

## ENERGY EXPENDITURE AND WATER TURNOVER OF INCUBATING RUDDY TURNSTONES: HIGH COSTS UNDER HIGH ARCTIC CLIMATIC CONDITIONS

THEUNIS PIERSMA<sup>1,2</sup> AND R. I. GUY MORRISON<sup>3</sup>

<sup>1</sup>Zoological Laboratory, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands;

<sup>2</sup>Netherlands Institute for Sea Research (NIOZ),

P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands; and

<sup>3</sup>Canadian Wildlife Service, National Wildlife Research Centre, 100 Gamelin Boulevard, Hull, Quebec K1A 0H3, Canada

**ABSTRACT**—To investigate whether shorebirds breeding in the High Arctic have relatively high rates of energy expenditure due to the harsh climatic conditions that prevail even in summer, we measured daily energy expenditure (DEE) and water turnover of Ruddy Turnstones (*Arenaria interpres*) during the incubation phase on Rowley Island in Foxe Basin, N.W.T., Canada, at 69°N, using the doubly-labeled-water technique. Simultaneously, we conducted detailed measurements of ambient climatic conditions, including *in situ* measurements with heated taxidermic mounts. A series of 11 doubly-labeled-water measurements with eight individual Ruddy Turnstones, of which at least seven successfully hatched eggs, yielded a mean DEE of 4.08 W. This is a relatively high value for a 108-g bird, equalling four times their basal metabolic rate (BMR). Most variation in DEE was attributable to standard operative temperature, which combines the effects of air temperature, wind and radiation on heat loss from the turnstone's point of view. On average, 25% of DEE was attributable to BMR, 31% to the cost of thermoregulation, and 44% to the cost of activity. The average value for water turnover of 96.6 g/day is high compared to published values for other birds and confirms the large requirement for food (which is water-rich) of incubating Ruddy Turnstones. An analysis of the climatic conditions prevalent in Foxe Basin during the breeding seasons of Ruddy Turnstones, based on the 33-year period 1958-1990, indicated that they faced thermostatic hardships, defined as energy expenditure exceeding the maximum sustained working level (estimated at 4.5 times BMR), on 15% of the days. Climatic conditions were most severe in the early 1960s, but have improved since. Received 7 June 1993, accepted 22 November 1993.

THERE ARE COMPARATIVELY few species of birds that have adapted to take advantage of the seasonal abundance of (especially arthropod) resources to reproduce in the productive parts of the High Arctic (Sage 1986). Compared to the temperate and tropical regions, two major costs are associated with using High Arctic tundra as an area of reproduction. First, most species face a large time and energy cost for migration to and from suitable nonbreeding areas (Alerstam et al. 1986, Davidson and Evans 1989, Drent and Piersma 1990, van Rhijn 1991). Furthermore, maintaining a body temperature of 40° to 41°C in a cold and windy arctic climate (e.g. Myers and Pitelka 1979) may, even in the summer, have a rather high energy cost (Piersma et al. 1991, Visser 1991). Birds breeding in temperate and tropical regions daily expend a modal energy value equivalent to only three times their basal metabolic rate (BMR; Bryant and Tatner 1991). In comparison, studies to date suggest that shorebirds breeding in the Arctic may have

daily energy expenditures equivalent to 3.7 to 5.5 times their BMR, mainly as a consequence of low temperatures and strong winds (Ashkenazie and Safriel 1979, Davidson and Morrison 1992). These estimates were not based on direct measurements, but on (indirect) time-energy budget studies using parameters derived from the literature. Apart from the preliminary results of E. Pierce (in Drent and Piersma 1990) on energy expenditure of Purple Sandpipers (*Calidris maritima*) breeding on Spitsbergen (79°N), no empirical data on daily energy expenditure for High Arctic breeding birds have been published (Bryant and Tatner 1991).

In this paper, we report the results of a study in which doubly-labeled-water loading experiments were conducted along with measurements of climatic conditions. We worked with Ruddy Turnstones (*Arenaria interpres*) during the breeding period on Rowley Island in the Canadian Arctic (latitude of 69°N). As comparative data on water turnover in free-living shorebirds

has not been published (Nagy and Peterson 1988), we also present our measurements of water-turnover rate, obtained during the field trials on turnstones.

Ruddy Turnstones are extremely wide ranging in the nonbreeding season, occurring along rocky, sandy and muddy coastal shores, from the North Temperate Zone to the Tropics and further to the south (Boere 1984, Cramp and Simmons 1983, Morrison and Ross 1989). They are only infrequently seen inland. Ruddy Turnstones have a wide latitudinal breeding range too, both in the Palearctic (55°N to 79°N) and Nearctic (63°N to 83°N), indicating a large variation in climatic conditions encountered during the breeding season. Ruddy Turnstones breed in rather dry, open habitats with low vegetation, from salt-marsh areas and small stony islands in and around the Baltic Sea (Bergman 1946, Cramp and Simmons 1983) to tundra slopes in the Canadian High Arctic (Nettleship 1973, Morrison and Piersma in prep.). The impressive geographical spread of this species suggests a large capacity to adapt physiologically to a range of climatic conditions (from cold and wet to hot and dry) by adjustments related to metabolic rate and water balance.

Although we acknowledge the existence of subtle behavioral mechanisms that affect the relationship between energy expenditure and diurnally fluctuating climatic variables (Cartar and Montgomerie 1985), we have taken a rather coarse-scale approach by relating the energy expenditure measured during the course of one or more days—using both standard meteorological methods and heated taxidermy bird models (Bakken et al. 1981, 1985)—to the average climatic conditions.

#### STUDY AREA AND METHODS

*Study area and field observations*—This study was carried out from 27 June to 18 July 1989 on the west-central coast of Rowley Island, Foxe Basin, N.W.T., Canada (68°56'N, 79°18'W). Our base camp was at an abandoned radar station close to an airstrip. We conducted experiments on Ruddy Turnstones found nesting in two main study areas. Near North Lake (ca. 95 ha), a few kilometers north of the station, five pairs nested in 1989. Near Butterfly Lake (ca. 135 ha), a few kilometers south of the station, the population fluctuated between five and eight pairs over a five-year period (1986–1990;  $\bar{x}$  = 6.6 pairs; 7 in 1989), with many banded birds returning to the study area from year to year (in prep.). Ruddy Turnstone nests were typ-

ically located on well-drained slopes or on raised beach ridges with moderate tundra vegetation cover consisting principally of *Dryas* sp. and lichens.

Nests were found by visually following alarm-calling birds returning to their eggs. Ruddy Turnstones were caught at the nest with walk-in traps and banded with aluminum and color bands. They were sexed on the basis of characteristic plumage differences (Ferns 1978, Whitfield 1986). Birds and eggs were weighed using Pesola spring balances; dimensions were measured with rulers and vernier calipers. Nests were checked every two to five days.

*Doubly-labeled-water protocol*.—The Ruddy Turnstones selected for doubly-labeled-water measurements were captured with walk-in traps, usually within 10 min of setting the trap, and were banded, weighed and measured. To obtain background values of the stable isotopes, a few small blood samples (25–50  $\mu$ l) were taken from the brachial vein in glass capillary tubes, which were sealed immediately by melting the ends. In the ventral region of the bird, we subcutaneously injected 1.9 to 2.5 ml of doubly-labeled water, consisting of 34% by volume of 99.84%-enriched  $^2\text{H}_2\text{O}$  (deuterium-oxide), and 66% by volume of 90.10%-enriched  $\text{H}_2^{18}\text{O}$ . In order to minimize stress in the injected bird, the doubly-labeled water was made up as "physiological saline" (0.9% NaCl), and was warmed to about 30°C by the researcher's body heat. The bird was then retained in an aerated dark space for an average time of 100 min (range 70–125 min) to allow the doubly-labeled water to be distributed evenly in its body. Thereafter, another series of blood samples was taken, and the bird weighed and released. In most cases it went off to bathe or preen, its partner having taken over incubation duties. Observations showed that handled birds were back on the nest within a few hours. After one to three days, we recaptured the experimental individuals on the nest, usually with an adapted Fundy pull trap (Hicklin et al. 1989), when the birds were bled again. In three cases, trapping and sampling were repeated on the same individual after a further interval of one day. Checks during the experimental periods indicated that the behavior of the injected birds appeared normal without exception.

The blood samples were stored in cool, dark conditions for six months. Isotope levels were measured with a mass spectrometer (Laboratory for Isotope Physics, University of Groningen). All calculations on water turnover and energy expenditure were made by the  $\text{D}_2\text{ONEW}$  software supplied by the same laboratory. Background concentrations were 0.01430 atom percent for  $^2\text{H}_2\text{O}$  and 0.1984 atom percent for  $\text{H}_2^{18}\text{O}$  ( $n$  = 3 birds). Percentage of body water was calculated by back-extrapolation of the  $\text{H}_2^{18}\text{O}$  enrichments above the average background concentration to the time of injection. The water-turnover values represent the averages of water influx and efflux. In all experiments, the mean water influx was  $0.97 \pm \text{SD of } 3.16 \text{ g/day}$

lower than water efflux, and the difference was similar to the daily mass loss the birds had during the experiments ( $\bar{x} = 1.09 \pm 2.2$  g/day). The daily energy expenditure (DEE) was calculated from the estimated CO<sub>2</sub> 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<sub>2</sub> as recommended by Gessaman and Nagy (1988). This estimate of DEE is robust and not susceptible to small deviations in RQ and energy-equivalent values (Gessaman and Nagy 1988) and, therefore, we use it for the entire period, including feeding bouts.

*Estimating maintenance metabolism.*—Maintenance metabolism (called “thermostatic costs” by Piersma et al. 1991) is defined as the net energy expenditure required to maintain a core temperature of about 41°C, excluding the costs of activity and tissue synthesis. Maintenance metabolism is the sum of the lowest rate of energy expenditure of homeotherms (i.e. BMR) and a possible extra “thermoregulation cost” under conditions where the environmental temperature causes the birds to produce extra heat to maintain their core temperature (i.e. below the lower critical temperature). To characterize the thermal environment we used a measure, called the “standard operative temperature” ( $T_{es}$ ), that combines the effects of air temperature, wind speed and solar radiation on heat loss (Bakken 1980, 1992).

In our study, the maintenance metabolism that Ruddy Turnstones experienced ( $M_{\text{maint, rutu}}$ ) was measured using three heated taxidermy mounts of Red Knots (*Calidris canutus*). One mount was placed in hummocky vegetation to simulate the situation of birds in vegetated habitats and on the nest, and two mounts were placed on a tundra ridge (measurements with the latter two never differed by more than 15% of the lower value, and were averaged). The mounts were calibrated in the laboratory under standard climatic conditions (wind speed = 1 m/s, range of air temperatures, no radiation) as described by Wiersma and Piersma (1994) before and after the study period.  $M_{\text{maint, rutu}}$  and  $T_{es}$  in the two microhabitats were calculated from the standardized heat loss of the mounts by equations 4 and 2a in Wiersma and Piersma (1994), using a body temperature of 41°C and a conductance ( $K_{es}$ )-value. The  $K_{es}$  value, 0.062 W/°C instead of 0.055 W/°C, was based on the average free convection value of 0.0505 W/°C for Ruddy Turnstones (Kersten and Piersma 1987), multiplied by a factor of 1.22 for forced-convection conditions obtained for Red Knots by Wiersma and Piersma (1994). We believe that Red Knot mounts represented Ruddy Turnstones fairly well in view of their similar mass (100–130 g), size (e.g. wing length of 16–17 cm), BMR (ca. 1 W), and free convection conductance (ca. 0.05 W/°C; see Kersten and Piersma 1987, Piersma et al. 1991). The heated taxidermy mounts were located at a maximum distance of 5 km from the experimental nests. Throughout

the experimental periods an automated data logger (Squirrel, Grant Instruments, Cambridge, United Kingdom) on the site registered the power requirements of the models at 20-s intervals (as well as air temperature, see below) and averaged them over 0.5-h periods. In presenting values for  $M_{\text{maint, rutu}}$  and  $T_{es}$ , we assume that Ruddy Turnstones spent 75% of their time in vegetated habitats and 25% on exposed tundra ridges (estimates based on our field observations over entire 24-h daylight period).

*Meteorological measurements.*—Throughout the experimental work, we recorded air temperature near the heated taxidermy mounts on the tundra ridge with a thermistor (NTC) placed under a sun screen. Every 0.5 h or 1 h, we recorded the global solar radiation with a Kipp solarimeter, the air temperature with a calibrated electronic probe and the wind speed with a calibrated cup anemometer at the base station, which was about 8 m higher than the study areas.

To place the observations made at Rowley Island in 1989 on a broader time scale, we analyzed the climatic data collected between 1958 and 1990 at the weather station at Hall Beach (68°47'N, 81°18'W) located 80 km WSW of our study area. There were relatively high correlations ( $r = 0.68$ – $0.70$ ,  $P < 0.01$ ) between the daily averages of air temperature and wind speed measured on Rowley Island for 15 days during the study period in 1989 and the averages of measurements taken every 3 h at Hall Beach on the same days (Fig. 1). The correlation between the daily averages of global solar radiation at the two sites is weakest ( $r = 0.45$ ,  $P < 0.05$ ), but values for Rowley Island were biased upwards in a systematic way, since we routinely did not make measurements during the nighttime low from 0100 to 0600 ST. The highest correlation between the three climatic variables at Rowley Island and Hall Beach ( $r = 0.77$ ) was given by  $T_{es}$ , the integrator of these variables (see below).

Having shown the correlation between the climatic conditions on Rowley Island and at Hall Beach, the next step was to predict maintenance metabolism of an average Red Knot ( $M_{\text{maint, knot}}$ ) based on air temperature, wind speed and global solar radiation in a microhabitat located on the tundra behind a hillock. The equation used to predict  $M_{\text{maint, knot}}$  (in Watts), derived by Wiersma and Piersma (1994), is as follows:

$$M_{\text{maint, knot}} = (0.045 + 0.00707u^{0.75})(41 - T_a) - 0.0014R_g \quad (1)$$

where  $u$  is the wind speed in m/s.  $T_a$  is the air temperature in °C, and  $R_g$  is the global solar radiation in W/m<sup>2</sup>. From a total of 342 direct measurements of maintenance metabolism ( $M_{\text{maint, rutu}}$ ), made every 0.5 h between 28 June and 18 July 1989 using heated taxidermy mounts for an average microhabitat use as outlined in the previous paragraph, and measurements of the three relevant climatic variables, we estimated that  $M_{\text{maint, rutu}}$  was a linear function of

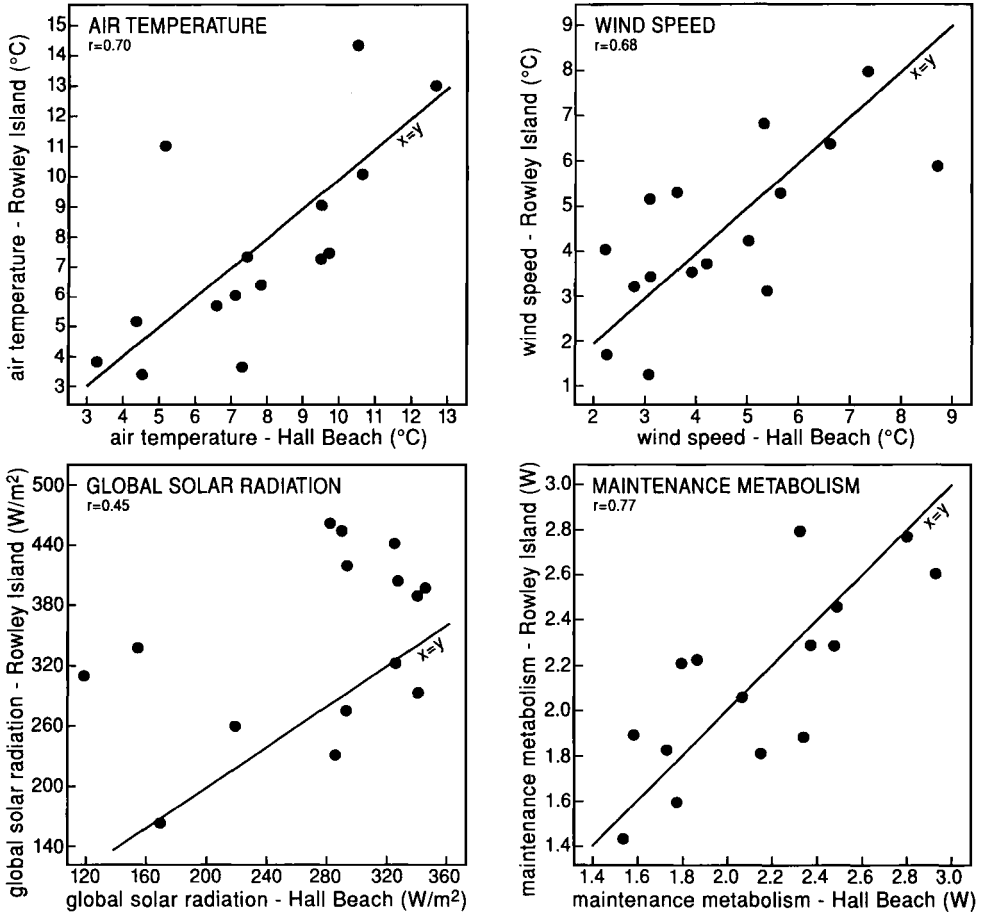


Fig. 1. Correlations between daily averages of three climatic variables measured on Rowley Island and at Hall Beach on 15 days between 28 June and 18 July 1989, and correlation between calculated maintenance metabolism incurred by Ruddy Turnstones at two sites for same set of days. Equations (1) and (2) in text are required to predict maintenance metabolism from air temperature, wind speed, and global solar radiation.

$M_{\text{maint, knot}}$  according to the following equation:

$$M_{\text{maint, rutu}} = 0.883M_{\text{maint, knot}} + 0.558 \quad (2)$$

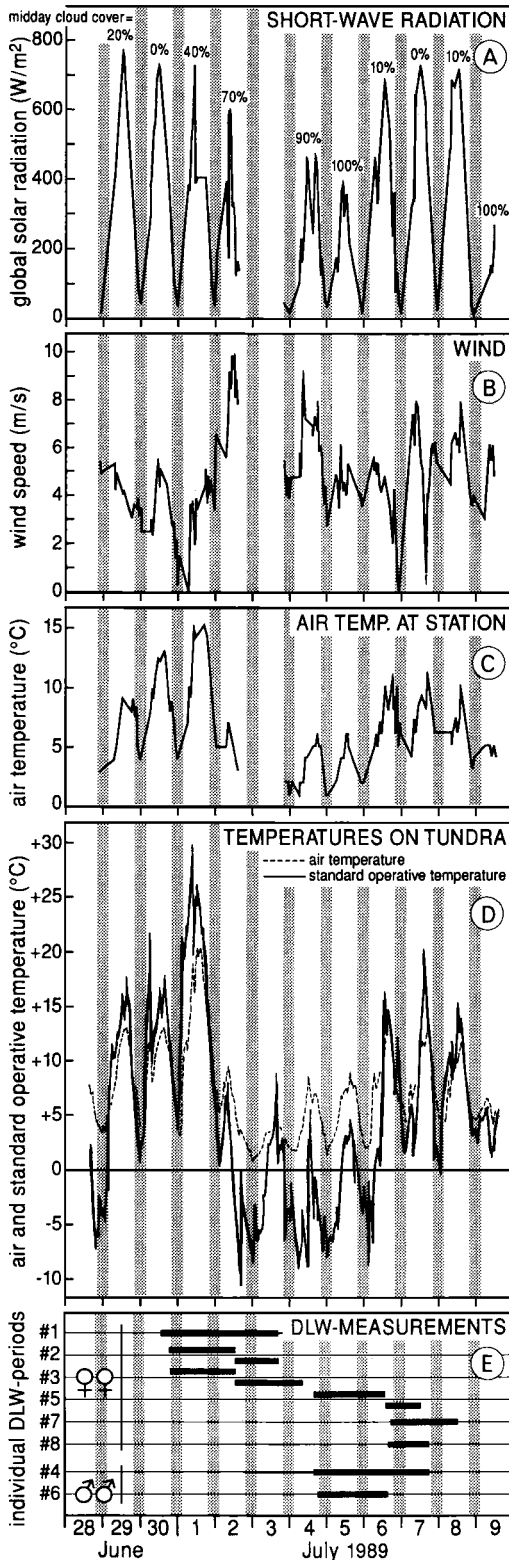
( $r^2 = 0.83, P < 0.01$ ). Using equations (1) and (2), maintenance metabolism of Ruddy Turnstones in the Foxe Basin could be calculated for all breeding seasons (defined here as 21 June–20 July) for which climatic data are available.

**Statistics.**—Data manipulations were made in Lotus 123 and the statistical analyses were made using SYSTAT (Wilkinson 1990). In order to investigate any categorical and continuous effects on DEE, the “multivariate general linear hypothesis (MGLH)”-procedures of SYSTAT were used. We constructed a mixed model similar to ANCOVA, which incorporated characteristics of the classic ANOVA (for the category variables “individual” or “sex”) and multiple-regres-

sion models (for the continuous variables maintenance metabolism,  $T_{\text{ea}}$  and  $T_{\text{a}}$ ).

RESULTS

There were clear diurnal patterns in the climatic variables measured repeatedly between 29 June and 9 July 1989 on Rowley Island (Fig. 2), in spite of the attention often given to the supposed “constancy” of arctic conditions (e.g. Remmert 1980, but see Cartar and Montgomerie 1985). Although daylight was continuous, values for global solar radiation varied between 800 W/m² at midday with clear skies and less than 10 W/m² at midnight. Air temperatures



fluctuated in a rather similar manner. Imposed on the diurnal fluctuations in radiation and temperature, there was a period of cold from 2 to 5 July, during which there was little sun, and the winds were stronger. The standard operative temperature ( $T_{es}$ ) experienced by the Ruddy Turnstones followed air temperature ( $T_a$ ) rather closely, but was more extreme. On days with low air temperatures, there was often a strong wind and cloud cover (i.e. little radiation) and  $T_{es}$  was usually lower than  $T_a$ , but on calm and sunny days  $T_{es}$  was usually higher than  $T_a$ . We were fortunate in measuring doubly-labeled-water loss over periods with rather varied climatic conditions (Fig. 2), especially when successive measurements of the same individual were made.

We obtained energy and water-turnover measurements for eight individual Ruddy Turnstones, two of which were males. With three females we made two successive measurements by recapturing and bleeding them twice (Table 1). The eight individuals had an average mass of  $109.0 \pm 6.2$  g and metabolism was measured over an average period of  $60.11 \pm 21.75$  h during which they lost an average of  $2.3 \pm 4.3$  g body mass. Of the six experimental nests, five successfully hatched chicks, while the fate of one (female 1) is unknown. The chicks of females 3 and 5 hatched on 15 July, the very day when mosquitoes first appeared. The three remaining experimental nests, occupied by female 2, paired male 6/female 7, and paired male 4/female 8, all had chicks that hatched on 17 July. With an incubation period of 22 to 24 days (Bergman 1946), and an average nest hatching date of 16 July, incubation started on 23 June. All doubly-labeled-water experiments (30 June–8 July), therefore, were conducted during the second week of incubation (i.e. halfway).

The average water content of the eight sampled individual Ruddy Turnstones was  $75.8 \pm 4.2\%$  based on fresh body mass. The average water turnover was  $97.1 \pm 22.9$  g/day, and the

Fig. 2. Fluctuations in (A) global solar radiation, (B) wind speed, (C) air temperature measured at base camp, and (D) air temperatures and standard operative temperatures measured on a nearby tundra ridge between 28 June and 9 July 1989 on Rowley Island, Foxe Basin. Shown in relation to timing of doubly-labeled-water experiments on eight individual Ruddy Turnstones (E, see Table 1).

TABLE 1. Basic data and results of doubly-labeled-water (DLW) measurements on individual Ruddy Turnstones studied on Rowley Island. For some individuals, two successive blood samples were obtained and, hence, two values of water turnover and daily energy expenditure (DEE) are available. Climatic variables maintenance metabolism, standard operative temperature ( $T_{es}$ ) and air temperature ( $T_a$ ) based on averages of all measurements taken every 0.5 h during experimental periods.

Individual no. and sex*	Start of experiment <sup>b</sup>	Duration <sup>c</sup> (h)	Mass (g)		DLW measurements			Climatic variables			
					Water		DEE (W)	Maintenance metabolism (W)	$T_{es}$ (°C)	$T_a$ (°C)	
					Content (%)	Turn-over (g/day)					
1	F	30 June (14, 14)	74.8	106	-2	77.9	93.98	3.925	2.14	6.49	7.57
2-A	F	30 June (18, 50)	41.9	117	-3	70.0	87.86	2.832	1.81	11.74	10.37
2-B	F	2 July (12, 45)	29.7	114	-7	68.6	81.34	4.465	2.71	-2.66	2.67
3-A	F	30 June (19, 04)	42.3	106	-4	73.8	91.33	3.118	1.83	11.54	10.32
3-B	F	2 July (13, 20)	42.9	102	-1	72.3	104.06	4.188	2.76	-3.51	2.48
5-A	F	4 July (16, 10)	46.1	105	-1	71.5	102.68	4.326	2.61	-1.11	5.42
5-B	F	6 July (14, 18)	22.8	104	2	71.8	105.68	3.547	2.04	8.02	7.21
7	F	6 July (18, 02)	42.9	112	-2	82.1	94.47	4.202	2.06	7.70	7.41
8	F	6 July (20, 18)	20.1	102	-3	78.5	55.25	3.907	2.01	8.51	6.98
4	M	4 July (15, 21)	72.1	105	-2	78.6	109.53	4.598	2.40	2.25	6.16
6	M	4 July (18, 03)	45.3	119	5	74.9	136.59	5.785	2.59	-0.75	5.49

\* F = female; M = male.

<sup>b</sup> Day and month (h, min).

<sup>c</sup> Duration of experiments is time elapsed between taking initial and final blood samples.

average DEE was  $4.21 \pm 0.72$  W. All values, including those for three experiments where individuals were sampled twice, are presented in Table 1, together with the experiment-specific values of maintenance metabolism,  $T_{es}$  and  $T_a$ .

Over all experiments, DEE, as measured by doubly-labeled-water experiments, correlated well with both  $T_a$  and  $T_{es}$ , the  $r$  values being  $-0.65$  and  $-0.74$ , respectively (Fig. 3). Of course, DEE correlated with maintenance metabolism as well, as it is, by definition, a mirror image of  $T_{es}$ . Although we were unable to show differences between individuals in the DEE-temperature relationships, either for  $T_a$  or  $T_{es}$  ( $P$ -values of 0.175 and 0.119, respectively) there was a significant sex effect ( $P$ -values of 0.005 and 0.017, respectively). The adjusted mean DEE of males (5.07 W) was a factor 1.31 larger than that of females (3.86 W). The temperatures  $T_a$  and  $T_{es}$  explained the variation in DEE remarkably similarly (Fig. 3). However,  $T_{es}$  was a slightly superior variable since: (1) the variation in the slopes of DEE on temperature in recaptured individuals was much smaller ( $SD/\bar{x} = 48.6\%$  for  $T_a$  and 19.6% for  $T_{es}$ ); and (2) in the ANCOVA with sex as the factor, slightly more of the variance was explained with  $T_{es}$  as the covariate (79.4%) than with  $T_a$  as the covariate (78.9%). The decision to sample a few individuals twice,

yielding two measurements of DEE, was made arbitrarily. The tendency of individual Ruddy Turnstones recaptured twice to show rather lower DEE levels (Fig. 3), therefore, must be a coincidence.

By plotting DEE on estimated maintenance metabolism, one can verify whether costlier climatic conditions lead to additional residual (i.e. activity, see below) costs. This is the case when the slope would be larger than one. Although the slope of DEE on maintenance metabolism, controlling for the effect of sex, was larger than 1 (1.302, SE = 0.383) and significantly different from zero ( $P = 0.009$ ), it was not significantly different from a slope of 1 ( $P = 0.453$ ).

### DISCUSSION

*Is the water turnover high?*—Over all 11 experiments, the water-turnover rate of Ruddy Turnstones (Table 1) averaged 96.6 g/day and was positively correlated with DEE ( $r = 0.57$ ), but the positive correlations were not found in two of the three individuals sampled twice. Nagy and Peterson (1988:table 1) provided two relevant allometric equations for making interspecific comparisons of water-turnover rates. For all sorts of carnivorous birds in the field, water flux (g/day) was related to body mass (g) as  $Y = 0.981 X^{0.746}$ , and for free-living seabirds  $Y =$

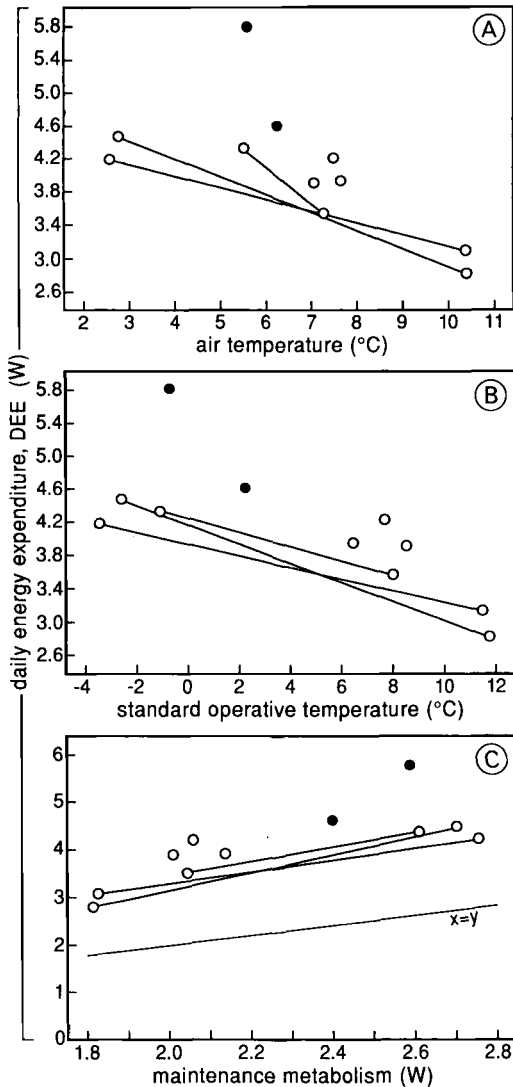


Fig. 3. Field metabolic rates (expressed as daily energy expenditure [DEE], in W) of free-living Ruddy Turnstones in relation to concurrent (A) average air temperature, (B) standard operative temperature, and (C) maintenance metabolism (note that Y-scale has been enlarged relative to A and B to allow comparison with  $X = Y$  line). Latter two variables measured using heated taxidermy mounts placed on exposed ridge or within tundra vegetation. Values for same birds are connected by lines. Data given in Table 1.

$0.270 X^{0.902}$ . For Ruddy Turnstones, which had an average body mass of 108.4 g on Rowley Island, these equations predict water-turnover rates of 32.3 g/day and 18.5 g/day, respectively, which are only 33% and 19%, respectively, of

the average empirical value obtained in this study. Thus, relative to carnivorous birds and seabirds, Ruddy Turnstones have a high water-turnover rate. Since it is likely that a high water turnover can be at least partially explained by a high DEE (this is so within our sample, see above), for comparative purposes we can also calculate the water economy index (WEI) according to Nagy and Peterson (1988). WEI is daily water flux rate (g/day) divided by DEE (kJ/day). For the 11 experiments with Ruddy Turnstones,  $WEI = 0.279 \pm 0.06$  g/kJ. This value is in the upper half of the distribution of WEI-values for free-living birds presented by Nagy and Peterson (1988:figs.18 and 19).

Assuming that the ash-free dry mass of the invertebrate prey ingested by Ruddy Turnstones on the tundra had an energy content of 21 kJ/g (Cummins and Wuycheck 1972), that the apparent metabolizable energy coefficient for ash-free dry matter was 0.70 (Castro et al. 1989), that the prey contained four times as much water as ash-free dry mass (pers. observ.), and that body mass was constant, it is possible to predict the water influx on the basis of DEE. We predict that the average food intake was  $24.0 \pm 4.4$  g ash-free dry mass per day during the 11 experiments listed in Table 1. This translates to an estimated average water intake of  $96.0 \pm 17.6$  g/day, which equals the empirical average water influx of  $96.1 \pm 20.0$  g/day. Although our estimates of water influx based on DEE and of predicted dry food intake are not independent and are undoubtedly inaccurate to an unknown extent, the close correspondence between the predicted and empirical values (based on parameter values chosen without hindsight) suggests that it is unlikely that excessive water drinking caused the high water-turnover rate in these Ruddy Turnstones. Water turnover is large as a consequence of a high DEE and the concomitant requirement of a high (and water-rich) food intake if body masses are to remain constant. The estimated total food mass required daily by Ruddy Turnstones in order to maintain energy balance is  $96 + 24 = 120$  g wet mass, and slightly exceeds their own body mass.

*DEE, maintenance metabolism, and estimating activity costs.*—The 30% higher DEE of male Ruddy Turnstones compared to females may have had three possible causes: (1) males were heavier and, therefore, had higher maintenance and transport costs; (2) males occurred in more exposed habitats incurring a higher maintenance

metabolism; and (3) males indulged in more energetically expensive activities. Males (average mass 112 g) were barely heavier than the females (108 g), but our occasional observations suggest that males were indeed more active in territory surveillance and defense, and occurred more frequently on exposed look-out posts than did females. Detailed individual time-budget studies of doubly-labeled birds are required to further examine the possibility of sexual differences in energetic costs throughout incubation and to attribute these costs to different activities (e.g. Brunton 1988a, b).

More of the variation in DEE was explained by the integrated measure of environmental temperature, standard operative temperature  $T_{es}$ , than by air temperature  $T_a$ , especially for the within-individual comparisons (Fig. 3). This finding encourages the use of heated taxidermy mounts, which are rather complicated measuring devices (Bakken 1992, Wiersma and Piersma 1994). Although the estimation of maintenance metabolism using these mounts additionally allows an interpretation of DEE in terms of thermoregulation and activity costs (Fig. 3C), the attribution of energy expenditure to the different cost factors is sensitive to correctly assigning the time spent in various microhabitats.

An estimate of the residual costs or "net cost of activity" (called net costs since the contribution of heat produced during activity to purposes of thermoregulation cannot be estimated and is assumed constant) can be gained from the regression of DEE on predicted values for maintenance metabolism. By definition, maintenance metabolism represents the nonactive part of DEE. The net activity cost includes the cost of incubation, the contribution of which also cannot presently be estimated (but see e.g. Drent 1975, Biebach 1979). Since the slope of DEE on maintenance metabolism is not significantly different from one, a good estimate of the net cost of activity can be made by averaging DEE over all 11 experiments ( $\bar{x} = 4.08$  W) and subtracting the predicted maintenance metabolism ( $\bar{x} = 2.27$  W). The average net cost of activity was thus  $4.08 - 2.27 = 1.81$  W. In this estimate, Ruddy Turnstones are assumed to spend 75% of their time in sheltered and 25% in exposed habitats. What would the estimates of maintenance and activity costs be if the birds spent the entire time either in the exposed areas or in sheltered places? In exposed habitats the values for maintenance and net activity costs

would be, respectively, 2.78 W and 1.30 W, and in sheltered habitats 2.10 W and 1.98 W. Estimates of the possible average net cost of activity of incubating Ruddy Turnstones, therefore, vary by a factor of 0.72 to 1.09 relative to the most likely estimate of 1.81 W, based on the given assumptions of time spent in sheltered and exposed habitats.

*Is breeding in Arctic costly for climatic reasons?*—BMR of Ruddy Turnstones has been reported as 0.99 W (Kersten and Piersma 1987). Of the average daily energy expenditure of 4.08 W, one-quarter ( $0.99/4.08$ ) thus is accounted for by BMR, 31% by the cost of thermoregulation (i.e.  $2.27 - 0.99 = 1.28$  W;  $1.28/4.08 = 0.31$ ), and the rest (almost one-half; 44%) by the net cost of activity. If the cost of activity were partially due to the level of foraging and food intake required to sustain a relatively high DEE, then the cost of activity would be higher than under favorable climatic conditions. Therefore, at least 31% but possibly more (40%, assuming the cost of activity to be 20% lower under thermoneutral conditions) of the DEE is due to the cost of climatic conditions in the Arctic study area. Taking this potential saving of 40%, the ratio between DEE and BMR would decrease from a factor of 4.1 to 2.5. This suggests that the Arctic is indeed a costly place for Ruddy Turnstones to breed, at least in comparison to climatically "neutral" places.

Drent and Daan (1980) were the first to argue for the existence of a maximum sustainable level of energy expenditure, or "metabolic ceiling," above which the fitness of the expending individual would decline steeply. From studies on the energy expenditure of breeding birds, they deduced that this metabolic ceiling was about four to five times greater than BMR. In spite of some disagreement in the literature as to the numerical value of this BMR-related factor (Peterson et al. 1990, Weiner 1992), there is now strong experimental evidence for the existence of a metabolic ceiling in incubating birds (Masman et al. 1989). For the sake of the argument, let us assume that such a ceiling occurs in breeding Ruddy Turnstones at 4.5 times BMR (i.e. 4.5 W). With an activity cost of 1.8 W, turnstones would have  $4.5 - 1.8 = 2.7$  W leeway to cover maintenance metabolism. How does maintenance metabolism incurred by Ruddy Turnstones in Foxe Basin vary from year to year, and is the metabolic ceiling often exceeded?

*Yearly variability and long-term trends in main-*



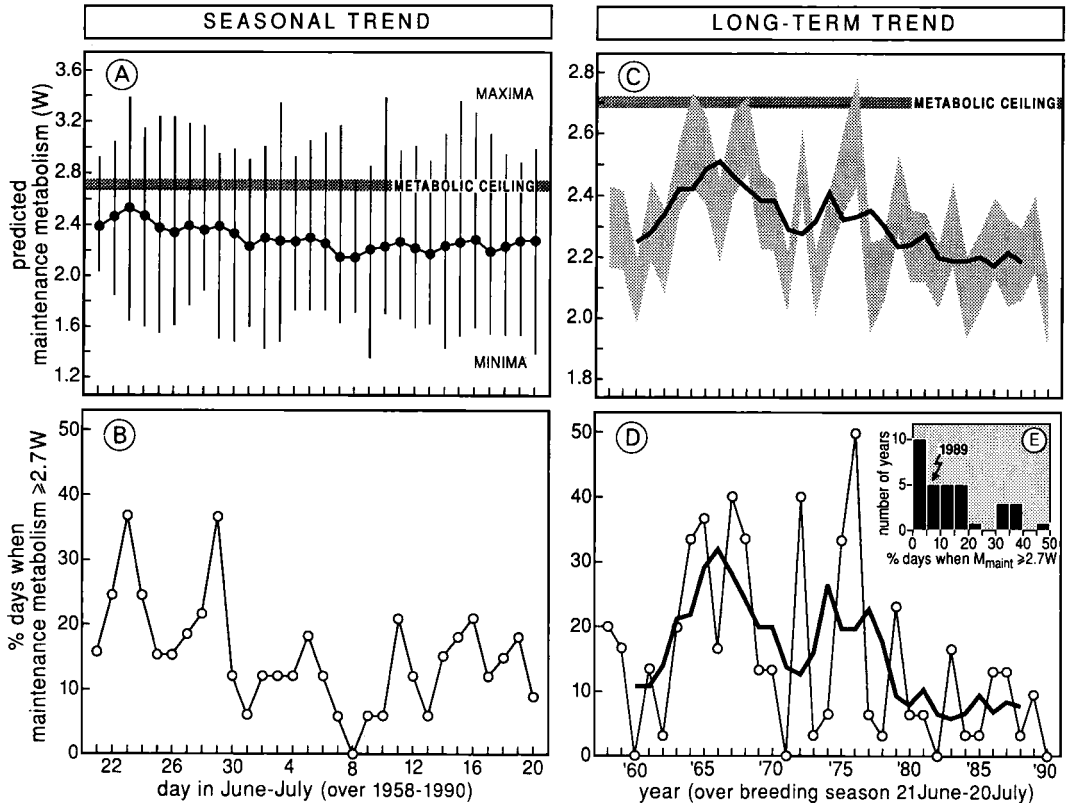


Fig. 4. Seasonal averages and long-term trends in maintenance metabolism of Ruddy Turnstones during breeding season (i.e. period of incubation, 21 June–20 July) in Foxe Basin, N.W.T., Canada, based on climatic data from Hall Beach. (A) Estimated maintenance metabolism predicted from air temperature, wind speed, and global solar radiation derived from equations (1) and (2) during course of breeding season. Vertical lines enclose date-specific minima and maxima over period 1958–1990. (B) Percentage of years when predicted maintenance metabolism on that date was larger than suggested "metabolic ceiling" (see text) of 2.7 W. (C) Trends in predicted maintenance metabolism during breeding season for years 1958–1990. Shaded area encloses 95%-confidence intervals of means, and heavy line connects the five-year running averages. (D) Percentage of days per breeding season on which maintenance metabolism was larger than metabolic ceiling of 2.7 W. Heavy line connects five-year running averages. (E) Frequency distribution of percentage of days where maintenance metabolism exceeds 2.7 W. Value for study season (1989) is indicated.

*tenance metabolism.*—The climatic data from Hall Beach during the period 1958–1990 suggest a slight decrease in maintenance metabolism in the course of the entire breeding season (21 June–21 July; Fig. 4A,B). Maintenance metabolism exceeded the inferred metabolic ceiling of 2.7 W on an average of 15.3% of the days per season. The variation between years over all dates ( $SD/\bar{x} = 89.2\%$ ; see Fig. 4C) was much larger than the variation between dates over all years ( $SD/\bar{x} = 52.9\%$ ; see Fig. 4A). Between 1958 and 1967, maintenance metabolism during the breeding season increased by a factor 1.14, from 2.2 W to 2.5 W (Fig. 4C). Thereafter, mainte-

nance metabolism showed an almost continuous decrease by the same factor from 1967 to 1983, and has leveled off since. There was considerable variation in the percentage of days per season when maintenance metabolism exceeded the metabolic ceiling (Fig. 4D). Between 1963 and 1976, there were seven seasons when more than 30% of the days were very costly to Ruddy Turnstones. Our study season (1989) belonged to the majority of seasons in which the weather was mild, and when the metabolic ceiling was exceeded for only a few days ( $<10\%$ ; Fig. 4E). In 1989 the turnstones bred successfully.

Although we are able to suggest that the maintenance metabolism of breeding Ruddy Turnstones can reach potential critical levels in Foxe Basin, the results do not enable us to evaluate the repercussions of the described variation in climate on breeding success, timing of southward migration and parental survival. Thus, it would be profitable to examine large-scale patterns in climate on the basis of the equations presented here, and to investigate any correlations between abundance parameters in the breeding and nonbreeding areas of Ruddy Turnstones. The 1960s were probably an energetically difficult period for Ruddy Turnstones in Foxe Basin, and this must have been true for other locally breeding bird species as well. Further field research should be directed toward relating energy expenditure to breeding performance, survival and site fidelity and to quantifying the maintenance component.

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