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Basal metabolic rate in migratory waders: intra-individual, intraspecific, interspecific and seasonal variation

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Summary

1. Basal metabolic rates (BMR) were measured in 36 adult and 119 juvenile waders of 19 species on autumn migration in southern Sweden.
2. In a comparison with literature data, it was found that juvenile BMR was generally lower than at the onset of migration in the Arctic and slightly higher than on African wintering grounds.
3. The seasonal differences may reflect local physiological adaptations or possibly a gradual decline from high premigratory levels due to growth. Our data contradict the idea that BMR is high during migration as an adaptation to generally high levels of energy expenditure.
4. The allometric exponent, scaling BMR to body mass, was significantly higher within individuals (1.19) and within species (1.82) than among species (0.62).
5. The high intra-individual exponent indicates that non-fat tissues, with a high metabolic activity, are involved in the mass changes during migratory stopover.
6. The high intraspecific exponent indicates that tissues with a high metabolic activity contributed disproportionately to variation in body mass among individuals or that larger individuals had elevated mass specific metabolic rates of some tissues.

Key-words: Allometry, phenotypic flexibility

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Introduction

Animals continuously adjust their physiology, morphology and metabolic functions to varying ecological conditions and demands. This phenotypic flexibility (*sensu* Piersma & Lindström 1997) involves the size of tissues and organs (Piersma & Lindström 1997; Piersma 1998; Battley *et al.* 2000; Lindström *et al.* 2000), hormone levels (Rising & Hudson 1974; Stokkan 1994) and enzyme activities (Lundgren & Kiessling 1985, 1986). Basal metabolic rate (BMR) is the energy expenditure of a non-productive, postabsorptive animal resting in thermoneutrality during the circadian rest phase (Aschoff & Pohl 1970). In essence, BMR is the summed energy expenditure of all tissues and organs working together under the influence of the regulatory systems in the living animal. Therefore, changes in organs and tissues of an animal should cause a change in BMR. Indeed, several studies have reported correlated variation between the size of metabolically highly active organs and BMR (Daan, Masman & Groenewold 1990; Konarzewski & Diamond 1994; Piersma *et al.* 1996; but see Burness, Ydenberg & Hochachka 1998).

The annual cycle of long-distance migratory waders involves drastic seasonal changes in living conditions. Several species completely change diet between seasons; they move between warm and cold climates, between terrestrial, limnic and estuarine environments and between the Arctic and the Tropics (Alerstam 1990; Piersma *et al.* 1996). Their objectives in the different environments also differ: breeding, migration or winter survival. The changing circumstances pose radically different demands on the birds. This will lead to physiological and morphological adjustments which, in turn, may be reflected in seasonal differences in BMR (Weathers 1980; Piersma *et al.* 1996; Lindström 1997; Kersten *et al.* 1998).

We measured BMR of waders during autumn migration in southern Sweden. Our first aim was to look for seasonal changes by comparing our BMR values with those of birds at the onset of migration in the Arctic (Lindström 1997) and on their wintering quarters in Africa (Kersten *et al.* 1998). Lindström (1997) found that BMR was higher on migration in the Arctic than on African wintering grounds. Supposedly, the high BMR in the Arctic reflects the large metabolic machinery required to cope with the energy-demanding migration (Kersten & Piersma 1987; Lindström 1997) and the low BMR in Africa reflects low-maintenance

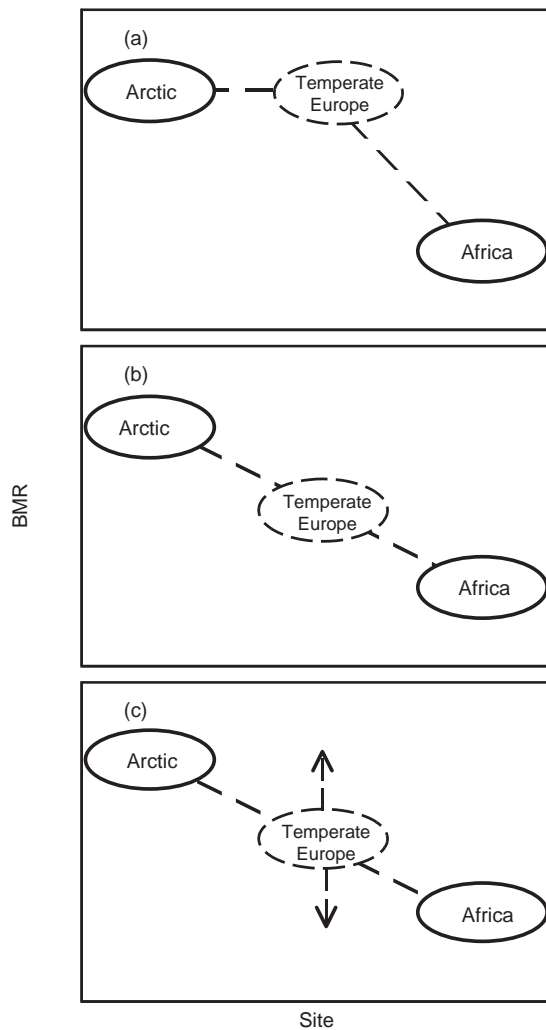


Fig. 1. Three scenarios for BMR at an intermediate migration site. (a) If a high BMR reflects a physiological adaptation to high energy turnover during migration, BMR on migration in temperate Europe should be as high as on migration in the Arctic. (b) If BMR gradually declines from high postnatal values in the Arctic to low winter values in Africa, BMR should be intermediate in temperate Europe. (c) If BMR mainly reflect local adaptations, BMR at an intermediate site could attain any value.

energy demands and may reduce the risk of heat stress (Weathers 1980; Klaassen, Kersten & Ens 1990; Lindström 1997; Kersten *et al.* 1998). But there are other possibilities for the pattern found.

We suggest three potential scenarios of how BMR can change between seasons and sites, and from them predict what the BMR at an intermediate migration site may be (Fig. 1). (1) If BMR does reflect a high energy turnover during migration, BMR should still be high at an intermediate migration site (Fig. 1a). (2) High BMR values in the Arctic could also be due to effects from the last stages of growth or other postnatal effects (Ricklefs 1974; Hume & Biebach 1996; Guglielmo 1999), although the waders measured by Lindström (1997) had completed moult and showed no signs of growth. If BMR declines gradually from high postnatal values in the Arctic to low winter values

in Africa, BMR should be intermediate at an intermediate migration site (Fig. 1b). (3) BMR at all three sites reflect local adaptations to the ecological conditions and demands at that site rather than one general physiological adaptation to migration or a slow decline from one local adaptation in the Arctic to another local adaptation in Africa. BMR could reflect physiological adaptations to local food sources or food supply, climate or other local factors. In this scenario, the BMR at an intermediate migration site could attain any value (Fig. 1c). The three hypotheses are not mutually exclusive (and there may be others), but we consider them useful when trying to interpret the seasonal variation in BMR in migratory waders.

Our second aim was to compare the relationship between BMR and body mass within individuals and species, and among species. A number of studies have treated the allometric scaling of BMR by comparing average species values (Aschoff & Pohl 1970; Kendeigh, Dolnik & Gavrilov 1977; Bennett & Harvey 1987; Reynolds & Lee 1996). There has been considerable debate on the scaling of BMR and if and how it varies between taxonomic levels. Comprehensive studies within genera and higher taxonomic levels indicate that there is a difference in the scaling of BMR between levels both in birds (Bennett & Harvey 1987) and in mammals (Elgar & Harvey 1987). Whether this difference has biological meaning or is simply a statistical artefact is uncertain (Bennett & Harvey 1987; Pagel & Harvey 1988). Basal metabolic rate also varies to a large extent within species and even within individuals (Daan *et al.* 1989; Piersma, Cadée & Daan 1995; Burness *et al.* 1998; Lindström, Klaassen & Kvist 1999). The data presented here for a large number of wader species and individuals form a homogeneous set suitable for investigating the allometric scaling of BMR at these lower taxonomic levels.

Materials and methods

Migrating waders were captured at Ottenby Bird Observatory, SE Sweden (56°12' N, 16°24' E) in late July to early September in 1995–1997. Birds were aged as juveniles or adults. The birds were kept indoors in separate cages measuring between 30 cm × 30 cm × 50 cm and 100 cm × 100 cm × 100 cm, depending on bird size. The temperature in the holding room varied between 18 °C and 25 °C and the light regime simulated the natural local light and dark periods. During night a small window let in some light from outside (moonlight, starlight and indirect light from a nearby lighthouse). The birds had access to water for drinking and bathing at all times. All birds were weighed and their fat stores scored according Pettersson & Hasselquist (1985) every day between 1700 and 1800 local time. Food supply (mealworms, *Tenebrio* sp.) was regulated so that new birds with higher fat stores gradually depleted their stores until they reached a fat score of 1–3 before BMR was measured. After the overnight

BMR measurement, the birds were given food *ad libitum* and consequently increased in mass. Some of the birds were measured again during one or more nights during the mass increase or after body mass had reached a stable high value. In 19 cases, BMR was also measured at higher fat scores directly after capture.

BMR MEASUREMENTS

Air from two metabolic chambers (5–11 l), and reference air was drawn at 12–60 l h⁻¹ (STPD), depending on the size of the birds (20–215 g), via separate dryers (silica gel), pumps, flow controllers (F-201C-FA-22-V, Bronkhorst High Tech, Ruurlo, the Netherlands) and valves to each of two oxygen analysers (Xentra 41002A1, Servomex, Crowborough, UK). A carbon dioxide sensor was connected after one of the oxygen analysers. The two birds connected to each oxygen analyser were measured alternately for periods of 25 min. Reference air was measured for 15 min every 90 min. In 1995, a different respirometer with one oxygen analyser (1100 A, Servomex), no carbon dioxide sensor and different flow controllers (5850E, Brooks, Veenendaal, the Netherlands) was used. In all other respects the 1995 respirometer and test protocol was identical to that used in 1996 and 1997.

Oxygen measurements were made between about 1900 and 0800 local time, in complete darkness at +26.0 °C (SD = 0.95 °C) in a temperature-controlled cabinet (BK600, Heraeus, Hanau, Germany). Few data on the lower critical temperature (LCT) of waders exist (*Arenaria interpres* L., mass, 120 g; LCT, +22–23 °C, Kersten & Piersma 1987; *Calidris canutus* L., mass, 130 g; LCT, +20 °C, Piersma *et al.* 1995). According to the equation for non-passerines of Kendeigh *et al.* (1977), the LCT for the smallest bird in our study (30 g) is +25.5 °C. In a separate test, the oxygen consumption of eight Dunlins (*Calidris alpina* L.) was on average 6% higher at +24.5 than at +28.5 °C, but the difference was not significant (paired *t*-test, $t_7 = 1.9$, $P = 0.11$). For the smallest birds the temperature may have been just below LCT, resulting in a somewhat overestimated BMR and an underestimate of the interspecific allometric exponent. The comparison with African data (Kersten *et al.* 1998) could also be somewhat biased, but not the comparison with the Arctic data (Lindström 1997) since the same temperature was used in that study.

Data on oxygen concentration, temperature and carbon dioxide production were logged automatically every minute to a data logger (Grant SQ1202; Grant Instruments, Shepreth, UK). Changes in flow due to the gas exchange of the bird was corrected for when calculating oxygen consumption (Klaassen, Lindström & Zijlstra 1997). When carbon dioxide production was not measured, a respiratory quotient (RQ) of 0.70 was assumed (the average RQ measured was 0.704 ± SD 0.028, with 93% of the values between 0.67 and 0.75). Oxygen consumption was recalculated to energy

metabolic rate assuming an energy equivalent of 20 kJ l⁻¹ oxygen consumed.

BMR was calculated as the lowest 10-min average metabolic rate. BMR estimates will clearly be influenced by the time period on which the estimate is based. However, the average metabolic rate from start to end of measurements was only 15% higher than the lowest 10-min average. Food was removed 2 h before measurements started. In 95% of the cases, the lowest 10 minute average metabolic rate occurred after midnight and the birds had thus been without food for at least 7 h. Thirteen of the 237 overnight measurements were discarded because the oxygen consumption readings clearly showed that the bird had been active during most of the night.

SEASONAL AND GEOGRAPHICAL VARIATION

The BMR of waders in southern Sweden (this study) was compared with that of waders at the onset of migration in the Eurasian Arctic (Lindström 1997) and on their winter quarters in tropical Africa (Kersten *et al.* 1998). For methodological reasons there is often some uncertainty involved when comparing BMR values from different studies. As far as the comparison with the Arctic data is concerned, we used the same experimental set-up and protocol of analysis as Lindström (1997) and therefore think direct comparisons can be justified.

The study of Kersten *et al.* (1998) is comparable to ours in most aspects. In both studies BMR was estimated overnight from oxygen consumption in an open flow system, and wild birds were measured within four days of capture. The generally low body masses in the African data set, and the fact that the birds were wintering in tropical Africa, suggest that these birds had small fat stores (Zwarts *et al.* 1990). Therefore, in both Lindström (1997) and the present study only birds with low fat scores (4 or less) are included in the between-site comparisons. Hence, fat stores should have been of comparable size in the three different data sets.

Since Kersten *et al.* (1998) did not present the age of their birds, a difference in BMR due to differences in age cannot be ruled out. However, as shown by our own studies (see below), there seems to be no generality in how BMR varies between age groups and it is difficult to know what kind of differences to predict. Kersten *et al.* (1998) estimated BMR graphically from curves of oxygen consumption over time, corresponding to the lowest 30-min averages (T. Piersma, personal communication). The small difference in length of time periods when calculating BMR (30 min for Africa and 10 min for our data) would tend to give, everything else being equal, slightly higher estimates for African birds than in our study.

ALLOMETRY OF BASAL METABOLIC RATE

Individuals or species with a sample size of three or more, and with a reasonable range in body mass (the highest body mass was at least 10% higher than the

lowest), were selected for the intra-individual and intraspecific analyses, respectively. For the intraspecific and interspecific analyses all measurements of very fat (fat score 5 or more) and very lean (fat score 0) birds were also excluded, to minimize variation due to the fat status of the birds.

STATISTICAL ANALYSES

Basal metabolic rate is normally assumed to show an exponential relationship to body mass:

$$\text{BMR} = a\text{Mass}^b.$$

In order to use linear models, all analyses were therefore done on log (base 10) transformed values. Accordingly, geometric means of BMR and body mass are used in the analyses for individuals and species. Body mass was always measured just prior to respirometer measurement in concordance with Kersten *et al.* (1998) and Lindström (1997). The average decrease in body mass overnight was 7%.

Reduced major axes analyses were used to estimate interspecific, intraspecific and intra-individual allometric exponents (b in equation). Least squares regression underestimates the true allometric exponent in proportion to the degree of correlation in the data (Pagel & Harvey 1988). It is not possible to test how well our data conform to the assumptions of reduced major axis analysis (error variances of x and y should be proportional to their respective underlying true variances), but simulation studies have shown that reduced major axis generally is less biased than both least squares regression and major axis (McArdle 1988; Pagel & Harvey 1988). Least squares estimates are presented only for comparison with other studies.

To examine the relative variability around the allometric regressions, a coefficient of variation (CV) was approximated from the standard deviation of the residuals from ANCOVA (with individual and species, respectively, as factors) and regression (interspecific) according to Garland (1984). Non-significant interaction terms were excluded from all ANCOVA. All statistical analyses were carried out using SPSS 8.0 for Windows (SPSS Inc., Chicago, IL, USA).

Results

We made 224 successful measurements of BMR in 36 adult and 119 juvenile waders of 19 species. Because of the large differences in size between sexes in the Ruff (*Philomachus pugnax* L.), males and females are treated as separate species.

SEASONAL AND GEOGRAPHICAL VARIATION: COMPARISONS WITH LITERATURE DATA

Using species averages, the BMR of juvenile waders was on average 16% lower in southern Sweden than

Table 1. Intraspecific comparison of BMR of juvenile waders measured in southern Sweden (Ottenby, this study), in the Eurasian Arctic (Lindström 1997) and in tropical Africa (unaged birds, Kersten *et al.* 1998). Differences in BMR between sites are tested for using ANCOVA with body mass as covariate and site nested within species as factor. The effect is the average difference in BMR between sites after the statistical effect of body mass and species has been removed. A positive effect means that the BMR in the Arctic or Africa is higher than the BMR in southern Sweden. Three *Calidris ferruginea* with very low body masses in the African data set are excluded from the analyses. The P -values refer to t -test between adjusted means. n_1 is the number of individuals measured at Ottenby and n_2 is the number of individuals measured at the other site (Arctic or Africa)

| Species | n_1 | n_2 | Effect | P |
|-----------------------------------|-------|-------|--------|-------|
| Southern Sweden – Eurasian Arctic | | | | |
| <i>Arenaria interpres</i> | 2 | 2 | +24% | 0.065 |
| <i>Calidris alpina</i> | 30 | 6 | +10% | 0.090 |
| <i>Calidris ferruginea</i> | 6 | 6 | +30% | 0.001 |
| <i>Calidris minuta</i> (Leisl.) | 1 | 7 | +0% | 0.975 |
| Southern Sweden – Africa | | | | |
| <i>Arenaria interpres</i> | 2 | 5 | -30% | 0.003 |
| <i>Calidris alpina</i> | 30 | 1 | -15% | 0.252 |
| <i>Calidris canutus</i> | 3 | 26 | +11% | 0.231 |
| <i>Calidris ferruginea</i> | 6 | 12 | +22% | 0.005 |
| <i>Charadrius hiaticula</i> (L.) | 6 | 2 | +0% | 0.967 |
| <i>Limosa lapponica</i> (L.) | 1 | 9 | +9% | 0.558 |
| <i>Tringa nebularia</i> (Gunn.) | 1 | 2 | -20% | 0.197 |
| <i>Tringa totanus</i> | 5 | 3 | -20% | 0.030 |

in the Arctic ($F_{1,17} = 13.876$, $P = 0.002$, ANCOVA with body mass as covariate, species with mass >100 g excluded to make size range comparable between studies). In contrast, BMR was on average 8% lower in tropical Africa than in southern Sweden, although the difference was not significant ($F_{1,28} = 3.268$, $P = 0.08$, ANCOVA, species with mass >250 g excluded to make size range comparable between studies).

Seasonal differences within species were also tested for, using individual values in ANCOVA with body mass as covariate and site nested within species as factor. Juvenile BMR was on average 16% higher in the Arctic than in southern Sweden ($F_{4,51} = 5.440$, $P = 0.001$). All four species in this comparison showed a higher BMR in the Arctic (Table 1). The difference was significant only for the Curlew Sandpiper (*Calidris ferruginea* Pont.).

In the comparison between southern Sweden and Africa, the interaction term between species and body mass was significant ($F_{7,93} = 5.487$, $P < 0.001$). However, the interaction was caused mainly by three Curlew Sandpipers with very low body masses in the African data (38, 41 and 41 g, being 10 and 7 g lighter than the lightest of the other birds). The low body masses indicate that the birds may have been in an emaciated state, which could have caused their very low BMR values. If the values for these three individuals are removed, the interaction term is no longer significant. BMR was on average 5% lower in Africa than in southern Sweden ($F_{8,97} = 3.553$, $P = 0.001$). However, the pattern was

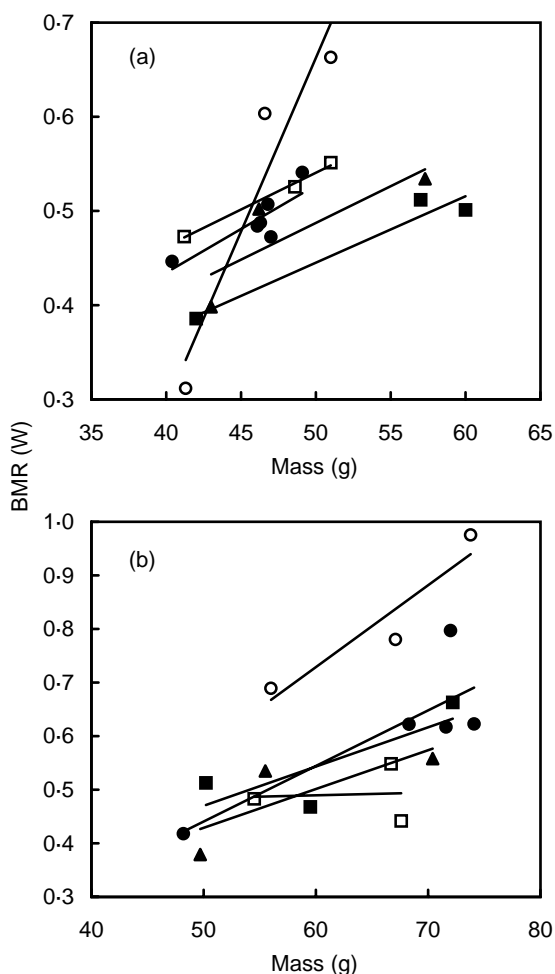


Fig. 2. Intra-individual variation in BMR in (a) Dunlins (*C. alpina*) and (b) Wood Sandpipers (*T. glareola*). Each dot represents one BMR measurement. Different individuals are represented by different symbols. The lines are intra-individual regression lines.

not consistent within species. Four of the species showed a lower BMR in Africa and an equal number showed a higher BMR (Table 1).

INTRA-INDIVIDUAL, INTRASPECIFIC AND INTERSPECIFIC ALLOMETRY OF BASAL METABOLIC RATE

Basal metabolic rate varied to a large extent within individuals at different measurement occasions (Fig. 2) and among individuals of the same species (Fig. 3). The coefficient of variation was largest around the intraspecific allometric regression and least around the intra-individual regressions (Table 2).

The sample size weighted mean intra-individual allometric exponent was 1.19 (Table 2) and did not differ significantly among species ($F_{4,15} = 0.188$, $P = 0.94$).

At the intraspecific level, age groups were first compared. In three species, there are measurements of at least three adults and three juveniles. In the Dunlin, juveniles had a significantly higher BMR than adults ($F_{1,45} = 7.402$, $P = 0.009$, ANCOVA, Fig. 3a). In the Knot

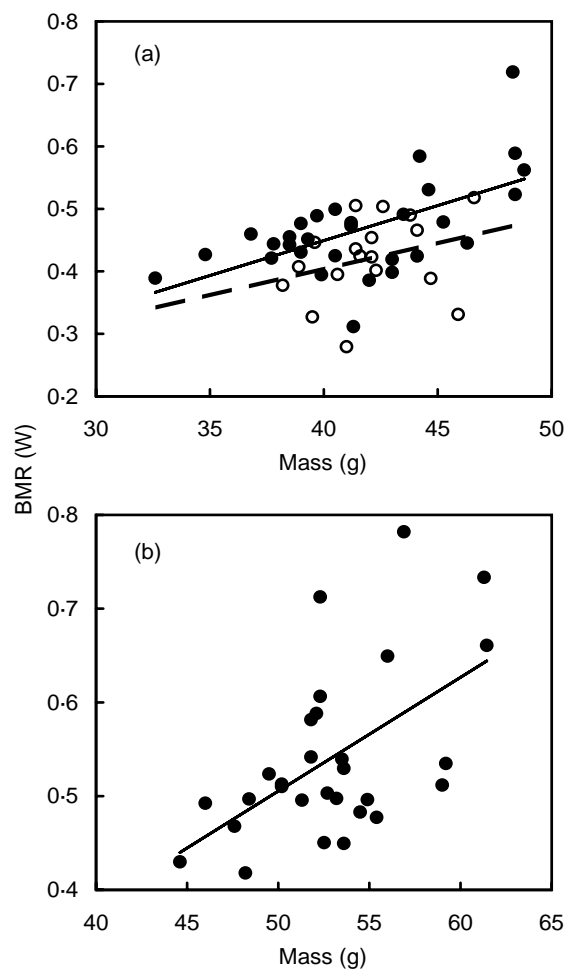


Fig. 3. Intraspecific variation in BMR in (a) Dunlins (*C. alpina*) and (b) Wood Sandpipers (*T. glareola*). Each dot represents the mean of all BMR measurements of one individual at fat scores 1–4. For most individuals there was only one available measurement. Dots and circles denote juveniles and adults, respectively. The solid lines are juvenile intraspecific regression lines. The broken line is the adult intraspecific regression line for the Dunlins.

Table 2. Intra-individual, intraspecific and interspecific allometric exponents of basal metabolic rate. The allometric exponents are estimated both by reduced major axis (RMA) and by ordinary least squares regression (OLS). Confidence intervals (95% CI) are only given for reduced major axis estimates. n_1 is the sample size at the specified level. n_2 is the sum of the sample size at the lower level (e.g. when n_1 is the number of individuals, n_2 is the summed number of measurements of all individuals). A coefficient of variation (CV in percentage) of BMR after the statistical effect of body mass is removed is estimated from the residuals of the least squares regression (see statistical analyses)

| | n_1 | n_2 | RMA | 95% CI | OLS | CV (%) |
|------------------|-------|-------|------|-----------|------|--------|
| Intra-individual | 16 | 54 | 1.19 | 0.80–1.58 | 0.96 | 8.5 |
| Intraspecific | 8 | 97 | 1.82 | 1.48–2.15 | 0.99 | 11.7 |
| Interspecific | 1 | 19 | 0.62 | 0.54–0.70 | 0.60 | 9.6 |

(*Calidris canutus* L.), adults had a significantly higher BMR than juveniles ($F_{1,3} = 10.3$, $P = 0.049$, ANCOVA). In the Curlew Sandpiper there was no difference between age classes ($F_{1,11} = 0.267$, $P = 0.616$, ANCOVA).

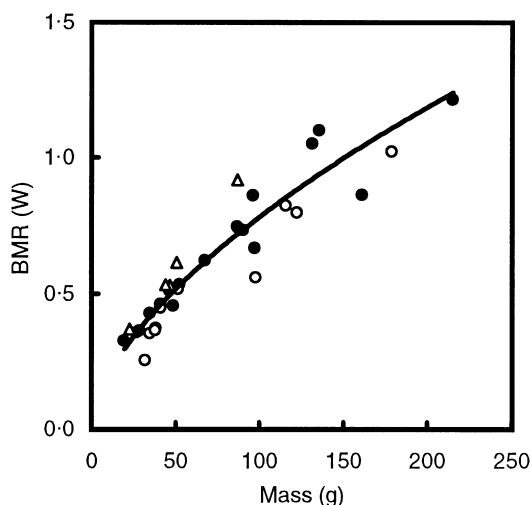


Fig. 4. Interspecific variation in BMR in juvenile waders. Each dot represent the geometric mean BMR of all individuals of one species at fat scores 1–4. Dots denote values from southern Sweden (Ottenby, this study), circles denote values from African winter quarters (Kersten *et al.* 1998) and triangles denote values from the Arctic (Lindström 1997). The regression line is based only on the values from southern Sweden.

Because of the differences between juveniles and adults, the estimates of allometric exponents below are based only on measurements of juveniles (too few adults were measured for a separate analysis). The sample-size weighted mean intraspecific allometric exponent was 1.82 (Table 2). The exponent of 1.82 is significantly higher than the intraindividual exponent of 1.19 ($t_{22} = 2.247$, $P = 0.035$).

The interspecific exponent was 0.62 (Table 2, Fig. 4). This exponent is significantly lower than both the intra-

individual ($t_{15} = 3.159$, $P = 0.006$) and the intraspecific ($t_7 = 8.520$, $P < 0.001$) exponents. Interspecific and intraspecific allometric equations calculated from reduced major axis and least squares regression can be found in Table 3.

Discussion

SEASONAL AND GEOGRAPHICAL VARIATION

Seasonal changes in BMR have been shown for a number of bird species (Kendeigh *et al.* 1977; Weathers 1980; Cooper & Swanson 1994; Piersma *et al.* 1995). Generally, these changes seem to follow seasonal changes in energy expenditure (Cooper & Swanson 1994; Piersma *et al.* 1995). Long-distance migration is considered an energy-demanding phase in the yearly routine. During migratory stopovers, waders deposit large amounts of fat (e.g. Gudmundsson, Lindström & Alerstam 1991). This fat deposition requires a high energy intake which, in turn, demands the support from a large and active digestive machinery. This machinery could generate a high BMR. Waders wintering in the tropics, by contrast, have low energy requirements and this should be reflected in a low BMR (Klaassen, Kersten & Ens 1990). Kersten *et al.* (1998) showed that 16 species of both resident and migratory waders in tropical Africa had lower BMR than waders wintering in temperate regions (Kersten & Piersma 1987). Lindström (1997) showed that the BMR of five species of waders at the onset of migration in the Arctic are on a level with waders wintering in temperate regions (Kersten & Piersma 1987) but are higher than those of waders in tropical Africa (Kersten *et al.* 1998). Piersma *et al.* (1996) showed that tropical wintering Knots have lower BMR than their temperate wintering conspecifics. The waders in our study showed BMR values distinctly lower than that of waders in the Arctic and only slightly higher than those of waders in Africa.

Our birds were all captured at a stopover site during active migration, and those of the birds that spend the winter in tropical Africa still had a long migration ahead. BMR was slightly higher than in Africa, but not significantly so. Thus, the low BMR of these birds speaks against the hypothesis that BMR is high throughout the migration season as an adaptation to a generally high level of energy turnover (Fig. 1a). Instead, the low BMR in southern Sweden is in line with the two other hypotheses.

The low BMR in southern Sweden could represent a gradual decline from high postnatal levels in the Arctic to low winter levels in Africa, as described in the second scenario (Fig. 1b). Our BMR measurements from southern Sweden are much closer in time to the measurements in the Arctic, yet more closely resemble the African winter values. The gradual decline in BMR of a tropically wintering passerine bird carrying out the equivalent of a full autumn migration in a windtunnel supports this hypothesis (Lindström *et al.* 1999).

Table 3. Interspecific and intraspecific allometric equations, $BMR (W) = a \text{ body mass}^b$ (g), estimated by reduced major axis analyses (RMA) and least squares regression (OLS). Interspecific allometric equations are presented for southern Sweden (this study), the Eurasian Arctic (Lindström 1997) and Africa (Kersten *et al.* 1998). Intraspecific equations are separated by age. Only equations based on at least three individuals are presented

| | RMA | | | OLS | | |
|--|----------|----------|----------|----------|----------|-----------------------|
| | <i>n</i> | <i>a</i> | <i>b</i> | <i>a</i> | <i>b</i> | <i>r</i> ² |
| Interspecific | | | | | | |
| Southern Sweden | 19 | 0.046 | 0.62 | 0.050 | 0.60 | 0.94 |
| Eurasian Arctic | 5 | 0.041 | 0.69 | 0.043 | 0.68 | 0.97 |
| Africa | 16 | 0.025 | 0.74 | 0.026 | 0.73 | 0.96 |
| Intraspecific | | | | | | |
| <i>Charadrius hiaticula</i> (juvenile) | 6 | 1.7E-3 | 1.49 | 0.01 | 1.16 | 0.61 |
| <i>Calidris canutus</i> (adult) | 3 | 101 | -1.01 | 13.0 | -0.57 | 0.32 |
| <i>Calidris ferruginea</i> (juvenile) | 6 | 3.5E-5 | 2.44 | 0.32 | 0.09 | 0.00 |
| <i>Calidris ferruginea</i> (adult) | 8 | 3.8E-8 | 4.21 | 0.00 | 2.37 | 0.32 |
| <i>Calidris alpina</i> (juvenile) | 30 | 1.2E-3 | 1.59 | 0.02 | 0.88 | 0.31 |
| <i>Calidris alpina</i> (adult) | 18 | 5.5E-6 | 3.01 | 0.02 | 0.83 | 0.08 |
| <i>Philomachus pugnax</i> fem. (juvenile) | 6 | 9.2E-6 | 2.53 | 0.00 | 1.32 | 0.27 |
| <i>Gallinago gallinago</i> (L.) (juvenile) | 6 | 6.3E-5 | 2.08 | 0.00 | 1.47 | 0.50 |
| <i>Tringa totanus</i> (juvenile) | 5 | 1.2E-2 | 0.93 | 0.01 | 0.91 | 0.95 |
| <i>Tringa glareola</i> L. (juvenile) | 29 | 1.8E-4 | 2.01 | 0.01 | 1.13 | 0.31 |
| <i>Actitis hypoleucos</i> (L.) (juvenile) | 9 | 1.1E-3 | 1.59 | 0.02 | 0.85 | 0.29 |

The variation in BMR among the three sites could also reflect local adaptations, as suggested in the third scenario (Fig. 1c). The cycles of flight and stopover during migration involve large and rapid changes in body mass and in the masses of many organs (reviewed by Piersma 1998; Battley *et al.* 2000). These changes in organ masses are likely reflected in large and rapid changes in BMR (Lindström *et al.* 1999; Battley *et al.* 2000). The relatively small decline in BMR of 24% from the Arctic to Africa would have to be superimposed on the much more rapid and probably larger variation in BMR between days during periods of rapid fattening (judging by the intra-individual allometric exponent of 1.19). Hence, BMR could change continuously and rapidly, reflecting physiological adaptations to the ecological conditions and demands at each site (Fig. 1c). For example, in the Arctic, BMR could be elevated owing to some latent effect of growth still present (Ricklefs 1974; Hume & Biebach 1996; Guglielmo 1999). In tropical Africa BMR could be low to avoid heat stress by minimizing endogenous heat production (Weathers 1980; Klaassen *et al.* 1990). Differences in food types, supply or demand at different sites could cause differences in the food processing organs (Guglielmo 1999), known to have a strong impact on BMR (Field, Belding & Martin 1939; Martin & Fuhrman 1955; Scott & Evans 1992).

Singling out the importance of one ecological factor causing seasonal changes in BMR may be a tricky task. Different organs and tissues may change in size or metabolic activity simultaneously as a result of different demands and changes in BMR just shows the net result. However, since size and metabolic intensity of organs and tissues were not measured in the present study, alternative causes for the variation in BMR cannot be ruled out. The true causal relationships behind the seasonal variation in BMR can only be elucidated through studies of the physiological or other changes that underlie changes in BMR and experiments designed to demonstrate the ecological factors underlying these changes.

INTRA-INDIVIDUAL, INTRASPECIFIC AND INTERSPECIFIC ALLOMETRY

Variation in BMR with body mass has previously been interpreted in terms of variation in organ and tissue masses (Daan *et al.* 1990; Piersma *et al.* 1996; Lindström *et al.* 1999). If variation in BMR were caused only by variation in organ and tissue masses, an allometric exponent of one (isometric scaling) would imply that the organs and tissues that caused the variation in mass had the same average mass-specific metabolism as the whole animal. A lower or higher exponent would imply that tissues with a lower or higher mass-specific metabolism, respectively, contributed disproportionately to the variation in mass. However, these interpretations should be done with caution since variation in BMR also can result from changes in

the mass-specific metabolism of tissues and organs, caused, for example, by hormonal differences and variation in enzyme activities.

The BMR of waders showed a significantly different relationship to body mass within individuals, within species and among species. Variation in body mass within individuals, within species and among species is likely to involve different tissues and organs and different variations in hormone and enzyme levels. The evolutionary forces that ultimately cause differences in size and metabolic rate among species are likely to be different from the forces that cause differences in size and metabolic rate within a species, not to mention the evolutionary forces that contribute to shaping the flexible phenotype of an individual (Piersma & Lindström 1997). Therefore, one allometric exponent that applies both within individuals, within species and among species is hardly to be expected.

Our birds on migratory stopover showed an average intra-individual exponent of 1.19. The few other available studies also reveal high intra-individual exponents, implying that the mass changes involved tissues with high mass-specific metabolism, both during migration (*Luscinia luscinia* L. 0.95 and 1.7, Lindström *et al.* 1999), winter (*Carduelis chloris* L. 2.8, Å. Lindström & M. Rosén, unpublished data; *Tringa totanus* L. 1.68, Scott, Mitchell & Evans 1996) and other parts of the yearly cycle (*Falco tinnunculus* L. 1.67, Daan *et al.* 1989; *Calidris canutus* 1.73, Piersma *et al.* 1995). The exponents were all recalculated to reduced major axis estimates. Whereas a large part of the mass increase is due to adipose tissue, which has a low metabolic activity (Scott & Evans 1992), it is, by now, a well-established fact that a significant part of the mass increase of birds on migratory stopover is due to protein in addition to the fat (Lindström & Piersma 1993; Piersma 1998). Organs with high metabolic activity, such as the gastrointestinal tract, liver, kidneys and flight muscles, have all been shown to be involved in the mass change during migratory stopover (Marsh 1984; Hume & Biebach 1996; Battley & Piersma 1997; Karasov & Pinshow 1998; Piersma 1998; Piersma, Gudmundsson & Lillendahl 1999). This may well be the reason for our high intra-individual allometric exponent.

There was no consistent pattern of age-related differences in BMR. We have not found any other study dealing specifically with the effect of age on BMR in full-grown birds. In Western Sandpipers (*Calidris mauri* Cabanis), a close relative of the Dunlin, juveniles have larger alimentary tracts than adults during autumn migration, but not when on their wintering grounds (Guglielmo 1999). Possibly the higher BMR of juvenile Dunlins in our study can be explained by the energy cost of maintaining a larger alimentary tract. However, this hypothesis cannot explain the age differences in knots since they showed the opposite pattern. The effect of age on BMR needs further study.

Our waders showed an intraspecific allometric exponent of 1.82. Other studies have also found

intraspecific allometric exponents higher than one (*Falco tinnunculus* 1.24, Daan *et al.* 1989; *Tringa totanus* 1.39, Scott *et al.* 1996, reduced major axis estimates). If individuals of a species were geometrically similar, with all tissues and organs contributing to body mass in exactly the same proportion and having the same mass-specific metabolic activity, the intraspecific allometric exponent would be 1. However, variation in mass within species is a result of both structural size differences, which will tend to produce geometrical similarity, and of deviations from proportionality within individuals. Some individuals may have tissues and organs that are comparatively large or small for their size. These deviations from proportionality tend to involve organs and tissues with high metabolic activity, especially in our data where we deliberately minimized variation in lipid stores. Most probably, the mass of the skeleton and plumage, with low metabolic activity, is proportionately the same in individuals of different size (Turček 1966). In contrast, the mass of muscles and many internal organs with high metabolic activity may deviate substantially from proportionality. An individual may commonly have a heavy or light breast muscle or liver for its size (Piersma 1998). Heavy individuals are likely to be the ones with proportionally big organs, and vice versa. The high intraspecific allometric exponents are consistent with the hypothesis that tissues and organs with a high metabolic activity contribute disproportionately to variation in mass among individuals. An alternative or additional explanation for high intraspecific exponents may be that larger individuals have an elevated mass-specific metabolic activity of some tissues.

The interspecific allometric exponent for the waders in our study was 0.62. This is within the range of 0.61–0.92 found in numerous other studies on birds (see Bennet & Harvey 1987). The interspecific exponent is thus well below 1 and much lower than both the intra-individual and the intraspecific exponents. A plethora of explanations for the decreasing mass-specific metabolic rate with size and the value of the interspecific allometric exponent in vertebrates has been proposed but no consensus has been reached (Kleiber 1975; Schmidt-Nielsen 1997). One proposed explanation is that larger animals need a relatively greater amount of skeletal and connective tissues, with low metabolic activity, to support their greater body weight (Kleiber 1975). However, it is also clear that homologous tissues have a lower mass-specific metabolic rate in larger animals than in smaller, when subject to the regulatory systems of the living animal (Kleiber 1975). We can conclude only that for a given difference in mass, BMR differs much less among species than within an individual or among individuals of a species.

Apart from the differences in how BMR relates to body mass, we have also shown that, even within a homogeneous group of birds, waders, there is considerable mass-independent variation in BMR within individuals, among individuals and among different

species. Part of this variation can be explained by seasonal changes in BMR and by differences between age classes. Other studies show that ecological parameters such as latitude (Weathers 1980), feeding regime (Daan *et al.* 1989) and natural daily energy expenditure (Daan *et al.* 1990) can explain some of the differences within and among species. However, a large part of the mass-independent variation in BMR remains unexplained. We are still far from being able to predict the BMR of an individual bird with precision from equations in the literature.

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