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Seasonality in basal metabolic rate and thermal conductance in a long-distance migrant shorebird, the knot (*Calidris canutus*)

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Abstract Knots *Calidris canutus* live highly seasonal lives, breeding solitarily on high arctic tundra and spending the non-breeding season in large social flocks in temperate to tropical estuaries. Their reproductive activities and physiological preparations for long flights are reflected in pronounced plumage and body mass changes, even in long-term captives of the *islandica* subspecies (breeding in north Greenland and northeast Canada and wintering in western Europe) studied in outdoor aviaries. The three to four fattening episodes in April–July in connection with the flights to and from the high arctic breeding grounds by free-living birds, are represented by a single period of high body mass, peaking between late May and early July in a sample of ten captive *islandica* knots studied over four years. There are consistent and synchronized annual variations in basal metabolic rate and thermal conductance in three *islandica* knots. Basal metabolic rate was highest during the summer body mass peak. Within the examined individuals, basal metabolic rate scales on body mass with an exponent of about 1.4, probably reflecting a general hypertrophy of metabolically expensive muscles and organs. Any potential effect of moult on basal metabolic rate was obscured by the large seasonal mass-associated variations. In breeding plumage, insulation (the inverse of thermal conductance) was a factor of 1.35 lower than in winter plumage. This was paralleled by the dry mass of contour

feathers being a factor of 1.17 lower. In this subspecies the breeding season is indeed the period during which the costs of thermoregulation are lowest. In captive knots seasonal changes in basal metabolic rate and thermal conductance likely reflect an anticipatory programme adaptive to the variable demands made by the environment at different times of the year.

Key words Basal metabolic rate · Thermal conductance · Physiological adaptations · Annual rhythms · Bird migration

Abbreviations bm body mass · BMR basal metabolic rate · MR metabolic rate(s) · SMR standard metabolic rate(s) · T_a air temperature(s) · T_b body temperature · TC thermal conductance

Introduction

The demands of the environment lead to continuous adjustments in the physiological and morphological characteristics of individual animals (Adolph 1964; Dill et al. 1964). Such variations are likely to be most prominent in species that either live a sedentary life in a highly seasonal environment (Kendeigh 1949; Steen 1958; Dawson et al. 1983), or – through their migrations – increase the range of environmental conditions they are exposed to (Drent and Piersma 1990; Piersma et al. 1991a). Knots *Calidris canutus* exemplify the latter mode of living; they migrate and their life is strongly seasonal (Piersma et al. 1991b). In the non-breeding season knots are grey-plumaged, mollusc-eating shorebirds roaming by the thousands in highly synchronized social flocks over intertidal flats (Piersma et al. 1993a). In summer, they are rufous-plumaged, arthropod-eating land-birds roaming quite solitarily over their high arctic tundra breeding grounds (Nettleship 1974; Cramp and Simmons 1983). At the time of migration to

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and from the high Arctic, knots increase their *bm* by half or more at a minimum of two stopover sites (Davidson and Wilson 1992; Piersma et al. 1992; Piersma and Davidson 1992). These dramatic morphological and behavioural seasonal changes in relation to migration are bound to be reflected in the birds' physiology (Berthold 1975; Meier and Fivizzani 1980; Marsh and Dawson 1989; Jenni-Eiermann and Jenni 1991).

In this study we address the question of whether changes in morphology and physiology are a response to the natural annual cycle or based on a seasonal programme exhibited also in captivity. We assessed seasonal fluctuations in *bm* and plumage, and in two basic physiological characteristics: BMR and TC. BMR is the metabolic rate of non-digesting animals measured at rest in the thermoneutral zone, and TC is the reciprocal of insulation, a measure of the rate at which body heat is lost by convection, conduction, radiation and evaporation.

To explain patterns of distribution of warm-blooded animals, many studies have examined correlations between climate and work-performance on the one hand, and physiological characteristics on the other, both between species (Scholander et al. 1950a,b,c; Hart 1964; Lasiewski and Dawson 1967; Herreid and Kessel 1967; Aschoff and Pohl 1970; Drent and Stonehouse 1971; Kendeigh and Blem 1974; Aschoff 1981), and within species (Wallgren 1954; Barnett 1970; Pohl 1971; Blem 1974; Dawson and Carey 1976; Weathers and Caccamise 1978; Dawson et al. 1983; Rintamäki et al. 1983; Wijnandts 1984; Hohtola et al. 1991). Recently, research has focussed on BMR as an indicator of a maximum sustained work level (Drent and Daan 1980; Masman et al. 1989; Peterson et al. 1990; Daan et al. 1991; Weiner 1992) and the causal basis for such a relationship (Daan et al. 1990; Hammond and Diamond 1992). Since Wallgren's (1954) comparative study of a migratory and a sedentary bunting species (showing a higher cold resistance in the species that remained at high latitudes throughout the winter), the link between migration and seasonal variations in BMR and TC has not been explicitly addressed. In this study we take up this line of enquiry again.

Material and methods

Experimental animals

We studied knots of the subspecies *Calidris canutus islandica*. These knots breed in northern Greenland and the most northeastern part of arctic Canada (Davidson and Wilson 1992). During the non-breeding season (August to April) they live in the large estuaries of western Europe, using Iceland and north Norway as staging posts on their way to and from (Iceland only) the arctic breeding grounds. Ten knots were captured on 15 October 1988 on the intertidal flats south of Schiermonnikoog in the Dutch Wadden Sea. Four of them were juveniles which had hatched in the arctic only a few months

earlier. The other six were adults in their third year of life or older. The juveniles and the adults were kept in separate flocks in outdoor aviaries (2 × 4 × 1.8 m high) at the Zoological Laboratory, Haren, The Netherlands. There was a shallow basin with continuously flowing fresh water. The sand on the floor was refreshed every week and the faeces cleaned out.

Knots were fed ad libitum with trout food pellets (Trouvit, Produits Trouw, Vervins, France). These consisted of 11% water, 12% fibers, 3% cellulose, 45% protein and 8% fat (manufacturer's specification). During the weekly cleaning, all birds were weighed and their moult and plumage scored. Contour feather moult was scored on the breast as none (0), light (1), medium (2) or heavy (3). Plumage was scored from 1 = winter plumage, 2 = trace or breeding plumage, 3 = 1/4 breeding, 4 = 1/2 breeding, to 7 = full breeding plumage, corresponding with grey (scores 1 and 2) to fully rufous-reddish (scores 6 and 7) coloured birds. Patches of vascularized naked skin, such as brood patches on birds' bellies, might increase TC, but none of the knots used in these experiments ever showed a brood patch in summer.

Oxygen consumption

MR and TC were measured every 6 weeks over an entire annual cycle (from October 1990 to October 1991) in three individuals.

Before entering the metabolic chamber, birds were kept in separate cages without food but with fresh water for 24 h to ensure that they were post-absorptive from the start of the measurements. Before the birds entered the metabolic chamber they were weighed to the nearest 0.1 g on an electronic balance. Metabolic chambers were made of Plexiglass and had a volume of 13 or 22 l. The walls were covered with black paper to avoid heat reflection (Porter 1969). Measurements started between 1600 and 1900 hours. At 0900–1000 hours the next morning the birds were removed from their metabolic chambers and weighed again. The *bm* values reported here were those of birds before they entered the metabolic chamber.

Birds were exposed to three different T_a per night. During the first night, T_a was -20 , -10 and $+5$ °C. After three nights and four days with their flock in the outdoor cage, they underwent the same treatment at T_a of $+15$, $+25$ and $+35$ °C. In this way we collected about 5 h of measurements for each T_a . T_a was monitored with thermistors inside the metabolic chambers. We used no more than three temperatures per night, since short-term temperature fluctuations can lead to an increase in metabolism (Prinzinger 1982). Temperatures were set in the same ascending order every night, since the climatic chamber warmed up faster than it cooled down. A series of measurements with descending T_a did not show differences with the procedure of increasing temperatures. In separate sessions where knots were held under constant conditions for longer periods, they failed to show any diurnal pattern in MR (cf. Aschoff and Pohl 1970), apart from a steady decline as the birds fasted longer (T. Piersma, pers. obs.). The absence of a diurnal rhythm may relate to the fact that non-breeding knots live a tidally rather than a diurnally structured life. With two nights of actual metabolic measurements and an intermediate period of three nights, almost a full week was needed to collect a series of MR measurements of BMR and TC of three individual birds.

Oxygen consumption was measured on three channels in an open-flow respirometer, using Applied Electrochemistry S-3A and S-3A/II oxygen analysers, with reference to the oxygen percentage of outside air (checked every 4 h). Oxygen consumption by the bird was computed according to Hill (1972), with a RQ-value of 0.73 (T. Piersma, P. Wiersma and L. Bruinzeel, pers. obs.). This is close to a value of 0.71 expected for a post-absorptive bird burning fat (Bartholomew 1982). For every minute of the experiment, air flow, T_a in the metabolic chamber and percentage oxygen consumed by each of the three birds were stored. Inlet air flow was set at 60 or 100 l · h⁻¹ depending on the volume of the metabolic chamber. An

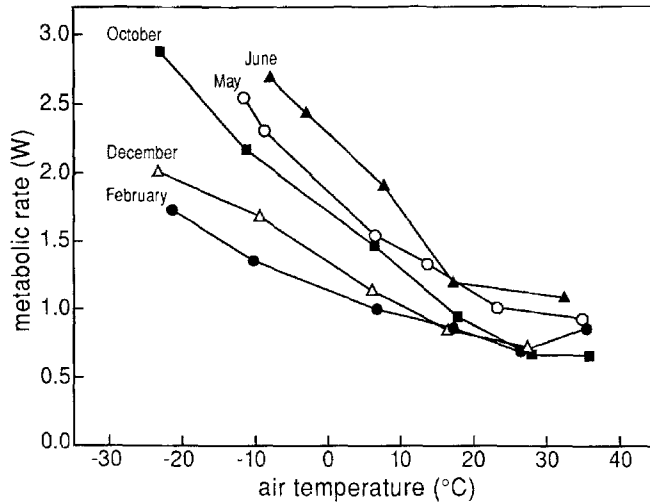


Fig. 1 Example of the relationships between air temperature and metabolic rate in one of the knots (#406) at different times of the year

energy equivalent of $20 \text{ kJ} \cdot \text{l}^{-1} \text{ O}_2$ was used (Schmidt-Nielsen 1975; Gessaman 1987; Gessaman and Nagy 1988).

Within the range of six temperatures the lowest value of MR is called BMR and was always obtained at $+25$ or $+35$ °C. During the first 1–1.5 h at a new temperature the knots normally showed an increase in oxygen consumption, and data from this period were omitted from the analyses. MR at constant T_a was estimated in two ways: (1) as the lowest value of the 60-min running means, and (2) as the lowest 1-min observation during the 60-min interval for which the running mean was used. The first estimate of MR is comparable to the values of MR as they are usually derived, and presented for other shorebirds by Kersten and Piersma (1987). The second estimate is to check for consistency (see Results).

Figure 1 illustrates the MR obtained for one bird at different times of the year. At each T_a , SMR is defined as the lowest MR measured at that temperature. Figure 1 clearly shows that the Scholander-model [a linear decrease in SMR with increasing T_a below the lower critical temperature with core T_b as the origin; Scholander et al. (1950: Fig. 3) does not apply. This is not unusual (McNab 1980) and the presented values of TC were therefore calculated assuming a constant body (core) temperature (T_b) of 41 °C for each given T_a , by the equation: $\text{TC} = \text{SMR}/(T_b - T_a)$ rather than by using a regression type of Scholander-model [see Wiersma and Piersma (1994) for an application of the latter]. TC per bird at each time of the year was calculated as the average of all values of $\text{SMR}/(T_b - T_a)$ obtained at $+15$ °C and lower temperatures. Note that the McNab and Scholander models, nevertheless, yielding comparable values for TC. Over 27 pairs of observations in three birds correlated with an r -value of 0.99, showing a slope approaching unity. Scholander values deviated between -10% and $+37\%$ from McNab-values.

Mass of contour feathers

A sample of 73 carcasses of knots of the *islandica* subspecies was assembled between 1979 and 1992 [see Piersma et al. (1993b) for origins]. Most birds died upon collision with the Westerhever lighthouse in Schleswig-Holstein, Germany, while others died during severe weather period in midwinter or during catching accidents in The Netherlands. A few birds had been in captivity for some time (less than a year) before dying. During analyses the contour feather tracts [all feathers except the flight feathers (remiges) and the tail feathers (rectrices)] were plucked and dried to constant mass at 60 °C in paper bags before weighing.

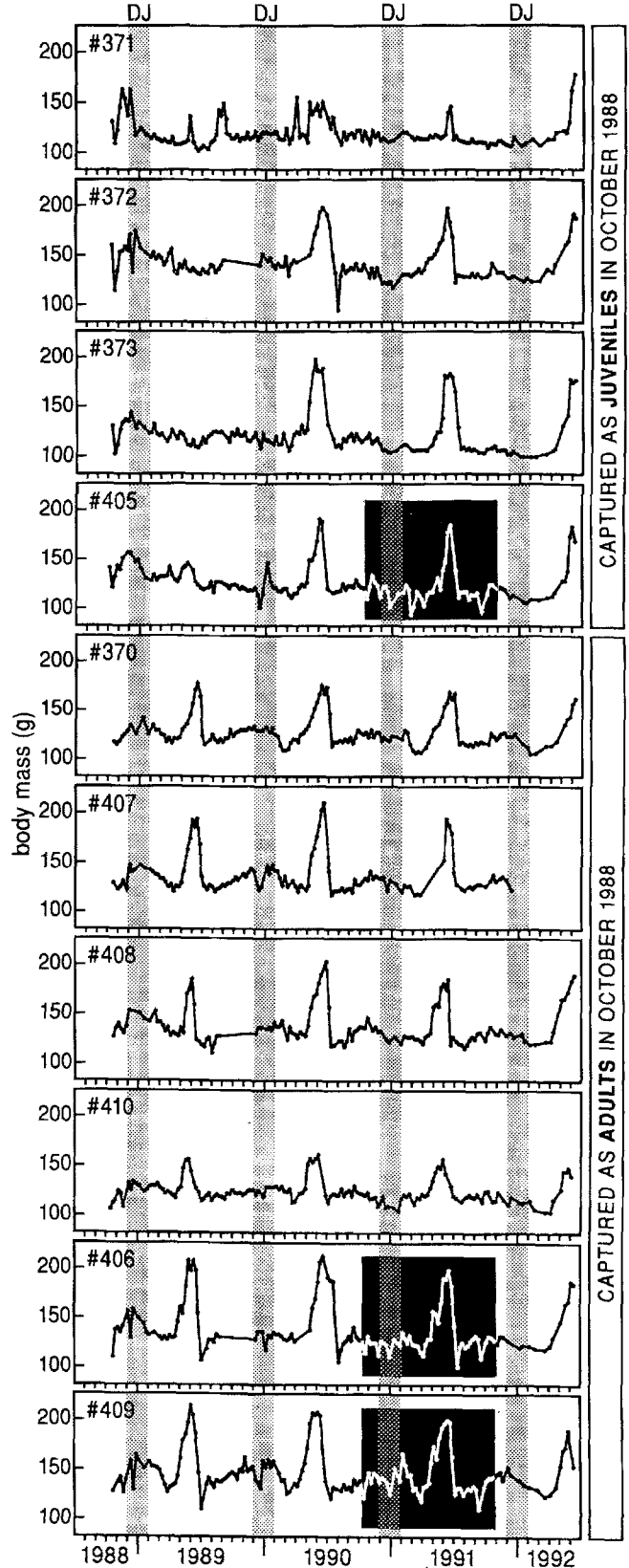


Fig. 2 Seasonal variations in body mass over a four-year period in ten knots of the *islandica* subspecies. The top four individuals were captured as juveniles, the remaining six as adults. The period over which metabolic measurements were made in three of the birds (#405, #406, #409) is indicated by the shaded boxes

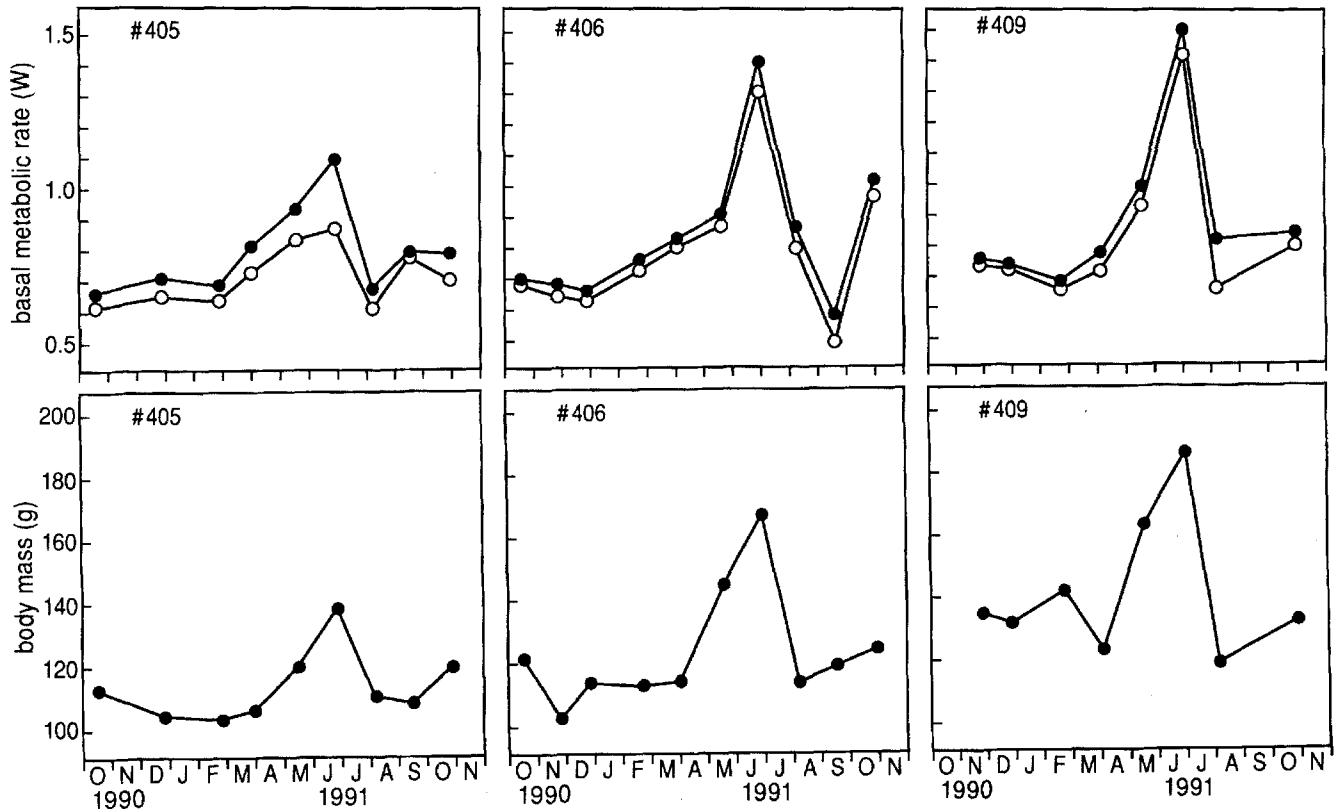


Fig. 3 Seasonal changes in basal metabolic rate (*top row*) and body mass (*bottom row*) in the three focal *islandica* knots measured up to ten times in one annual cycle. The closed dots per BMR indicate 60-min running means. The open circles show the lowest 1-min observations of BMR

Results

Seasonal variations in body mass

In the outdoor aviaries knots maintained recognizable seasonal cycles in bm (Fig. 2), as well as alternating winter and breeding plumages (only presented for the three focal knots in Fig. 6, but apparent in all adults). Body mass of all individuals varied between 110 and 120 g in early spring and late summer, and 170 and 210 g during the late spring mass peak. Especially in their first winter in captivity, birds showed another low 'peak' in bm in early winter, but this bm increase was much smaller and more protracted than the one in summer (Fig. 2).

Free-living adult *islandica*-knots show three to four mass peaks during the breeding season, two in preparation for the northward flights and one or two for the southward migration [Piersma and Davidson (1992: Fig. 6)]. In the captive knots only one high peak in bm was distinguishable in all adult birds in May-June, i.e. in all years for the six birds taken captive as adults, and from the second summer season in captivity for the four birds captured as juveniles.

During their first summer in captivity the juveniles also failed to show a clear moult into breeding plumage. According to the timing of the recurring May-June mass peaks, the total cycle in bm lasted close to 12 months (Fig. 2). BMR and TC of the three focal knots #405, 406, 409) were examined during their third annual cycle in captivity. During this year (1990-1991), bm and plumage showed the usual seasonal alterations.

Seasonal variation in basal metabolic rate

The three knots showed pronounced seasonal variations in BMR (Fig. 3), with peak values during the early summer highs in bm. BMR varied by a factor of 1.7 (highest/lowest) in birds #405, by 2.4 in bird #406, and by 2.2 in bird #409. The minimal MR over a 1-min period tracked the seasonal variations in BMR closely (Fig. 3). Since our knots were always measured at rest, the fluctuations in BMR cannot be caused by clear behavioural changes. The coefficients of variation (among data points for 1-min intervals) were always in the order of 2-6%, confirming the interpretation that variations in BMR were not due to variation in nocturnal activity.

An allometric analysis (Fig. 4) shows mass exponents of 1.437 (SE = 0.410) in bird #405, 1.359 (SE = 0.399) in bird #406 and 1.338 (SE = 0.385) in bird #409. We examined the extent to which moult affected log(BMR),

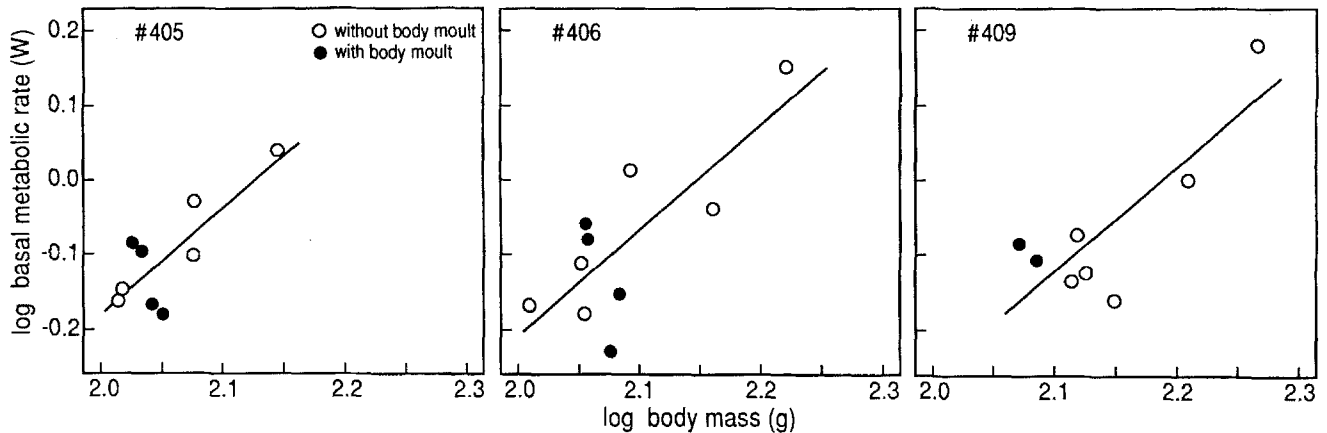


Fig. 4 Allometry of basal metabolic rate on body mass of three individual knots. Each measurement throughout the annual cycle (Fig. 3) is taken as a data point. Values for non-moulting birds are indicated by open circles, for moulting birds by closed dots. The

allometric regression lines for the three birds are indicated. For bird #405 $Y = 0.00088 \cdot X^{1.437}$ ($r^2 = 0.64$, $n = 9$); for bird #406 $Y = 0.00120 \cdot X^{1.359}$ ($r^2 = 0.59$, $n = 10$); for bird #409 $Y = 0.00167 \cdot X^{1.338}$ ($r^2 = 0.67$, $n = 8$)

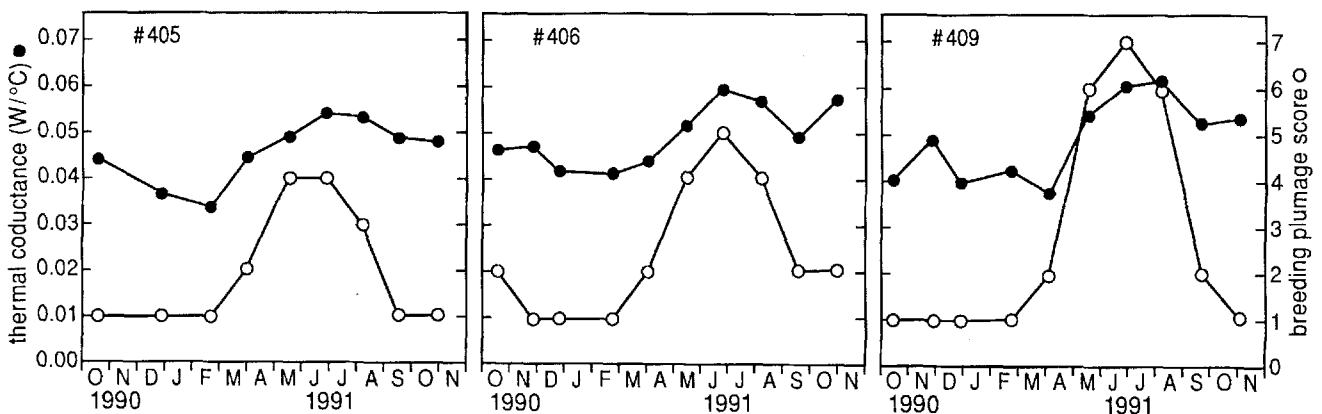


Fig. 5 Seasonality in thermal conductance (●, in $W \cdot ^\circ C^{-1}$ per bird) and plumage status (○, ranging from 1 = winter plumage to 7 = full breeding plumage) of the three focal *islandica* knots

as shown in raptors (Wijnandts 1984; Dietz et al. 1992) and songbirds (Doľnik and Gavrilov 1979; Lindström et al. 1993), by an analysis of covariance with individual and body moult (scores of 0, 1 and 2) as factors and $\log(\text{bm})$ as the covariate. The effect of the covariate was significant ($F = 34.7$, $df = 1$, $P < 0.0001$), but there were no effects of individual ($F = 2.0$, $df = 2$, $P = 0.17$) and moult status ($F = 0.4$, $df = 2$, $P = 0.68$). On the basis of the allometric relationships between BMR and bm (Fig. 4), the individual BMR-values at a bm of 130 g work out at 0.96 W, 0.89 W and 0.79 W for #405, #406 and #409, respectively.

Seasonal variation in thermal conductance

As the knots moulted into breeding plumage their TC increased (Fig. 5). It decreased with moult into winter

plumage. In none of the birds did TC return to the same level as a year earlier (Fig. 5). TC was apparently a function of plumage status (Fig. 6), and not of bm (no correlations; compare Figs. 3 and 5). It was highest for birds in full breeding plumage. The increase in TC is mirrored by a decrease in the mass of the contour feathers in a different sample of birds (Fig. 6C). Whereas insulation (inverse of TC) was a factor of 1.35 lower in birds in full breeding plumage compared to birds in winter plumage, contour feather mass was a factor of 1.17 lower.

Discussion

Annual rhythmicity

The data reported here show that under ad libitum food conditions shorebirds in captivity can maintain annual bm cycles similar to those they show in the wild. Similar evidence was obtained by Clark (1983) in

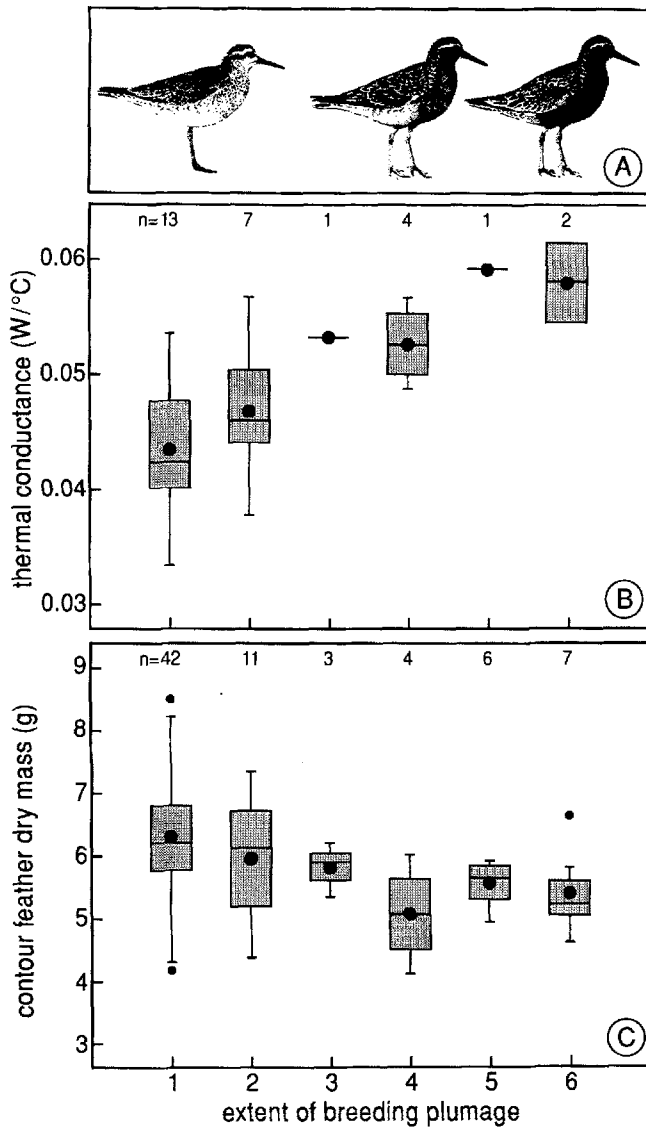


Fig. 6A–C The relationship between the extent of the rufous-red coloured breeding plumage (A) of *islandica* knots and thermal conductance (B) measured in three captive birds, and contour feather dry mass (C) measured in another sample of 72 birds, mainly from the wild. Thermal conductance and feather mass are given as box plots (Wilkinson 1990), showing the median and the quartiles by the split-box and the statistical outliers as *small dots*. Average values are indicated with *fat dots*

dunlins *Calidris alpina*, by M. Kersten and T. Piersma (pers. obs.) in oystercatchers *Haematopus ostralegus* and turnstones *Arenaria interpres*, and by Goede (1993) in different groups of oystercatchers. This phenomenon implies that the variations in *bm* are not the result of seasonal food shortages (Pienkowski et al. 1979). They also are not a response to the extreme variations in climate and daylengths knots encounter on their migratory pathway (Piersma and Davidson 1992; Wiersma and Piersma 1994). Most likely they are under endogenous circannual control [Gwinner

(1986a, b); N. Cadée, T. Piersma and S. Daan, unpubl. obs.], although the possibility that they emerged in response to the variations in daylength and/or temperature at the study site must be considered.

Seasonal variation in BMR

The average BMR of a 130-g knot in this study was estimated to be 0.88 W. This is close to the value of 0.95 W for a sample of captive *islandica* knots weighing on average 130 g (Wiersma and Piersma 1994). It is smaller than the prediction of 1.14 W for a 130-g shorebird according to the interspecific allometric relationship proposed by Kersten and Piersma (1987). In knots, long-term captivity leads to a reduction in BMR, mainly as a consequence of decreases in the size of the digestive system (Piersma et al. 1994a). The TC, varying between 0.04 and 0.06 W·°C⁻¹ in this study, covers the average value of 0.045 W·°C⁻¹ estimated by Wiersma and Piersma (1994) for winter-plumaged *islandica* knots.

The large seasonal variability in BMR of individual knots, expressed by the ratio highest BMR/lowest BMR (varying between 1.7 and 2.4 with a mean of 2.1) is only partly explained by simultaneous variation in *bm*. On a mass-specific basis the ratio varied between 1.34 and 1.68, with a mean of 1.55. This exceeds all the ratios (winter/summer ratios rather than the summer/winter ratios for knots) assembled by Weathers and Caccamise (1978: Table 3) for 20 resident bird species and short-distance migrants. Ratios varied between 0.8 in birds weighing more than 1000 g to 1.5 in birds weighing 30 g or less, the ratio of winter/summer mass-specific fasting MR (i.e. BMR) being a negative function of *bm*. Their equation (ratio = 1.49 *bm* (g)^{-0.077}) predicts a ratio of 1.02 for the mean *bm* of 144 g for knots. In addition, the season with the highest MR is reversed in this long-distance migrant. The highest mass-specific MR occurs in summer rather than in winter.

Intraspecific allometry of BMR

The mass exponent of BMR considerably exceeded proportionality in all three knots (average 1.38). Similar high values (1.67) have been reported for kestrels kept on low and high maintenance food regimes (Daan et al. 1989). Intra-individual mass exponents are thus considerably steeper than for homomorphic change [i.e. 0.667; Heusner (1984)], for interspecific comparisons within a group of similar bird species [e.g. shorebirds: 0.729; Kersten and Piersma (1987)] and for mass proportionality (i.e. 1.00). This suggests that the mass of metabolically highly active tissue varies more than *bm* mass in the course of the annual cycle of an individual knot, or that some of the major tissues show seasonal variation in mass-specific metabolism.

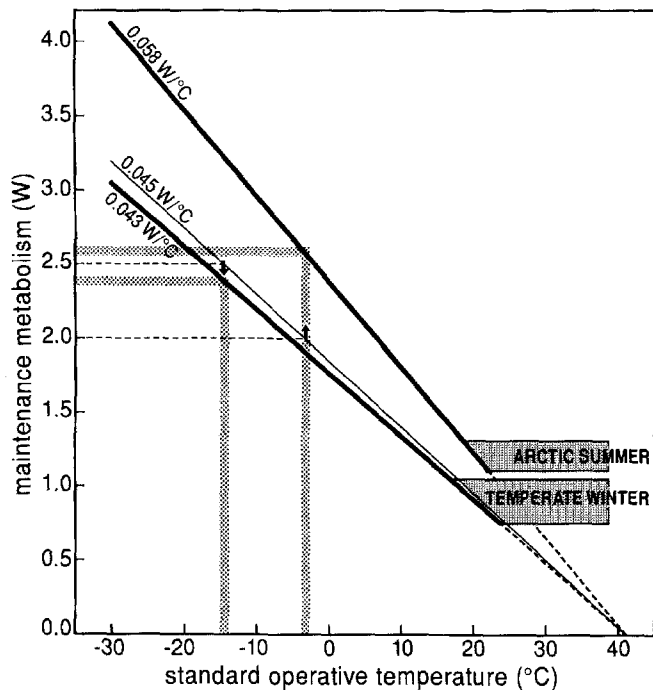


Fig. 7 Idealized Scholander-curves for the relationship between the maintenance metabolic rate (called SMR under lab-conditions) and environmental temperature (standard operative temperature or air temperature in a metabolic chamber) for *islandica* knots in winter and in summer. The presented ranges in BMR are bordered by the rather low values of captive birds in this study (Fig. 3) and the higher values of freshly captured wild knots (Piersma et al. 1994b). Values for thermal conductance are derived for a full winter and a full summer plumage (Fig. 6)

Thermal conductance

To ensure that the reported seasonal changes in average TC (from $0.043 \text{ W} \cdot \text{°C}^{-1}$ in a winter to $0.058 \text{ W} \cdot \text{°C}^{-1}$ in a breeding plumage) were not merely an effect of a seasonal shift in the setpoint of the core T_b , we carried out a sensitivity analysis of TC values estimated with the McNab-model. A deviation of 2 °C in T_b resulted in deviation in TC of $0.002 \text{ W} \cdot \text{°C}^{-1}$ at standard operative temperatures between -10 and $+10 \text{ °C}$. Since this relatively huge change in T_b has only a small effect on TC, we conclude that the seasonal change of $0.015 \text{ W} \cdot \text{°C}^{-1}$ is mediated by changes in plumage.

Indeed, seasonal variations in TC were mirrored by changes in the mass of the insulative layer (Fig. 6). This is not usually found in studies of seasonality in bird physiology (Dawson and Carey 1976; Marsh and Dawson 1989).

Wiersma and Piersma (1994) were unable to show a difference between the insulative capacity of one breeding-plumage skin and three winter-plumage skins on heated taxidermic mounts. However, their study does present a detailed assessment of the thermal envi-

ronment encountered by *islandica* knots in the course of the year. This showed that the cost of thermoregulation is higher in winter (1.55 W) than during the breeding season in the high arctic [1.05 W ; Wiersma and Piersma (1994); Fig. 10]. The lower insulation of birds in breeding plumage can thus be interpreted as an adaptation to a reduced heat loss in the arctic summer compared to the European winter.

Seasonal adjustments in thermal physiology

The values for BMR and TC of *islandica* knots in an arctic-breeding and a temperature-non-breeding situation can be summarized schematically in the form of the Scholander model (Fig. 7). For BMR a rather large range is indicated, since the BMR values obtained in our set of long-term captives are certainly underestimates relative to knots in the wild (T. Piersma, unpubl. data). The most interesting feature of the comparison between a breeding-plumaged bird during the arctic summer and a winter-plumaged bird during winter in the Wadden Sea is their maintenance cost under the prevailing thermal conditions. Wiersma and Piersma (1994) present predictive equations for maintenance costs of 'standard-knots' with a TC of $0.045 \text{ W} \cdot \text{°C}^{-1}$ for the two situations. These are based on extensive series of measurements with heated taxidermic mounts under a range of weather conditions in different microhabitats. The resulting predictions (2.0 W in the Canadian Arctic and 2.5 W for the Dutch Wadden Sea) can be converted into 'true' values of the maintenance costs of birds with different plumage characteristics. Figure 7 shows that maintenance costs tend to converge to rather similar values. *Islandica* knots in a plumage normal for the time of the year incur maintenance costs of 2.4 – 2.6 W in summer as well as in winter. The decrease in insulation by birds in a full breeding plumage is partly offset by the lower thermal stress in the breeding season compared to the non-breeding period.

An understanding of the adaptive value of the strong seasonal variations in BMR of *islandica* knots is complicated because we are not yet able to disentangle the effects of migratory hypertrophy of metabolically active body parts (T.P. Weber and T. Piersma, unpubl. data) and the effects related to the actual breeding episode (which birds, of course, were not breeding in the cages). Further studies on changes in functional organ size of free-living birds at different phases of the summer period need to be combined with field studies on the levels of energy expenditure of knots during these phases.

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