

High Levels of Energy Expenditure in Shorebirds; Metabolic Adaptations to an Energetically Expensive Way of Life

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HIGH LEVELS OF ENERGY EXPENDITURE IN SHOREBIRDS; METABOLIC ADAPTATIONS TO AN ENERGETICALLY EXPENSIVE WAY OF LIFE

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1. INTRODUCTION

The ability to maintain a favourable energy balance is one of the major factors that determines survival or mortality of free-living birds. King (1974) was the first to state that the daily energy expenditure (DEE) of free-living unrestrained adult birds parallels basal metabolic rate (BMR, defined as the rate of energy expenditure of an inactive, post-absorptive animal in a thermoneutral environment during the resting phase of its daily cycle) as a function of body weight. Drent *et al.* (1978) showed that DEE converges at 2.6 BMR, whereas cage existence metabolism (EM) at 10 °C amounts to approximately 2 BMR.

Both King (1974) and Drent *et al.* (1978) believed that DEE was geared to BMR at the species level, implying that a high BMR relative to the species' body weight should coincide with a relatively high DEE, but none of these authors gave any explanation for the phenomenon. Several studies on daily food intake in shorebirds indicate that DEE in these species tends to be high for birds of this size (Smith 1975, Hulscher 1974, 1982, Goss-Custard 1977, Pienkowski 1982). Unfortunately, no measurements of BMR were available for shorebirds at that time, so it was not possible to say whether these high DEE values were accompanied by a relatively high BMR. We measured BMR and EM in three shorebird species, Turnstone *Arenaria in-*

terpres, Grey Plover *Pluvialis squatarola* and Oystercatcher *Haematopus ostralegus* and will show that both are above the values expected on the basis of their body weights. We hypothesize that a high DEE requires a high BMR, and develop a functional explanation for the phenomenon.

Most species of shorebirds are migratory. To fuel their migratory flights they periodically deposit large amounts of fat (McNeil 1969, Summers & Waltner 1978, Pienkowski *et al.* 1979, Davidson 1984, Johnson 1985). The weight patterns of our captive shorebirds closely resembled those of their conspecifics in the wild. This enabled us to measure the costs of fat deposition and to determine how energy expenditure relates to body weight in the individual bird.

2. METHODS

The study was conducted in the period October 1980–July 1983. Experimental birds were caught with mistnets (Turnstones, Grey Plovers) or cannon nets (Oystercatchers) in the Wadden Sea area, The Netherlands (53° 10'–53° 30' N, 4° 50'–6° 20' E). Two groups of Turnstones were kept. Group A consisted of three birds caught in their first calendar year in August 1982. Group B varied in number (3, 4, 5 or 6) and consisted of four adults caught in January 1981, one adult and a juvenile caught in August/September 1981 and three adults caught in August 1982. Group B suffered some losses: two individuals escaped in November 1981 and another bird died in June 1982. Three adult Grey Plovers were caught in late May 1982. Seven adult male Oystercatchers were caught in October 1980 and another adult male was brought to the laboratory in December 1980. Six of these birds survived the three-year study period.

The birds were kept in outdoor cages near the Zoological Laboratory in Haren, The Netherlands (53° 11' N, 6° 36' E). The cages measured 4 by 1.5 m. The lower 0.5 m of the sides (with a total height of 1.5 m) were made of wood to provide the birds some shelter. The bottom of the cage was covered with regularly refreshed sand, and a few elevations were provided. A 30 by 60 cm basin with continuously flowing water to a depth of 3–7 cm gave the birds the opportunity to drink and to bathe. A male and a female Oystercatcher were kept indoors from November through March 1982 at constant air temperature (19 °C) but with the normal photoperiodic regime.

The birds were fed with commercial (mink-)food pellets,

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Table 1. Basal Metabolic Rate (Watts) and the Lower Critical Temperature (LCT) of individual shorebirds.

Species	Individual	Body weight (g)		BMR (W \pm SD)	n	LCT (°C)	BMR Predicted ^a
		mean	range				
Turnstone	A	117	111–120	0.99 \pm 0.03	3	22	0.74
	B	118	108–143	0.98 \pm 0.04	4	23	0.74
	C	106	—	1.01	1	— ^b	0.69
Grey Plover	A	169	160–173	1.52 \pm 0.06	3	15	0.97
	B	251	240–256	1.78 \pm 0.15	3	16	1.29
	C	259	259	2.04 \pm 0.21	2	20	1.32
Oystercatcher	A	543	540–545	2.71 \pm 0.02	2	9	2.27
	B	479	479	2.68 \pm 0.00	2	— ^b	2.07

^a Aschoff & Pohl's (1970) allometric relation for non-passeriform birds in the resting phase of their daily cycle converted into appropriate units BMR (Watts) = 3.56 BW (kg)^{0.734}.

^b Not determined.

consisting of 41% protein, 19% fat, 22% carbohydrates and 7% water (manufacturers indication). The energy content was determined with a Gallenkamp adiabatic bomb calorimeter and averaged (\pm SD) 22.8 \pm 2.3 kJ/g fresh weight (n = 3). Food was available *ad libitum*.

All captive birds were weighed with Pesola spring balances at regular, usually one week intervals. Readings were accurate to the nearest 1 g (Turnstones, Grey Plovers) or nearest 5 g (Oystercatchers). Food was removed from the cages at about 10.00 and renewed after the birds were weighed in the afternoon. The average daily food consumption per bird was calculated as total food consumption divided by the number of days between two consecutive weighings and the number of birds in the cage. The water content of both the food presented (average \pm SD = 7.2 \pm 2.8%, n = 7) and the food removed (6.9 \pm 4.5%, n = 2) was close to the figure supplied by the manufacturer. Sometimes, after periods of heavy rains, the food was obviously wet and these data were excluded from the analysis. The average of the body weights of birds from one cage, determined after a period during which total food consumption was measured, is called average body weight. The average daily weight change per bird was calculated from the difference between average body weights at the start and end of such a period of food intake measurement, divided by the length of that period.

We determined the assimilation efficiency of Oystercatchers, individually confined to small outdoor cages (c 0.2 m²). Every two or three days the amount of food eaten by the bird was measured and the faeces produced collected and dried to constant weight at 60 °C. Energy content of both food and faeces was determined with a Gallenkamp adiabatic bomb calorimeter.

Average daily air temperature (T_a) was obtained from the weather station at Eelde airport, a few km from the laboratory. Daily air temperatures were averaged over the periods between successive weighings.

Oxygen consumption was measured in an open flow respirometer using a Taylor Servomex OA 184 paramagnetic analyzer. The birds were weighed before and after each testing procedure. Early in the afternoon the birds were put in the metabolic chamber. Measurements were taken six to ten hrs later during the night. To avoid increased metabolic rates due to frequently changing temperatures (Prinzinger 1982), each bird was tested at only two or three different air

temperatures in a night. Consequently, most measurements cover periods of constant oxygen consumption of several hours (minimal test periods: Turnstones 1 h, Grey Plovers 0.5 h and Oystercatchers 2 h). All data were corrected to standard temperature and pressure (0 °C, 760 mm Hg, dry gas). Metabolic rate, expressed in Watts (= J/sec), was then calculated from oxygen consumption, assuming an energetic equivalent of 20.08 kJ/l O₂.

3. RESULTS

Metabolic rate at rest

Fig. 1 shows the relationship between metabolic rate and air temperature for one individual of each species. The data of the other birds followed the same pattern but there were some slight differences between individuals. We therefore analyzed the data for each bird separately. Basal metabolic rates and lower critical temperatures (LCT) are presented in Table 1. In each bird BMR was well above the value predicted from the allometric relation between BMR and body weight derived by Aschoff & Pohl (1970). The discrepancies amounted to 37% in Turnstones, 50% in Grey Plovers and 24% in Oystercatchers. It is unlikely that these high levels were due to the testing procedure or to any systematic error in the apparatus. The BMR of Long-eared Owls *Asio otus* measured with the same equipment, were consistently lower than the Aschoff & Pohl (1970) prediction (Wijnandts 1984).

Metabolic rate increased linearly with decreasing air temperature below thermoneutrality (Fig. 1, Table 2). The regression equations extrapolate to temperatures between 35 °C and 45 °C when metabolic rate is set equal to zero,

Table 2. Standard metabolic rate in relation to the air temperature (T_a) for individual shorebirds. r^2 = explained variance.

Species	Individual	SMR(W)	r^2	n	T_b^a
Turnstone	A	$-0.048T_a + 2.02$	0.98	8	42
	B	$-0.053T_a + 2.19$	0.98	6	41
Grey Plover	A	$-0.064T_a + 2.47$	1.00	4	39
	B	$-0.078T_a + 3.03$	0.87	6	39
	C	$-0.085T_a + 3.82$	0.99	3	45
Oystercatcher	A	$-0.103T_a + 3.60$	0.97	3	35

^a Estimated body temperature, extrapolated value of T_b when SMR is set equal to zero.

Table 3. Measured and predicted Temperature Coefficients of individual shorebirds.

Species	Individual	Body weight (g)		Temperature coefficient (W/°C)		measured/ predicted
		mean	range	measured	predicted ^a	
Turnstone	A	118	111–121	–0.048	–0.037	1.30
	B	117	112–135	–0.053	–0.036	1.47
Grey Plover	A	169	168–173	–0.064	–0.045	1.42
	B	258	251–259	–0.078	–0.058	1.34
	C	286	259–310	–0.085	–0.062	1.37
Oystercatcher	A	540	540	–0.103	–0.090	1.14

^a Allometric equation derived by Kendeigh *et al.* (1977) for non-passeriform birds in winter $TC(W/°C) = -0.0022 BW(g)^{0.5886}$ ($n = 12$).

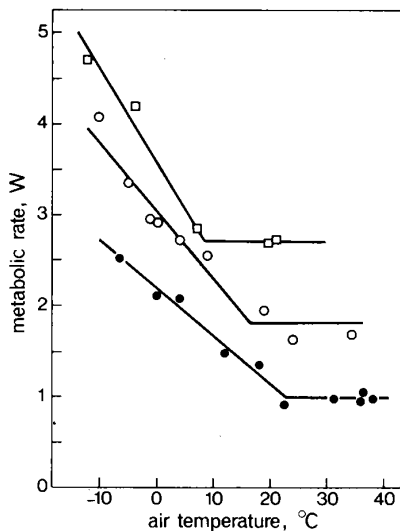


Fig. 1. Standard metabolic rate at night in relation to air temperature of three shorebird species. Data from selected individuals are shown. Squares; Oystercatcher A, open dots; Grey Plover B and closed dots; Turnstone B (see Tables 1 and 2).

i.e. close to the expected body temperature of about 40 °C. The temperature coefficients are high compared to values predicted by Kendeigh *et al.* (1977) (Table 3), indicating that these birds are relatively poorly insulated.

That metabolic rate increases with body weight in interspecific comparisons was already well known (for a review see Kendeigh *et al.* 1977). Our data on individual Grey Plovers (Table 1) indicate that this relation may hold in intraspecific comparisons as well. Since the weight differences between individuals were maintained throughout the study period, we infer that they reflect size differences between these birds.

Like many other migratory bird species, shorebirds display cyclic variations in their body weight over the annual cycle (Pienkowski *et al.* 1979). These variations are mainly due to the deposition or utilization of lipid reserves (Mascher & Marcström 1976, Summers & Waltner 1978). In our Turnstones these individual weight variations were much larger than the

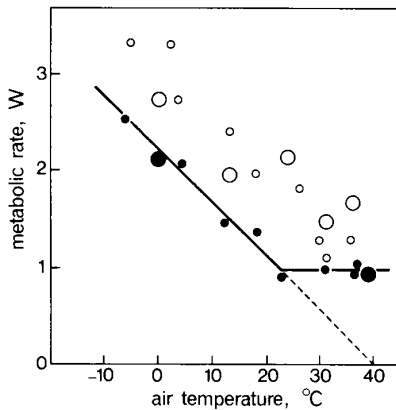


Fig. 2. Standard metabolic rate in relation to air temperature in Turnstone B during nighttime (closed symbols) and daytime (open symbols). Large dots show data points from measurements when the bird weighed 142–153 g, whereas small dots are from times when it weighed 110–120 g.

weight differences between individuals. Fig. 2 shows that even a 30% weight increase has no effect on the metabolic rate of a resting bird. This indicates that the metabolic rate of adipose tissue must be very small, as was suggested by Hayward (1965), who noticed that *Peromyscus* races with a high lipid content had a low weight specific metabolic rate.

Food consumption in outdoor cages

The daily food consumption of Oystercatchers was negatively correlated with air temperature below $T_a = 10^\circ\text{C}$ (Fig. 3), but was independent of air temperature above $T_a = 10^\circ\text{C}$. We did not find such 'zones of thermoneutrality' in daily food consumption of Turnstones (Fig. 4) and Grey Plovers (Fig. 5). However, the air temperature during the cage-experiments was

always below the lower critical temperatures of these species, as determined during energy consumption measurements of inactive birds (above).

Table 4 shows that in addition to air temperature, daily weight change also had a strong effect on daily food consumption. To increase its body weight by one g, a shorebird required 1.3 to 2.6 g of additional food.

Above, it was shown that fat reserves had no discernable effect on metabolic rate at rest. In contrast, active birds must carry the extra weight around. We therefore expected an effect of average body weight on daily food consumption in the caged (but active) birds. In all groups

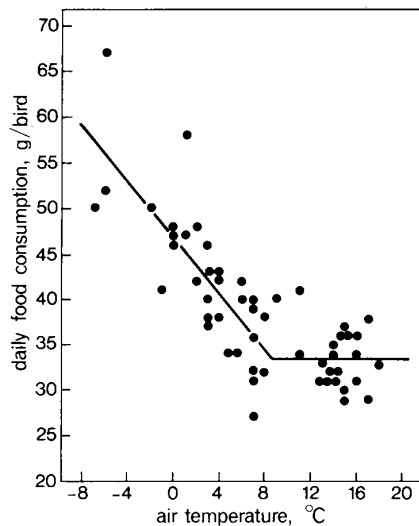
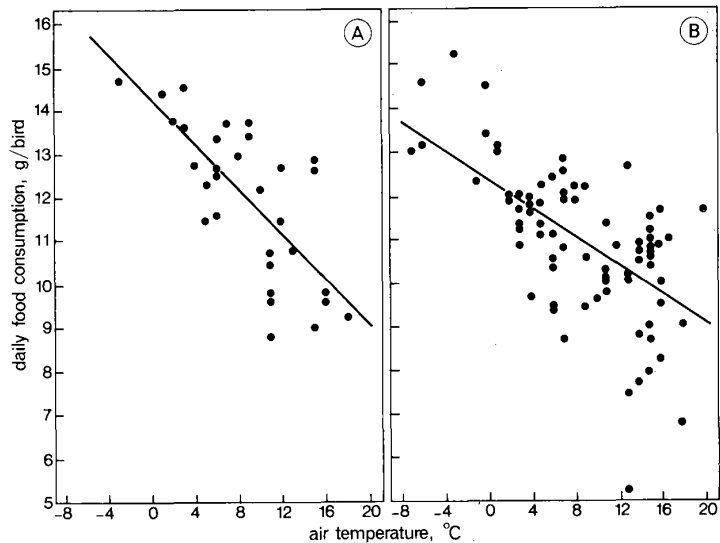


Fig. 3. Average daily food consumption of male Oystercatchers in relation to air temperature. Daily food consumption was corrected for the effect of daily weight change (DWC = 0; Table 4).

Table 4. Multiple regression equations that relate daily food consumption (g/bird) of three shorebird species in captivity to air temperature (T_a) and daily weight change (DWC). n refers to the number of different food measurements. All regression coefficients are significant at the 1%-level. r^2 = explained variance.

Species	Category	Daily food consumption	r^2	n
Turnstone	group A	$-0.20 T_a + 2.4 \text{ DWC} + 14.3$	0.76	40
Turnstone	group B	$-0.16 T_a + 2.5 \text{ DWC} + 13.7$	0.63	77
Grey Plover		$-0.47 T_a + 2.0 \text{ DWC} + 23.6$	0.84	30
Oystercatcher	$T_a \leq 10^\circ\text{C}$	$-1.56 T_a + 1.3 \text{ DWC} + 46.6$	0.66	34
Oystercatcher	$T_a > 10^\circ\text{C}$	$1.5 \text{ DWC} + 33.5$	0.26	21
Oystercatcher	indoors, $T_a = 19^\circ\text{C}$	$2.6 \text{ DWC} + 30.2$	0.51	12

Fig. 4. Average daily food consumption in relation to air temperature of Turnstones kept in separate cages (A: juveniles; B: adults). Daily food consumption was corrected for the effects of daily weight changes (DWC = 0) and average body weight (BW = 100 g).



of caged birds, body weight had a positive effect on daily food consumption, in addition to that of air temperature and daily weight change. This effect was only significant in group A of Turnstones. The discrepancy between group A and the other shorebird groups may be related to the relatively large range in body weight in group A (highest BW – lowest BW)/lowest BW \times 100% = 40%, compared with 25% in the other groups. When included in a multiple regression model, BW of Turnstone-group A explained an extra 11% of the variance in daily food consumption ($-0.27 T_a + 2.1 \text{ DWC} + 0.09 \text{ BW} + 4.4$, $r^2 = 0.87$). One extra g of food per day was thus needed to carry an additional 11 g of body weight.

Assimilation efficiencies for one Oystercatcher were 87% and 89%, and for the other bird 82%, at air temperatures between 10 and 15 °C. To estimate the EM (Kendeigh 1970) of our experimental shorebirds, we assumed that their average assimilation efficiency was 85%. Table 5 shows the dependence of EM on air temperature. The temperature coefficients (kJ/day °C) of 3.9 and 3.1 for the two groups of Turnstones are close to the value of 3.3 predicted by Kendeigh *et al.* (1977) for a non-passerine bird of 105 g under a LD 10/14 photoperiodic regime. However, the temperature coefficients of 9.0 for Grey Plovers and 30.3 for Oystercatchers are

much higher than the predicted values for birds of their body weight, 4.3 and 5.6 respectively.

4. DISCUSSION

4.1. COSTS OF FATTENING

Table 4 showed that 1 g change of body weight requires a 1.3 to 2.6 g difference in daily food consumption. Part of this variation may be due to differences in energy values of the tissues being deposited. The very low value of 1.3 was measured in outdoor Oystercatchers at air temperatures below 10 °C. This low value may have been caused by a strong intercorrelation between DWC and air temperature, which could lead to the positive effect on food consumption of DWC being underestimated and the negative effect of air temperature overestimated.

On average, a 1 g increase in body weight requires a 2.0 g increase in food intake, or $2 \times 22.83 = 45.66$ kJ/g. Body composition analyses of 82 Oystercatchers showed that, on average, weight differences consist of 85% fat, 10% water and 5% dry nonfat material (probably protein) (own obs., L. Zwarts pers. comm.). Energy values of fat and protein are 39.3 kJ/g and 17.8 kJ/g, respectively (Schmidt-Nielsen 1975) and the energy value of body weight-gain therefore equals: $(0.85 \times 39.3) + (0.05 \times 17.8) = 34.3$ kJ/g. Using these two averages, it means

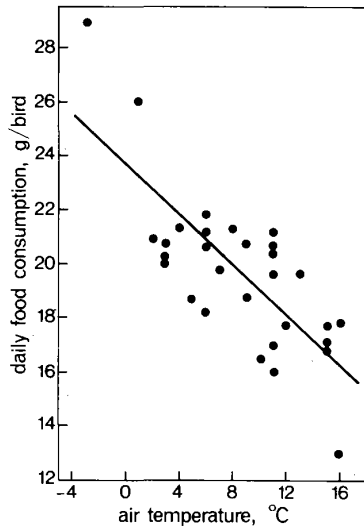


Fig. 5. Average daily food consumption of Grey Plovers in relation to air temperature. Daily food consumption was corrected for the effect of daily weight change (DWC = 0; Table 4).

that $34.3/45.66 \times 100\% = 75\%$ of the additional energy intake of shorebirds is deposited in body tissue. However, only 85% of the energy intake is actually assimilated, which implies that the energy deposition efficiency is $75/0.85 = 88\%$. Literature values for the energy deposition efficiencies of fat from protein, fat and carbohydrate substrates in Domestic Fowl *Gallus domesticus* are 61%, 84% and 75% respectively (Hoffmann & Schiemann 1971, cited by De Groote 1974).

4.2. LEVEL OF ENERGY EXPENDITURE

We have found that for three shorebird species BMR is between 24% and 50% above the predicted level for birds of their size (Aschoff & Pohl 1970). BMR of the Little Ringed Plover *Charadrius dubius* is also above the Aschoff & Pohl (1970) prediction by 34% (Kendeigh *et al.* 1977). Speakman (1984) measured BMR in adult Oystercatchers and Redshanks *Tringa totanus* and found them to be respectively 29% and 77% above prediction. Finally, Sanderlings *Calidris alba* have a BMR 41% above the expectation (Castro 1987). When we combine this information with our own results, the relationship between BMR and body weight of

shorebirds, as presented in Table 6 and depicted in Fig. 6, is best described by the allometric relation

$$\text{BMR (Watts)} = 5.06 \text{ BW(kg)}^{0.729}, \\ r^2 = 0.97, n = 6.$$

It is noteworthy that despite the small sample size, the exponent relating BMR to body weight (range 36 to 554 g) almost equals the 0.73 power generally encountered (Peters 1983, Calder 1984).

In addition to BMR, Fig. 6 shows all available values for cage EM of shorebirds at $T_a = 10^\circ\text{C}$. These data were derived from this study and from work by Gavrilov & Dol'nik, quoted by Kendeigh *et al.* (1977). We have not used their figures for Oystercatcher and Curlew *Numenius arquata*, since these certainly concern emaciated individuals, nor their value for European Woodcock *Scolopax rusticola* because this individual had an aberrantly high body weight. Drent *et al.* (1978: Fig. 6) found that EM at $T_a = 10^\circ\text{C}$ for Charadriiform birds (mostly gulls and auks) and waterfowl species with body weights between 100 and 1000 g, were approximately twice the level of BMR, predicted by Aschoff & Pohl's (1970) equation. As Fig. 6 shows very clearly, all EM-values for shorebirds lie above this line, but very near the line representing two times BMR as determined for shorebirds in this study. EM in shorebirds is related to body weight with the equation

$$\text{EM (kJ/ bird.day)} = 912 \text{ BW}^{0.704} \\ (r^2 = 0.96, n = 9),$$

and is proportional to BMR (the exponents are

Table 5. Existence metabolism (kJ/day) in relation to air temperature (T_a) of three shorebird species in captivity. The relationships between EM and T_a were calculated from the equations presented in Table 4, assuming the energetic value of fresh food 22.83 kJ/g (Methods) and the assimilation efficiency of the birds as 85% (see text).

Species	Existence metabolism	Average body weight (g)
Turnstone, group A	$- 3.9 T_a + 277$	105
Turnstone, group B	$- 3.1 T_a + 266$	105
Grey Plover	$- 9.0 T_a + 459$	220
Oystercatcher, $T_a \leq 10^\circ\text{C}$	$- 30.3 T_a + 904$	505
Oystercatcher, $T_a > 10^\circ\text{C}$	650	505

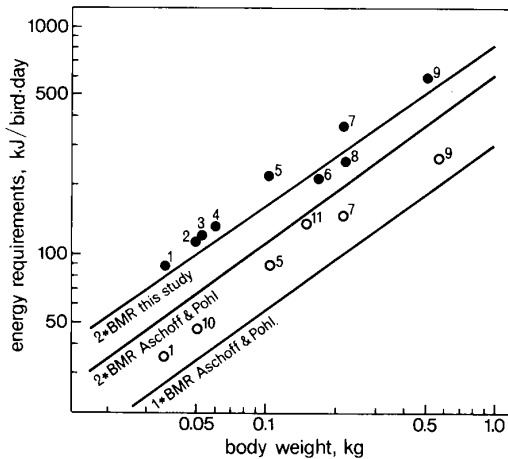


Fig. 6. Basal metabolic rate (open symbols) and cage existence metabolism at $T_a = 10^\circ\text{C}$ (closed symbols) of shorebirds in relation to body weight. Figures refer to different species. 1. Little Ringed Plover, 2. Ringed Plover, 3. Common Sandpiper *Actitis hypoleucos*, 4. Wood Sandpiper *Tringa glareola*, 5. Turnstone, 6. Ruff *Philomachus pugnax*, 7. Grey Plover, 8. Lapwing *Vanellus vanellus*, 9. Oystercatcher, 10. Sanderling and 11. Redshank. See text for data sources. Aschoff & Pohl's (1976) predictions for one, and two times BMR and our predicted line for two times BMR frame the observations.

0.704 and 0.729 respectively). Therefore, the finding of Drent *et al.* (1978) about the general level of the energy requirements of caged birds in relation to BMR still holds when we use the relatively high empirical values for BMR of shorebirds.

Although the foregoing EM-body weight comparison supports our suggestion that energy expenditure of shorebirds is relatively high, a cautionary note about such use of EM is required. We have shown above that in Oystercatchers EM is independent of air temperature at $T_a > 10^\circ\text{C}$ (very close to their LCT as determined during energy consumption mea-

surements at rest in the laboratory), but that no such zone of thermoneutrality was found in the two smaller species. Presumably this is because the maximum air temperatures during which EM was measured were about $18\text{--}20^\circ\text{C}$, which is below the LCT of these species. Over a range of species, the LCT may be above or below $T_a = 10^\circ\text{C}$, depending on body size. A comparison of the level of EM between species, at a given air temperature, thus incorporates a cost of thermoregulation for the smaller species, but not for the larger ones. This would cause the slope of the allometric relation between EM and body weight to go down. As will be shown below, costs of thermoregulation in shorebirds are considerable. It would therefore have been better to consider EM at thermoneutrality in all species, but these data are not presently available.

The DEE of free-living shorebirds seems to be relatively high as well. Table 7 summarizes the available information on net energy intake (NEI) of free-living shorebirds. These estimates should be considered minimum estimates, since in all but one case it was assumed that no food at all was taken outside the daylight period. We may equate net energy intake with DEE if we additionally assume that the values represent the intake of birds with constant energy content, which is obviously not the case during periods of rapid migratory fattening (e.g. May values for Grey Plovers and Bar-tailed Godwits *Limosa lapponica*). Outside these periods, DEE is on average 4.1–4.4 times Aschoff & Pohl's prediction of BMR. This is considerably higher than the multiplication of two to three times BMR which was derived by Drent *et al.* (1978) and Walsberg (1980), as the normal level of DEE in non-passerine birds over 10 g. When we use our prediction of BMR for shorebirds instead of As-

Table 6. Basal metabolic rate (BMR) and body weight (g) of six species of shorebirds. n refers to the number of different individuals per species on which the averages for BMR and body weight are based.

Species	Body weight	BMR(W)	n	Authority
Oystercatcher	554	2.91	4	Speakman 1984, this study
Little Ringed Plover	36	0.41	1?	Kendeigh <i>et al.</i> 1977
Grey Plover	226	1.78	3	This study
Sanderling	50	0.56	9	Castro 1987
Redshank	149	1.56	6	Speakman 1984
Turnstone	114	0.99	3	This study

Table 7. Net energy intake (NEI, kJ/bird.day) of free-living shorebirds as a function of basal metabolic rate (BMR). Values have been selected from studies where reasonably reliable information about the (absence of) nocturnal feeding was available. NEI was (re-)calculated from gross energy intake assuming an 85% assimilation efficiency. BMR (kJ/bird.day) was calculated from body weight (BW, kg) either by Aschoff & Pohl's (1970) equation $BMR = 308 BW^{0.734}$ (1) or by this study's equation $BMR = 437 BW^{0.729}$ (2, see text). In all but two studies it was assumed that no food was taken during the night. Petersen (1981) measured foraging activity throughout the night and assumed intake rate identical with daytime intake rate. Zwarts measured food intake when both low water feeding periods were in daylight hours.

Species	Locality	Period	Body weight	NEI	NEI/BMR (1)	NEI/BMR (2)	Authority
Oystercatcher	Wash, U.K.	January	0.555 ^b	1052	5.3	3.7	Goss-Custard 1977
Ringed Plover	Lindisfarne, U.K.	Aug., Sept., Apr.	0.070 ^c	159–192	3.6–4.4	2.6–3.1	Pienkowski 1982
Grey Plover	Lindisfarne, U.K.	Sept., Apr.	0.220 ^c	309–392	3.1–3.9	2.1–2.7	Pienkowski 1982
Curlew Sandpiper	Langebaan, S. Africa	year round	0.060 ^b	153	3.9	2.7	Puttick 1979, 1980
Bar-tailed Godwit	Lindisfarne, U.K.	Oct., April	0.300 ^c	610	4.8	3.4	Smith 1975
Redshank	Ythan, U.K.	April	0.183 ^b	405	4.6	3.2	Goss-Custard 1977
Curlew	Wadden Sea, Netherlands	July	0.925 ^b	1096	3.6	2.6	Zwarts pers. comm.
Grey Plover	Lindisfarne, U.K.	May ^a	0.250 ^c	698	6.3	4.4	Pienkowski 1982
Bar-tailed Godwit	Tipperne, Denmark	May ^a	0.300 ^b	886	7.0	4.9	Petersen 1981

^a period of migratory fattening.

^b given in text or table.

^c estimated from values in literature.

choff & Pohl's, we end up with a factor 2.9–3.1 (Table 7).

Hence, both at rest, and under restrained and unrestrained conditions, shorebirds utilize more energy than other non-passerine birds of their size, but the ratios between active/rest metabolism are almost identical to those in other bird species. We will try to give a functional explanation for this coupling and the high levels of energy expenditure in shorebirds.

The high level of BMR at which shorebirds seem to operate is in no way exceptional. Many bird species have BMR's which differ considerably from the values predicted from their body weight alone. The magnitude of these differences tends to be concealed when data are plotted on a log-log scale in interspecific comparisons. Ellis (1984) compared the BMR's of 41 species of seabirds (orders Sphenisciformes, Procellariiformes, Pelecaniformes and Charadriiformes without shorebird species) with values predicted by Lasiewski & Dawson (1967) for non-passerines. The majority (28 out of 49 measurements) differed by more than 20% from the predicted values; the extremes being 69% of the predicted value in the Magnificent Frigatebird *Fregata magnificens* (1078 g) and 200% in the Glaucous Gull *Larus hyperboreus* (1200 g). Much of this variation around predicted levels can be related to geographic distribution, as

was already shown for terrestrial birds by Weathers (1979) and Hails (1983). Among 16 species of Charadriiformes (mainly Laridae) the ratio between measured and predicted BMR increased from 0.8 in the tropics to 1.8 in arctic breeding species (Ellis 1984). Our shorebird data fit into this pattern. In the temperate breeding Oystercatcher the ratio is 1.24, whereas the more northerly breeding Turnstones and Grey Plovers have ratios of 1.42 and 1.49 respectively.

Natural selection may favour a low BMR in the tropics since this lowers the demand for food, while heat stress might be avoided by reduced internal heat production. It is, however, much more difficult to understand why BMR should increase with latitude. Obviously, the energy requirements for thermoregulation increase as one moves away from the tropics, but thermogenic and basal heat are produced in different tissues. In birds, shivering of the skeletal muscles is the main, if not the only, source of thermogenic heat production (Calder & King 1974). Basal metabolic heat is mainly produced by the brain and the organs in the abdominal cavity (more than 70% in humans), whereas the muscles contribute only 15% (Aschoff *et al.* 1971). It is therefore unlikely that a higher level of BMR will directly result in a considerable extension of the thermogenic potential of a bird.

It is probably more realistic to interpret the relative level of BMR as an adaptation to the rate of energy expenditure in nature. Energy expenditure above basal levels, both for activity and thermoregulation, is produced by the skeletal muscles. Hence, high levels of DEE involve a relatively high level of muscular activity. This will require a high level of support by the organs in the abdominal cavity since the muscles depend on them, not only for the supply of fuel and the degradation of waste materials, but also for repair of tissue as a result of wear. In this perception a high BMR is the inevitable consequence of a high DEE.

Assuming that the ability to mobilize energy at a high rate, for example in thermogenesis or extended activity such as long distance flights, is an advantage at higher latitudes, we have a functional explanation for the general correlation between relative level of BMR and latitude. There are several notorious exceptions to this pattern. Might these be explained as well? White Terns *Gygis alba* breeding in the tropics have a BMR which is 115% of the value predicted from their body weight (Pettit *et al.* 1985). In other tropical tern species this value typically ranges between 80% and 95%. The White Tern, however, is the only tropical tern species mentioned to hover without wind assistance, a particularly energy demanding task (Ellis 1984), indicating a high DEE. At the other extreme, the Snowy Owl *Nyctea scandiaca* living in the arctic has a very low BMR, 70% of the value predicted from its 2026 g body weight (Gessaman 1972). However, its DEE is also relatively low, the ratio DEE/BMR being 3.13. This is close to the values derived by Drent *et al.* (1978) and Walsberg (1980), and also close to the ratio found for shorebirds in the present study (Table 7).

From the observation that parent birds caring for their young could not be pressed to increase their energy expenditure above certain thresholds, Drent & Daan (1980) hypothesized the existence of a common 'maximum sustained working level' at about four times BMR. They inferred that energy expenditure above this level for more than one or two days would have detrimental effects on the bird's subsequent survival. The interpretation of BMR as a measure

of the level of support that can be given to the muscles gives a functional explanation to the mere existence of such a common maximum sustained working level and predicts that it should be directly related to BMR.

Seasonal changes in BMR have been demonstrated in several bird species (for reviews see Kendeigh *et al.* 1977, Weathers 1980). These changes also seem to be related to variations in DEE. In winter, when thermoregulatory demands are highest, many Passerines have a higher BMR than in summer. In another study changes in BMR coincide with changes in the activity levels of the birds. Male Long-eared Owls do most of the hunting during the period of courtship feeding in late winter. This coincides with an elevated BMR whereas the incubating females reduce their BMR at the same time (Wijnandts 1984).

The extent to which BMR may vary within individuals according to changes in DEE is probably rather restricted. Energy expenditure of birds living in captivity ($EM = 2 \times BMR$) is well below that in nature ($DEE = 3 \times BMR$). Yet, the BMR of captive and freshly caught birds is about the same. After one year in captivity, the BMR of Apapane *Himatione sanguinea* had not decreased significantly (Weathers *et al.* 1983).

4.3. WHAT CAUSES THE HIGH DEE IN SHOREBIRDS?

In the current absence of an annual energy budget for any shorebird species only tentative suggestions can be offered to explain the functional context of the relatively high DEE. We do not know to what extent the high DEE in shorebirds is due to thermoregulation or activity. Walsberg (1980, 1983) supposes that thermoregulation contributes little to seasonal variations in DEE. He argues that birds may reduce the amount of energy needed to maintain their body temperature by behavioural thermoregulation; *i.e.* by selection of favourable microclimates. This might be true for landbirds, on which Walsberg's analysis is mainly based, but we doubt whether behavioural thermoregulation is a realistic option for seabirds and shorebirds. The possibilities for finding shelter on the open sea or mudflats seem rather limited. In shore-

birds (Table 7) the highest ratio between NEI and BMR (3.7) occurred in January at the Wash (U.K.) (Goss-Custard 1977), whereas the lowest values (2.6 and 2.7) were obtained during the summer in the Dutch Wadden Sea (L. Zwarts pers. comm.) and year round in South Africa (Puttick 1980). This suggests that thermoregulation does affect DEE in shorebirds.

There are, however, two possible responses to increased thermoregulatory demands. One is a higher metabolic rate, the other is a better thermal insulation. From an energetic point of view the insulation option is the most economical. This raises the question why the thermal insulation of the shorebirds in the present study was rather poor, as indicated by the relatively high temperature coefficients under both resting and cage activity conditions (Tables 2, 5). It is possible that living in captivity had a detrimental influence on the plumage which provides most of the bird's thermal insulation (Robinson *et al.* 1976). However, the dry plumage weights of three of our birds (one Oystercatcher and two Grey Plovers), that died after the experiments were finished, did not differ from those of free-living conspecifics in the Wadden Sea (Fig. 7). The dry plumage weight of shorebirds in general is also not below that of other bird species (Wetmore 1936).

The poor thermal insulation of shorebirds as suggested by our experiments may be misleading for the natural situation. Free-living shorebirds rarely face the situations without wind which are typical during our experiments. In temperate areas strong winds prevail along the seashore, and wind is known to have a dramatic effect on the insulative quality of the plumage (Robinson *et al.* 1976). Wind resistance of the plumage may be extremely important for shorebirds living in this environment and might be incompatible with maximal thermal insulation in windless conditions. We therefore expect that the shorebird plumage provides a better isolation in windy conditions. There is some evidence which supports this idea. The relative increase of the CO₂-production of the Canary *Serinus canaria* and the Quail *Coturnix coturnix* in response to wind was about 2.5 times as high as that of the Oystercatcher (Whitlock 1979).

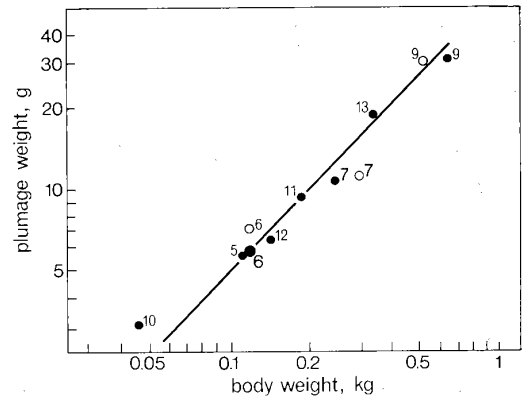


Fig. 7. Dry plumage weights of captive (open symbols) and free-living (closed symbols) shorebirds in relation to their body weight. Figures refer to different species as in Fig. 6, including 12. Knot *Calidris canutus* and 13. European Woodcock. The line shows the prediction-equation of Kendrigh (1970; after Wetmore 1936), recalculated for dry plumage weight as: $DPW(g) = 0.06 BW(kg)^{0.96}$ (water percentage of plumage is approx. 10%).

In our concept, a high DEE required at some period of peak demand, could well lead to a higher-than-expected BMR. Candidate times for high metabolic activity are the periods of mid-winter cold spells with high costs of thermoregulation (Table 7, Dugan *et al.* 1981) and possibly the periods of migration and premigratory fattening so characteristic for this group. Provisionally we will therefore argue that the energetic repercussions of wintering in unsheltered habitats and of long distance migrations under the constraints of the arctic breeding regime are important evolutionary pressures leading to interrelated metabolic adjustments yielding an upward extension of the ability to metabolize energy. This line of argument can be described as the 'energetic margin hypothesis'.

The energetic repercussions of premigratory fattening can be made more tangible by taking another look at Table 7. In spring, just before the departure from the wintering areas to the arctic breeding grounds, shorebirds increase their weights rapidly. During this period the net energy intake of Grey Plovers is 1.8–2.3 times the NEI for maintenance in September and April, whereas the comparable figure for Bar-tailed Godwits is 1.5 (Table 7). A part of this

additional intake is necessary for the acquisition of this food, whereas the remainder can be deposited as reserve tissue.

Bar-tailed Godwits captured during May in Friesland, The Netherlands show an average population weight increase of 6.0 g/day (J. Jukema pers. comm.). Assuming a net cost of $0.85 \times 45.66 = 38.8$ kJ per g weight increase, they would require an additional NEI of 233 kJ/day. Table 7 shows that the achieved difference between NEI in May and in October/April (276 kJ/day) is actually 18% higher than the expected value (233 kJ/day). The difference between achieved and expected NEI equals 0.24 times BMR and may give an impression of the additional energy expenditure of the birds during spring fattening. The average population weight increase of Grey Plovers in early May on the Wash, Great Britain, is 3.3 g/day (Branson & Minton 1976: Fig. 3). This implies an additional NEI of 128 kJ/day. However, the difference in NEI between May and September/April amounts to 306–389 kJ/day (Table 7), *i.e.* two to three times as high as the amount required for a 3.3 g/day weight increase. It seems unlikely that the cost of additional food acquisition is that high. The large difference may therefore also indicate that there is appreciable turnover in the migratory Grey Plover population on the Wash. Since arriving birds are likely to be lighter than those departing at the same time, the average population weight increase may severely underestimate the actual weight increase of individual birds. Unfortunately, the data required for a more accurate evaluation of the level of energy expenditure during pre-migratory fattening, *i.e.* energy intake and rate of body weight increase of individual birds, are not yet available.

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6. SUMMARY

We measured basal metabolic rate (BMR), existence metabolism (EM) and costs of thermoregulation in three species of captive shorebirds, Oystercatcher, Grey Plover and Turnstone. In all three species BMR was above the values predicted from their body weight (Aschoff & Pohl, 1970).

Including results of other studies, BMR of six shorebird species ranging in body weight from 36 g to 543 g, was on average 42% above the predicted level for a non-passerine. EM and DEE (daily energy expenditure) were relatively high as well. However, the ratio between BMR on the one hand and EM and DEE on the other, were not unlike those in other bird species, *i.e.* 2 and 3 times BMR respectively.

We hypothesize that a high DEE, mainly generated by the skeletal muscles, requires a high level of support by the organs in the abdominal cavity, which inevitably results in a high BMR. This interpretation provides a functional explanation for the constant ratio between BMR and DEE in many bird species and explains the existence of a 'maximum sustained working level' (Drent & Daan 1980) of parent birds feeding their young at approximately four times BMR. We suggest that the high DEE of temperate wintering shorebirds must be considered in relation to peak energy demands during their annual cycle. Candidate times are the periods of pre-migratory fattening and mid-winter.

The captive birds showed annual fluctuations in body weight associated with premigratory fattening, resembling those of their conspecifics in the wild. From the measurements of food intake we estimated the additional amount of energy needed for a 1 g increase in body weight at 45.66 kJ. Using this value, we estimate the efficiency of energy deposition at 88%.

Food intake increased with average body weight in all captive groups, but the BMR of an individual Turnstone did not, suggesting that fat has a low metabolic activity. This implies that the additional energy requirements for carrying around a fat load is associated with activity.

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8. SAMENVATTING

Om het energetische uitgaven-niveau van steltlopers te bepalen, hebben wij metingen verricht aan het basaalmetabolisme (basal metabolic rate BMR), de energetische opname van vogels onder beperkte bewegingsvrijheid in kooien (existence metabolism EM), en de kosten van thermoregulatie van drie steltloper-soorten: Scholekster, Zilverplevier en Steenloper. Bij alle drie was het BMR hoger dan verwacht op grond van hun lichaamsgewicht volgens de formule van Aschoff & Pohl 1970.

Als we de resultaten van andere studies aan energetische uitgaven van steltlopers met onze gegevens vergelijken, dan blijkt dat het basaalmetabolisme van steltlopers met lichaamsgewichten tussen 36 g en 543 g, gemiddeld 42% boven het gemiddelde BMR-niveau van niet-zangvogels ligt! Echter, EM en de dagelijkse energie-uitgaven in het vrije veld (daily energy expenditure DEE, geschat uit voedselopname-metingen uit de literatuur) blijken ook relatief hoog te zijn. Als we nu de ratio's tussen enerzijds BMR en anderzijds EM en DEE uitrekenen, dan zijn deze gelijk aan die van andere vogelsoorten, namelijk respectievelijk twee en drie keer BMR.

We veronderstellen dat een hoge DEE, die voornamelijk veroorzaakt wordt door de activiteit van de spieren van romp en ledematen, een grote mate van ondersteuning (toevoer brandstof, afvoer afvalstoffen, reparaties) door de organen in de buikholte (lever, nieren) vereist. Aangezien BMR juist in deze organen wordt gegenereerd, zal een verhoogde dagelijkse energie-uitgave zonder meer leiden tot een verhoogd basaalmetabolisme. Deze interpretatie geeft een functionele verklaring voor de constante verhouding tussen BMR en DEE bij een groot aantal vogelsoorten. Tevens verklaart deze interpretatie het bestaan van een langdurig-gehouden maximaal werkniveau (maximum sustained working level) op een energetisch maximum van ongeveer vier keer BMR (Drent & Daan 1980) bij oudervogels die hun jongen verzorgen.

We veronderstellen dat de hoge dagelijkse energie-uitgaven van steltlopers die in gematigde streken overwinteren, moet worden gezien in relatie tot de piekwaarden in energie-uitgaven gedurende hun jaarcyclus. Vooral de perioden

van aanleg van vetreserves om lange afstanden vliegend te overbruggen en koude-perioden in de winter, zouden tijden zijn dat de energetische kosten van steltlopers piekwaarden vertonen.

De steltlopers die wij in gevangenschap hielden, vertoonden jaarlijkse fluctuaties in lichaamsgewicht die erg leken op die van hun vrijlevende soortgenoten. Aan de hand van metingen van de dagelijkse voedselopname, schatten we dat de hoeveelheid extra energie die nodig is om 1 g in gewicht toe te nemen 45,66 kJ bedraagt. Uitgaande van deze waarde, berekenden we dat de efficiëntie van de aanleg van energiereserves 88% bedraagt.

De gemiddelde voedselopname van in kooien gehuisveste vogels nam toe met het gemiddelde lichaamsgewicht. Het basaalmetabolisme nam echter niet toe met het lichaamsgewicht, hetgeen suggereert dat vet (dat het grootste deel van de gewichtsverschillen uitmaakt) een erg lage metabolische activiteit heeft. Dit betekent dat de extra energetische kosten van een verhoogd lichaamsgewicht bij beperkte bewegingsvrijheid in kooien (het meesjouwen van meer vet) veroorzaakt worden door de toenemende kosten van lichamelijke activiteit.

NOTE ADDED IN PROOF

Since this manuscript was completed, one further measurement of BMR of a shorebird species came to our notice. Prinzinger & Hänsler (1980) measured BMR in one Green Sandpiper *Tringa ochropus* and found a value of 0.92 W. This is only 5.7% above the value of 0.87 that would be predicted for a shorebird weighing 90 g, on the basis of our equation ($BMR(W) = 5.06 BW(kg)^{0.729}$, see Table 6).

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