

# Time budgets of pre-breeding Knots on Ellesmere Island, Canada

N.C. Davidson & R.I.G. Morrison

Davidson, N.C. & Morrison, R.I.G. 1992. Time budgets of pre-breeding Knots on Ellesmere Island, Canada. *Wader Study Group Bull.* 64, *Suppl.*: 137-143.

The energetic costs faced by arctic-breeding shorebirds when they reach their breeding grounds are poorly known, yet this may be a critical time in their annual cycle. Knots arriving at Alert, in northernmost Canada, in early June generally spend 40-90% of their time feeding, but are relatively inactive in the first few days after arrival. During the first week after arrival they respond to periods of high windchill by becoming less active but switch to being more active during later periods of bad weather, perhaps because of improvements in food availability. Daily energy expenditure (DEE) estimated from observed time budgets is high, averaging 3.45 and 3.72 times Basal Metabolic Rate (BMR) in two springs. Estimated DEEs for the smaller Turnstones and Sanderlings at Alert are even higher, in Sanderlings averaging 4.73•BMR. High DEE estimates may be an artefact of the estimation technique, but some evidence from elsewhere suggests that high metabolic activity may be typical of shorebirds in cold weather. If so, carrying large reserves of fat and protein, which must be accumulated at late spring staging areas, is a vital part of the survival strategy of high arctic shorebirds.

N.C. Davidson, Joint Nature Conservation Committee, Monkstone House, City Road, Peterborough PE1 1JY, U.K.

R.I.G. Morrison, National Wildlife Research Centre, Canadian Wildlife Service, 100 Gamelin Boulevard, Hull, Quebec K1A 0H3, Canada.

## INTRODUCTION

In spring, migrant birds need to complete successfully their return to the breeding grounds at the appropriate time to breed. Birds breeding in the High Arctic have only a short summer in which to breed, yet to reach their breeding grounds they must make rapid long-distance migrations over inhospitable land and sea. To do this, such migrants store large amounts of fat and protein at migration staging areas. Knots *Calidris canutus islandica* which breed in high arctic Greenland and Canada fly direct to their breeding grounds from staging areas in May in Iceland and northern Norway, arriving on their breeding areas in late May and early June. Their migration system is reviewed by Davidson & Wilson (1992).

Much of the reserves of fat and protein accumulated at late spring staging areas provides the fuel and the power for the flight of over 3,000 km to the breeding grounds. Davidson & Evans (1988) predicted,

however, that part of this fat and protein load was retained during the flight and was carried to the breeding grounds as a pre-breeding reserve. This could be used either for balancing energy and protein demands during food shortage soon after the birds' arrival, for example during years of late snow melt or severe weather, and/or to contribute to the breeding attempt, for example by drawing on a protein store for egg production.

Knots do appear to arrive on their breeding grounds with reserves of both fat and protein remaining and seem then to draw on these reserves (as judged by changes in total body mass) during the two weeks after their arrival (Morrison & Davidson 1990; Davidson & Wilson 1992). Hence the energy expenditure incurred by high arctic waders during this brief period between their breeding-ground arrival and the onset of breeding may greatly influence the timing and success of the breeding attempt, and even the survival of adult birds themselves and so population size (see also Boyd 1992).

This paper examines this poorly understood feature of the biology of arctic-breeding birds. An understanding of what the birds face during their pre-breeding period is, however, very important for an interpretation of their strategy for the preceding migration. The paper summarizes the behaviour and estimated energy expenditure of Knots during their pre-breeding period at Alert (82°30'N, 62°20'W) on Ellesmere Island in the Canadian Arctic, based on data collected mostly in May and June 1987 and 1988. It reports part of continuing international studies on the behaviour and ecological energetics of high arctic shorebirds at Alert, which at less than 800 km from the North Pole is one of the most northerly breeding grounds for birds in the world. Despite its northerly location the presence of a sewage outfall and rubbish tip (associated with a meteorological station and military base) at Alert probably provide relatively favourable early-season feeding conditions for waders (Morrison 1975; Morrison & Davidson 1990).

In the absence of direct measures of the free-living energy expenditure of waders, we have estimated daily energy expenditure from time budgets and standard equations for the energetic costs of different activities. We also compare the estimated energy expenditure of Knots with those of other pre-breeding shorebirds (Turnstone *Arenaria interpres* and Sanderling *Calidris alba*) at Alert, based on data collected at the same times.

## METHODS

21 Turnstones and 3 Knots were caught and individually colour-marked using colour-dye and temporary leg-flags. Regular checks and counts of birds were made on the slopes surrounding Alert camp and its runway. Most Knots and Turnstones fed in the vicinity of the garbage dump and the sewage outfall, although use was also made of naturally occurring wet flushes on the surrounding slopes, particularly in 1988.

The presence of marked birds was noted and the behaviour of each bird in the flock noted by scan-sampling at 1-5 minute intervals depending on the size of the flock. For Knots we collected a total of 1,161 bird-observations in 1987 and 8,084 bird-observations in 1988. Whenever possible the behaviour of individually marked birds was recorded separately. The observations were then used to construct time-activity budgets for each species in 3-hourly

periods. Data on males and females were combined for these budgets since the sexes could not always be distinguished during scan-samples and the data on sexes or individual birds were generally too scarce to permit separate analysis. Similar observations were made also on Turnstones and Sanderlings feeding in the same areas.

Behaviour was recorded in 10 categories: walking; feeding (including walking about looking for food); flying; flight display; ground display; aggression; standing alert; resting (sitting or standing in non-alert posture); roosting; and preening/bathing.

Meteorological data were available from the Atmospheric Environment Service Meteorological Station at Alert, within 1 km of our main study sites. Air temperature, wind speed and direction were measured 3-hourly; other data were collected daily.

Daily energy expenditure (DEE) was estimated from the proportion of time spent in each activity, and the estimated energetic cost of that activity. Although this widely used approach makes substantial assumptions about the energetic costs of various activities and of thermoregulation costs (see Bryant *et al.* 1985; Goldstein 1988) it does permit a first estimate of the energy expenditure of shorebirds at Alert.

Very few other studies have yet examined energy costs of shorebirds in the High Arctic. We have based our energy cost estimates on formulae derived from those developed by Ashkenazie & Safriel (1979) for Semipalmated Sandpipers *Calidris pusilla* breeding in Alaska - the only other published study of the energetics of arctic-breeding shorebirds. Use of these formulae has the added advantage that it permits direct comparisons between our DEE estimates and those made by Ashkenazie & Safriel. The formulae allow for the effect of air temperature on the energetic costs of different activities to be taken into account for birds below their thermoneutral zone. It is particularly important to allow for this in our study since air temperature varied from +1°C to as low as -15°C. We have, however, modified Ashkenazie & Safriel's equations in the light of recent information showing that shorebirds have a relatively higher Basal Metabolic Rate (BMR) than is usual for non-passerines (Kersten & Piersma 1987; Castro 1987).

Following Ashkenazie & Safriel (1979) we calculated DEE as follows:

$$DEE = DEE_T + DEE_A \quad (1)$$

where  $DEE_T$  is the daily energy cost of production and thermoregulation and  $DEE_A$  is the daily energy cost of maintenance and other activities.

$DEE_T$  is calculated from Standard Metabolic Rate (SMR), the energy costs of maintenance and production at temperatures below the thermoneutral zone and BMR:

$$DEE_T = SMR - BMR \quad (2)$$

We have used the BMR equation for shorebirds given by Kersten & Piersma (1987):

$$BMR = 437.18 \cdot M^{0.729} \text{ kJ/d} \quad (3)$$

where  $M$  is total body mass in kg.

SMR is species-specific and depends on BMR, lower critical temperature and the rate of increase of energy cost of thermoregulation with decreasing temperature. For Turnstones we have used the equation given by Kersten & Piersma (1987):

$$SMR_{\text{Turnstone}} = 181.87 - 4.406 \cdot T \text{ kJ/d} \quad (4)$$

where  $T$  is ambient temperature in °C.

No SMR equations have been published for Knots or Sanderlings, so we have derived SMR estimates from the average body masses and metabolic data for other shorebirds given by Kersten & Piersma (1987):

$$SMR_{\text{Knot}} = 200.01 - 4.834 \cdot T \text{ kJ/d} \quad (5)$$

$$SMR_{\text{Sanderling}} = 126.14 - 2.592 \cdot T \text{ kJ/d} \quad (6)$$

$DEE_T$  was adjusted to exclude costs of thermoregulation during flight, since flight is considered to produce enough heat to maintain body temperatures (Ashkenazie & Safriel 1979).

$DEE_A$  is estimated as the sum of the costs of each activity, multiplied by the proportion of time ( $P$ ) spent in that activity, derived from our time-budget observations. For details of the derivation of the formulae see Ashkenazie & Safriel (1979). For the calculation of energy budgets we reduced the 10 activity categories to four groups, so:

$$DEE_A = DEE_{A1} + DEE_{A2} + DEE_{A3} + DEE_{A4} \quad (7)$$

$DEE_{A1}$  is the energy cost of roosting:

$$DEE_{A1} = BMR \cdot P_1 \text{ kJ/d} \quad (8)$$

$DEE_{A2}$  is the energy cost of feeding, walking, standing alert, aggression, and ground display:

$$DEE_{A2} = BMR \cdot (1.94 - 0.021 \cdot T) \cdot P_2 \text{ kJ/d} \quad (9)$$

$DEE_{A3}$  is the energy cost of resting and preening, and is intermediate between  $DEE_{A1}$  and  $DEE_{A2}$ :

$$DEE_{A3} = [(BMR + DEE_{A2})/2] \cdot P_3 \text{ kJ/d} \quad (10)$$

$DEE_{A4}$  is the energy cost of flight:

$$DEE_{A4} = 4.186 \cdot 7.05 \cdot M^{0.73} \cdot P_4 \text{ kJ/d} \quad (11)$$

Our observations indicated that the combined effects of the sometimes strong winds and low temperatures at Alert in late May and early June could greatly decrease the effective temperature the birds faced. Accordingly we have used windchill temperature equivalents as input into the temperature-dependent equations. On days of strong winds this increased the estimated DEE by up to 33% more than the DEE based on air temperature alone. For analysis of behaviour in relation to windchill we have, however, calculated a windchill factor,  $T \cdot V^{0.6}$ , derived by Gessaman (1973) for arctic birds, where  $T$  is the temperature deficit below 20°C and  $V$  is the windspeed in knots.

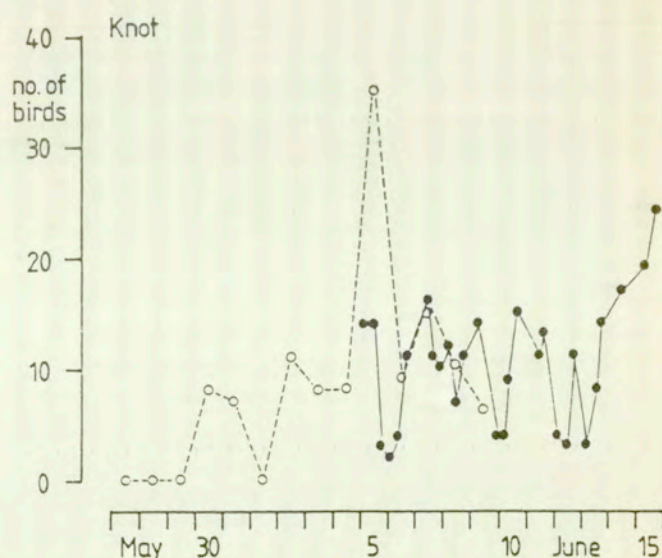


Figure 1. Daily maximum numbers of Knots counted at Alert during each observation period in late May and early June 1987 (open circles) and 1988 (dots).

## RESULTS AND DISCUSSION

### Numbers of birds

In some years large numbers of Knots and Turnstones congregate at Alert during the period of arrival in late May and the first week of June. Maximum numbers recorded were 150 Turnstones on 9 June 1976 and 118 Knots on 6 June 1974. Numbers of Knots at Alert varied greatly from day to day (Figure 1). In 1987 Knots were first seen on 30 May. Numbers increased to 35 birds during severe weather on 5 June. Thereafter numbers decreased rapidly. In 1988 numbers fluctuated between 2-15 birds between 5-13 June, before numbers increased to a maximum of 25 birds on 15 June.

This arrival pattern of numbers is consistent with some birds using Alert as a brief pausing place when they first arrive in the Arctic. The fluctuations in numbers could arise because of the arrival of successive waves of new migrants or the reappearance of a local population. Each of the three marked Knots (two females and one male) were seen on some days throughout the period after their capture so it seems that at least some birds were taking up breeding territories around Alert and were returning to the station regularly to feed during the two weeks after their arrival. At the same time Knots also feed in small groups in the area surrounding Alert in snow-free marshes and on likely breeding slopes: 15 Knots were found in such areas within 10 km of Alert on 14 June 1988. A similar pattern of regular appearances at Alert by at least some early arriving birds was found for Turnstones (Davidson & Morrison in prep.)

Numbers of Knots also fluctuated greatly on a much shorter timescale. Observations on Knots show almost continuous arrivals and departures of small groups of birds and sometimes individuals to a feeding area such as around the sewage outfall. Major temporary departures of most of the birds present were often induced by the appearance of an Arctic Fox *Alopex lagopus*. Groups or individuals watched after their departure were seen flying for over 2 km directly back towards probable breeding grounds on the surrounding hillsides.

### Time budgets

From the occurrence patterns of Knots it seems that we were observing a largely local population, at least some of which were flying from the surrounding area to Alert to feed regularly. The time budgets are therefore likely to underestimate the amount of time

spent flying. Activity patterns when birds were away from Alert may also have differed, although our limited observations of such birds suggested that they followed a broadly similar pattern of feeding and resting.

The daily time budgets for 1987 and 1988 (Figure 2) show that Knots generally spent 40-90% of their time feeding. Birds were least active in the days shortly after their arrival at Alert. They also, however, spent substantial periods of inactivity in preening, roosting

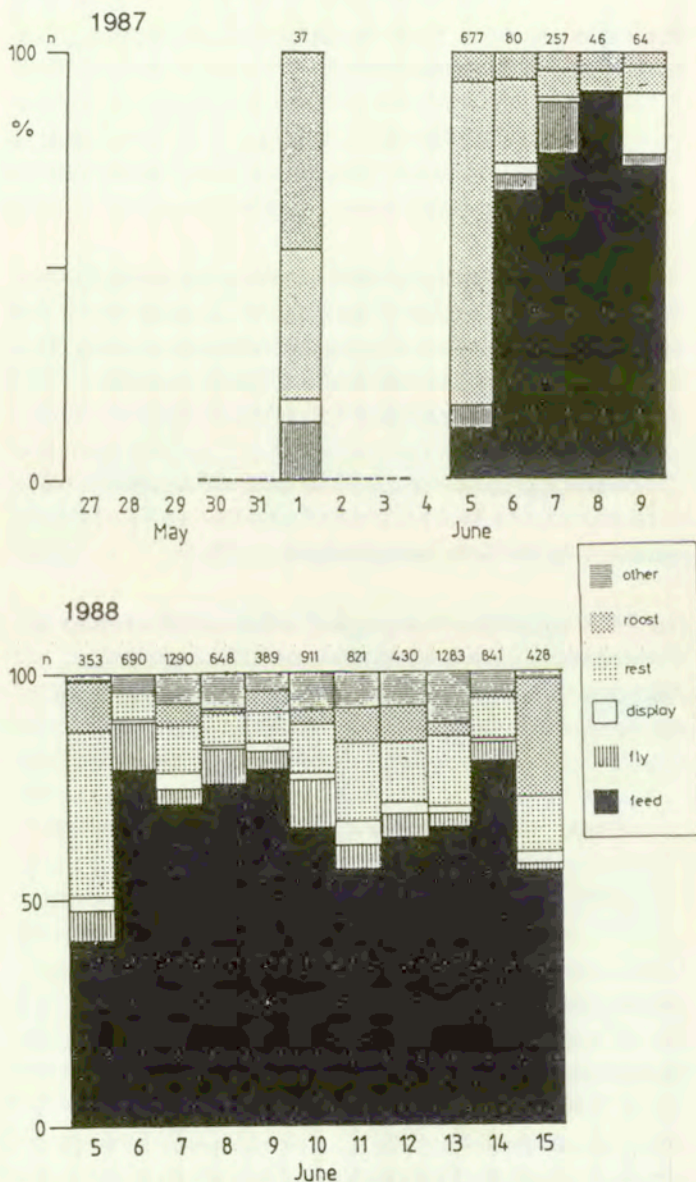


Figure 2. Time-activity budgets of Knots at Alert in late May and early June 1987 and 1988 (1987 figures are from Morrison & Davidson 1990). Data are shown separately for each day, except for Knots between 30 May and 3 June 1987 for which data are lumped because few birds were present and few observations made. The number above each column gives the number of bird-observations per day.

and resting. An appreciable part of the remaining time was spent flying, usually in response to disturbance from an obvious source such as a fox or a Long-tailed Skua *Stercorarius longicaudus*, but sometimes seemingly in response to an alarm call from one of the waders. Courtship activity whilst the birds were at Alert took up only 10% of time at most, and usually considerably less.

If birds are waiting for snow and feeding conditions to improve after their arrival at Alert, they would be expected to respond to severe weather by becoming

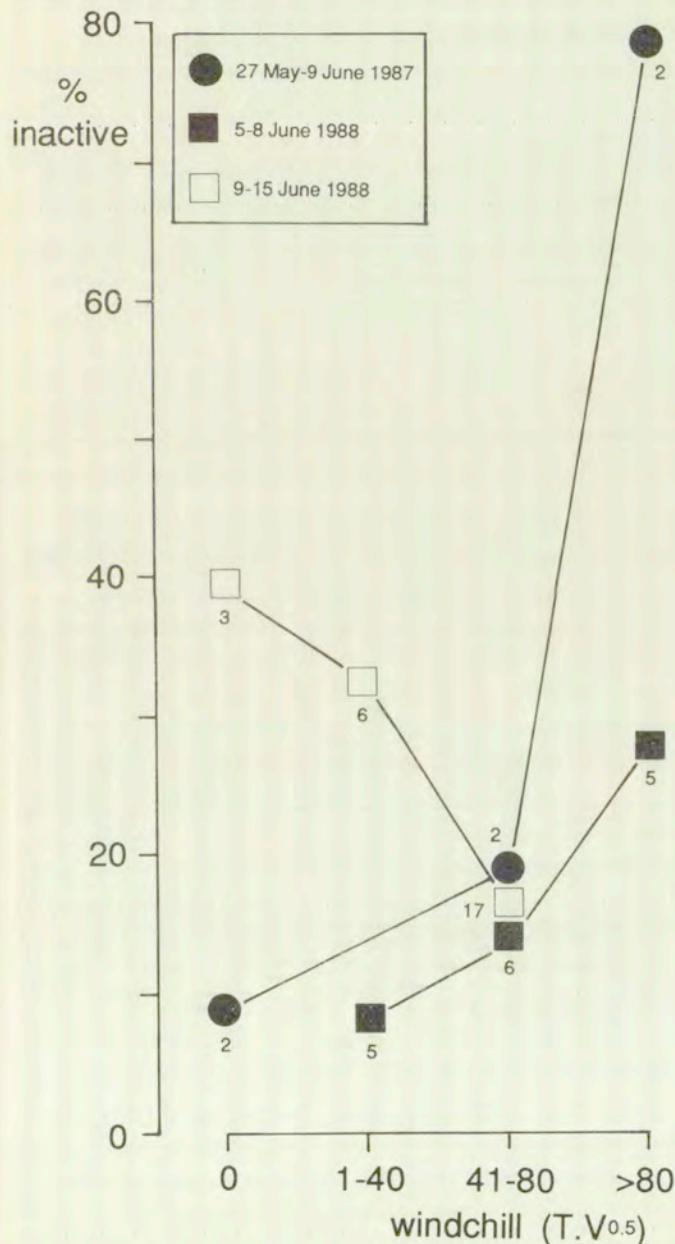


Figure 3. The percentage of available time spent inactive (resting, roosting, preening, standing) by Knots at Alert in late May and early June 1987 and early-mid June 1988 in relation to windchill. Mean values for each windchill category are shown, with the number of observation periods beside each symbol.

less active so as to minimize energy expenditure. Data from the periods up to 9 June in 1987 and 8 June in 1988 show that in both years Knots became much less active during periods of severe weather (Figure 3). The relationships between inactivity and windchill were statistically significant (Spearman rank correlation  $r_s$ ,  $p < 0.05$ ) and were stronger than with either temperature or windspeed alone, perhaps because windchill is a better measure of the energy requirements for thermoregulation.

In the second week of June 1988 there was a marked switch in the behaviour of Knots: birds became more active ( $r_s$ ,  $p < 0.05$ ) and fed more as windchill increased (Figure 3). Similar trends were found in Turnstones and Sanderlings (Davidson & Morrison in prep.). By this time of the year there was much more snow-free ground available and the birds were likely to be approaching the time of their egg laying. Greater availability of food may mean that the birds had no longer to rely on their nutrient reserves to meet their energy requirements. In the lead up to breeding there appears, therefore, to be a shifting trade-off between the need to conserve energy reserves through the pre-breeding period so as to carry reserves of fat and protein into the breeding attempt, and to feed so as to balance daily energy requirements.

#### Estimated daily energy expenditure

Estimated mean daily energy expenditure in 1987 and 1988 is summarized for Knots, Turnstones and Sanderlings in Table 1. No Sanderlings were present at Alert in May/June 1987. Estimated DEE ranged from 228 kJ/d for Sanderlings in 1988 to 388 kJ/d for Knots in 1988. Total estimated DEE of Turnstones was below that of Knots in 1988 but above in 1987. The mean estimated DEE did not differ significantly between years in either Knots or Turnstones (Student's  $t$ ,  $p > 0.05$ ).

As a multiplier of Basal Metabolic Rate (BMR), mean estimated DEE varied between  $3.45 \cdot \text{BMR}$  in Knots in 1987 and  $4.73 \cdot \text{BMR}$  in Sanderlings. As might be anticipated from the formulae used in estimating DEE, the BMR multiplier is related interspecifically to the mass of the birds with the largest, Knots, having the lowest estimated DEE relative to BMR (Table 1). The estimated DEE of Semipalmated Sandpipers in the same part of their breeding season (recalculated from data in Ashkenazie & Safriel (1979) using Kersten & Piersma's (1987) value for BMR) also fits this relationship ( $\text{DEE} / \text{BMR} = 8.69 - 2.285 \cdot \log \text{Mass}$ ,  $n = 7$ ,  $r = 0.957$ ,  $p < 0.001$ , where

Mass<sub>i</sub> = total body mass). The Semipalmated Sandpiper is smaller and lighter than the Sanderling and has an estimated BMR-multiplier of about 5.5.

All the DEEs for these arctic-breeding species at the start of the breeding season are, however, considerably higher than would be predicted from the general relationship between DEE and body mass of non-breeding non-passerines given by Bryant *et al.* (1985). This predicts a DEE ranging from 3.02 • BMR for male Semipalmated Sandpipers to only 2.58 • BMR for Knots. At temperate latitudes, Brunton (1988) estimated a DEE of 2.2 - 2.6 • BMR for pre-laying Killdeers *Charadrius vociferus*, and this is similar to most of the estimated DEEs of between 2 • BMR and 3 • BMR derived from net energy intake for various wintering shorebirds summarized by Kersten & Piersma (1987).

It is not yet clear, therefore, whether these high estimated DEEs at Alert are an artefact of the formulae employed in this study or whether they reflect a genuinely high daily energy demand during the pre-breeding period in the Arctic. Although we have attempted to take into account the effects of temperature and windspeed on metabolic rate in our calculations there are many other sources of potential error in generating estimates of the energy expenditure of free-living birds (for a recent review see Goldstein 1988).

Some support for high levels of energy expenditure does, however, come from direct measurements

Table 1. Mean estimated daily energy expenditure (DEE) of Knots, Turnstones and Sanderlings at Alert in May/June 1987 and 1988. Values are expressed as a) kJ/d, and b) a multiplier of estimated Basal Metabolic Rate (BMR). *n* = number of days of observations.

	1987			1988		
	<i>n</i>	mean	sd	<i>n</i>	mean	sd
a) kJ/d						
Sanderling	-	-	-	7	228.0	13.9
Turnstone	13	378.9	87.6	11	370.6	46.7
Knot	6	359.5	50.4	11	387.7	35.6
b) x BMR						
Sanderling	-	-	-	7	4.73	0.29
Turnstone	13	4.33	1.00	11	4.24	0.54
Knot	6	3.45	0.49	11	3.72	0.34

(using doubly-labelled water) of DEE in Sanderling overwintering in the Americas (Castro 1988). Castro found an average DEE varying from 2 to 4.2 • BMR at different wintering latitudes, rather lower than the estimate for Alert. On cold days, however, with temperatures of *c.* -5°C, DEE increased to up to 5 • BMR (G. Castro pers. comm.), even higher than the average of 4.73 • BMR estimated for Sanderlings at Alert (Table 1).

We tentatively conclude that in the low temperatures and sometimes high winds faced by shorebirds arriving on their arctic breeding grounds in spring levels of energy expenditure are high even when birds remain relatively inactive in the early days after their arrival. DEE appears to be similar at this time to that of shorebirds during cold weather on their wintering grounds, when large nutrient reserves are known to be vital for the birds' survival when feeding is poor or impossible (e.g. Davidson 1981). Energy reserves may be similarly important for birds such as Knots arriving on their breeding grounds, especially when spring weather is severe and feeding restricted, since we have found that the average mass of Knots at Alert declines rapidly during the two weeks after their arrival (Morrison & Davidson 1990).

Accumulating sufficient nutrient reserves on their spring staging areas both to fuel migratory flight and to balance energy expenditure on the breeding grounds seems therefore to be a vital part of the migration strategy of Knots. Further work is, however, needed to provide accurate values for DEE during the period between arrival in the Arctic and breeding, and on the relationships between weather conditions, behaviour and energy expenditure at this time.

## ACKNOWLEDGEMENTS

Financial support for parts of this work were provided by the NATO Cooperative Research Programme and the Canadian Wildlife Service, the latter also providing logistical support and equipment. We particularly wish to thank the Canadian Armed Forces for permission to work at Alert, the Commanding Officer and staff at Alert for their professional and most enthusiastic help during our studies, and the staff of the Atmospheric Environment Service at Alert Weather Station for providing meteorological data. Theunis Piersma and Hugh Boyd made helpful comments during the preparation of this paper.

## REFERENCES

- Ashkenazie, S., & Safriel, U.N. 1979. Time-energy budget of the Semipalmated Sandpiper *Calidris pusilla* at Barrow, Alaska. *Ecology* 60: 783-799.
- Boyd, H. 1992. Arctic summer conditions and British Knot numbers: an exploratory analysis. *Wader Study Group Bull.* 64, Suppl.: 144-152.
- Brunton, D.H. 1988. Energy expenditure in reproductive effort of male and female Kildeer (*Charadrius vociferus*). *Auk* 105: 553-564.
- Bryant, D.M., Hails, C.J. & Prys-Jones, R. 1985. Energy-expenditure by free-living dippers (*Cinclus cinclus*) in winter. *Condor* 87: 177-186.
- Castro, G. 1987. High basal metabolic rates in Sanderlings (*Calidris alba*). *Wilson Bull.* 99: 267-268.
- Castro, G. 1988. *Ecophysiology of Sanderlings migrating to four different latitudes*. Ph.D. Thesis, University of Pennsylvania, Philadelphia.
- Davidson, N.C. 1981. Survival of shorebirds (Charadrii) during severe weather: the role of nutritional reserves. Pp. 231-249 in: Jones, N.V. & Wolff, W.J. (eds.), *Feeding and Survival Strategies of Estuarine Organisms*. Plenum Press, New York.
- Davidson, N.C., & Evans, P.R. 1988. Prebreeding accumulation of fat and muscle protein by arctic-breeding shorebirds. *Acta XIX Congr. Internat. Ornithol. (Ottawa)*: 342-352.
- Davidson, N.C., & Wilson, J.R. 1992. The migration system of European-wintering Knots *Calidris canutus islandica*. *Wader Study Group Bull.* 64, Suppl.: 39-51.
- Gessaman, J.A. 1973. *Ecological energetics of homeotherms*. Utah State Press, Logan.
- Goldstein, D.L., 1988. Estimates of daily energy expenditure of birds: the time-energy budget as an integrator of laboratory and field-studies. *Amer. Zool.* 28: 829-844.
- Kersten, M., & Piersma, T. 1987. High levels of energy expenditure in shorebirds; metabolic adaptations to an energetically expensive way of life. *Ardea* 75: 175-187.
- Morrison, R.I.G. 1975. Migration and morphometrics of European Knot and Turnstone on Ellesmere Island, Canada. *Bird-Banding* 46: 290-301.
- Morrison, R.I.G. & Davidson, N.C. 1990. Migration, body condition and behaviour of shorebirds during spring migration at Alert, Ellesmere Island, N.W.T. Pp. 544-567 in: Harington, C.R. (ed.), *Canada's missing dimension. Science and history in the Canadian Arctic Islands*. Canadian Museum of Nature, Ottawa.

