the European wintering grounds. Estimates of the thermostatic costs, or costs of maintenance metabolism, for medium-sized shorebirds such as knots and turnstones suggest that the climatic conditions prevailing allow a large enough energetic margin for the birds to cope successfully with the demands of reproduction and breeding.

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