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## SHORT COMMUNICATIONS

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### BASAL METABOLIC RATE DECLINES DURING LONG-DISTANCE MIGRATORY FLIGHT IN GREAT KNOTS

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**Abstract.** Great Knots (*Calidris tenuirostris*) make one of the longest migratory flights in the avian world, flying almost 5500 km from Australia to China during northward migration. We measured basal metabolic rate (BMR) and body composition in birds before and after this flight and found that BMR decreased 42%. The mass-specific BMR based on lean mass decreased 33%. We also starved a group of pre-migratory Great Knots in captivity to determine whether they showed the same reduction in BMR without having undergone the hard work of flight. The captive birds showed a similar range and reduction of BMR values as the wild birds. Exponents of relationships between BMR and body mass in different comparisons were high, indicating large changes in BMR as a function of body mass. Analysis of the body composition of ten wild and three captive birds found that the flight muscle mass and intestine mass positively correlated with BMR.

**Key words:** BMR, *Calidris tenuirostris*, fasting, metabolism, migration, shorebirds.

#### La Tasa Metabólica Basal Disminuye durante Vuelos Migratorios de Larga Distancia en *Calidris tenuirostris*

**Resumen.** *Calidris tenuirostris* realiza uno de los vuelos migratorios más largos entre las aves, volando desde Australia hasta China durante la migración al norte. Medimos la tasa metabólica basal (TMB) y la composición corporal en aves antes y después del vuelo y encontramos que TMB se reduce en 42%. La

TMB específica por masa, o sea la TMB corregida por masa magra, se redujo en 33%. También expusimos un grupo premigratorio de *Calidris tenuirostris* a un periodo de ayuno en cautiverio, para determinar si mostraban una tasa de reducción similar en la TMB sin haber soportado la dura tarea de volar. Las aves en cautiverio mostraron un rango y una reducción de los valores de la TMB similares a los de las aves en libertad. Los exponentes de la relación entre TMB y masa corporal en diferentes comparaciones fueron altos, indicando grandes cambios de la TMB en función de la masa corporal. El análisis de la composición corporal de diez aves libres y tres en cautiverio mostró que la masa de los músculos del vuelo y la masa de los intestinos esta positivamente correlacionada con la TMB.

Long-distance migration induces dramatic and substantial changes in body mass and composition in birds. Changes may be very rapid, and decreases in body mass of over 40% can be achieved in only a few days of flight (Barter et al. 1997). Given that birds making long-distance flights catabolize metabolically active protein as well as fat (Jenni and Jenni-Eiermann 1998, Battle et al. 2000), it is likely that migration may induce rapid changes in metabolic rates of individuals.

Regional differences in basal metabolic rate (BMR) have been shown within shorebird species wintering in West Africa, in Europe, and on the breeding grounds in Siberia (Piersma et al. 1996, Lindström 1997, Kersten et al. 1998). It is not clear how much these differences reflect metabolic flexibility rather than fundamental metabolic differences among populations (Klaassen et al. 1990). Metabolic flexibility has been shown in captivity. Red Knots (*Calidris canutus*) from a tropical-wintering origin and a cold-temperate win-

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tering origin had different BMR levels soon after capture, but these converged over time (Piersma et al. 1996). This convergence was thought to reflect changes in body composition. Piersma et al. (1996) advanced the idea that migrants might strategically lower their BMR in response to a decrease in metabolic needs associated with living in tropical climates. In agreement with this idea, Kersten et al. (1998) showed that BMR of shorebirds in Africa did not differ between migrant and resident species, suggesting that BMR of the migrants was reduced upon arrival in the tropics (juvenile migrants on the breeding grounds had higher BMR values; Lindström 1997).

Metabolic variation had not been demonstrated in migrants in the wild until recently. We measured BMR and body composition in Great Knots (*C. tenuirostris*), a large sandpiper (Charadriiformes: Scolopacidae), before and after migration from Australia to China, and found a decrease in BMR of 42% (Battley et al. 2000; reported as 46% due to a calculation error). This was based on a comparison of groups of individuals caught before and after migration, so we could not follow changes in BMR of individuals. As long-distance flight may be equivalent to an intense period of fasting (Piersma 1990, Lindström et al. 1999), in this paper we expand our analysis to include an experimentally fasted group of Great Knots. We aim to determine whether the BMR changes observed in migrating wild birds are paralleled by equivalent changes of fasting individuals in captivity. We fasted birds caught before migration down to an expected "arrival mass" to simulate the change in body mass associated with migration without the hard work of flight.

## METHODS

We studied Great Knots at Roebuck Bay, Western Australia (18°00'S, 122°22'E), and Chongming Island, near the mouth of the Yangtze River, China (30°48'N, 121°27'E), in 1998. They are 5420 km apart.

### PROTOCOL: WILD BIRDS

We determined BMR in five birds during the fueling period (we use the term 'fueling' to refer to the mass increases of fat and lean tissue before migration) at Roebuck Bay, Australia (one from 20 February, two from 6 March, two from 21 March; BMR was not significantly related to date so we treat these values as representative of all pre-migratory birds;  $r = 0.61$ ,  $P = 0.27$ ), and in five birds caught in China (two caught on 3 April, one on 6 April and two on 9 April, the latter pair being measured on 10 April, having been maintained on a fish diet in the interim). The birds were placed in darkened metabolic chambers (9 or 11 L) between 18:53 and 00:58 hr local time, and removed from the chambers between 06:25 and 08:00 the following morning. Oxygen consumption was measured with a portable one-channel open-flow respirometry unit. The O<sub>2</sub> analyzer (Servomex A570, Servomex BV, Zoetermeer, The Netherlands) was calibrated before and after each measurement, using nitrogen gas for 0% O<sub>2</sub> and ambient air for 21% O<sub>2</sub>. Reference air was sampled every hour for 10 min. When two birds were measured per night, channels were sampled alternately for 10 min. Switching between sample air and reference air was done automatically. Flows were

adjusted so that the decrease in O<sub>2</sub> concentration was between 0.5% and 1% (200–850 mL min<sup>-1</sup>, Brooks Mass Flow Meters 5860S, Brooks Instruments, Hatfield, Pennsylvania). Inlet and outlet air of the metabolic chambers and reference air were dried with molecular sieve 3Å (Merck KgaA, Darmstadt, Germany). Chamber temperatures were within the expected thermoneutral zone for a Great Knot (Piersma et al. 1995, Kersten et al. 1998): mean 30.8°C in Australia (ambient temperature) and 23.3°C in China (heated). After measurement, birds were killed by cervical dislocation, and frozen for subsequent body composition analyses.

Oxygen consumption was calculated using equation 6 of Hill (1972) thereby assuming an RQ-value of 0.706, the mean value for birds fasted in captivity in this study. An energy equivalent of 19.7 kJ per L O<sub>2</sub> consumed was used to calculate energy expenditure. Data from the first half of the measurement period were discarded to minimize the chance of residual handling effects elevating metabolic rates. The first 2 min of each 10-min block were also discarded, to allow flushing of air through the respirometry system. Calculated BMR values represent the mean of the lowest two consecutive ten-minute periods in the latter half of the measurement period. For comparison with other studies, figure axes contain both BMR in Watts and volume of oxygen consumed (VO<sub>2</sub>).

### PROTOCOL: CAPTIVE BIRDS

Eight birds were caught in Australia by cannon-net on the afternoon of 21 March 1998, taken into captivity, and flown to the Netherlands Institute for Sea Research (NIOZ). Between capture and arrival at NIOZ they were force-fed kitten pellets or Trouvit trout pellets in an attempt to maintain their body mass before measurements during the fast could start. Birds were housed in an indoor aviary with a light:dark cycle of 12:12 and a temperature of 17–21°C with free access to fresh water. The timing of the light:dark cycle was partly shifted with the night starting at 12:00, to simulate conditions in Australia. Birds were weighed daily during the fast, which lasted 12–16 days. The involuntary fast was stopped when birds reached their individual predicted "arrival mass in China" (which, for all birds, was close to 130 g; Barter et al. 1997).

Metabolic rate measurements were similar to those in the wild birds, except that CO<sub>2</sub> as well as O<sub>2</sub> was measured (in a two-channel open-flow respirometer with a Servomex 1440C and Servomex Xentra 4100 respectively). Measurements started around the beginning of the Australian night. Nine-liter metabolic chambers were used, housed inside a darkened Weis Enet temperature cabinet (24°C). Reference air was sampled in one channel, while the second channel switched between the two chambers every 14 min (incorporating a flush time of 4 min). Flows were adjusted so that the decrease in the O<sub>2</sub> concentration was between 0.5% and 1% (50–60 mL min<sup>-1</sup>, Brooks Mass Flow Controllers 5850s).

Oxygen consumption was calculated using a modified equation 6 of Hill (1972) because we measured the CO<sub>2</sub> concentration as well as O<sub>2</sub>. The average RQ-value of all measurements was 0.706, indicating that the birds used predominantly fat as fuel. Therefore we used an energy equivalent of 19.7 kJ per L O<sub>2</sub> to cal-

culate energy expenditure. Three of the birds were sacrificed by cervical dislocation for body composition analyses. The remaining five birds were maintained in captivity for ongoing annual-cycle studies.

For the majority of measurements, coefficients of variation (CV) in oxygen consumption were lower during the periods we took to represent the minimum metabolic rate than during the rest of the measurement period. CVs were generally low: average 2.1% in Australia, 1.1% in China and 3.6% in captivity. Periods of apparent activity in the chambers were obvious in four birds, when CVs increased five to ten-fold. For methods of body composition analysis methods see Battley et al. (2001).

#### STATISTICAL ANALYSES

Means are given  $\pm$  SD for body masses and metabolic rates. Slopes of log-log regressions are given  $\pm$  SE. Reduced major axis (RMA) regression was used to calculate the dependence of BMR on body mass. Because RMA calculates the ratio of two SDs, significance tests for a slope being different from zero are meaningless (the slope would only be zero if one SD was itself zero). The SE of the slope and the CI can be used to roughly assess the fit of the relationship. Slopes of different regression lines were considered different if the slope of one did not overlap the 95% confidence interval of the other. To test whether organ mass correlated with BMR, we generated residuals from log-log least-squares regressions of BMR and internal-organ lean dry mass on total fat-free dry mass (rather than total body mass because much variation in body mass was due to fat content, which is unrelated to allometric scaling). Residual BMR was then regressed against residual organs in least-squares multiple regressions to determine significance. Because sample sizes were small, we decided to test only four key organs that were important in other studies and for which we had directly measured fat-free dry mass. Different combinations of the organs were tested separately, to determine whether the patterns of significance were consistent between comparisons. Statistical significance was accepted at  $P \leq 0.05$ .

#### RESULTS

##### BODY MASS AND BMR CHANGES IN THE WILD

Mean body masses of the birds measured in Australia and China were  $198.2 \pm 19.1$  g and  $122.2 \pm 9.2$  g, respectively ( $n = 5$  for each; Fig. 1A). Total BMR was 42% lower in China than in Australia (means of 1.08 and 1.85 W respectively; Fig. 1B). Because much of the lost body mass consisted of fat, which is an order of magnitude less metabolically active than lean tissue (Scott and Evans 1992), we calculated the mass-specific BMR based on either lean tissue mass or a weighted estimate of lean and fat tissue masses ( $\text{lean} + 0.1 \times \text{fat}$ ). Mass-specific Chinese BMRs were respectively 33% or 30% lower than that of the Australian birds (Fig. 1C). This indicates that the difference in total BMR before and after migration reflects either a decrease in the mass of metabolically especially active tissues or a reduction in metabolic intensity of tissues (e.g., lower enzyme activity).

Because Great Knots are sexually monomorphic, we

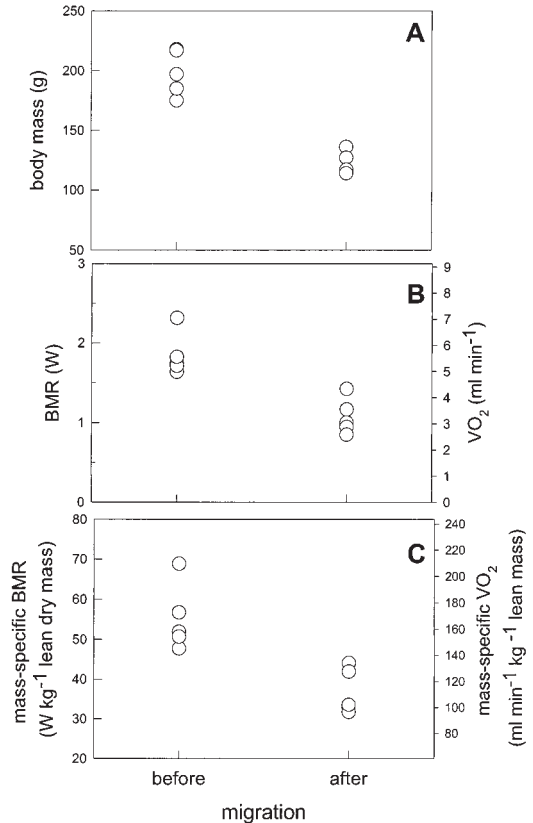


FIGURE 1. Comparison of (A) total body mass, (B) total BMR, and (C) mass-specific BMR in Great Knots caught before and after a 5400-km flight from Australia to China. For both groups,  $n = 5$ ; some points overlap in the plots.

could not select birds according to sex. The Australian sample comprised 4 males and 1 female, while the Chinese sample comprised 5 females. This difference in sex ratio is unlikely to have caused BMR differences between sites. Birds were nonreproductive, so we do not expect any sex effects as a consequence of reproductive state. Any sex effects could therefore only come from differences in body size (which were small) or body composition. In addition, the metabolic rate decrease we measured among individuals in the field was mirrored within individuals in captivity (below), so is unlikely to be due to the sex of the samples.

##### BODY MASS AND BMR CHANGES IN CAPTIVITY

When caught, the eight experimental birds weighed on average  $227.6 \pm 10.2$  g. By the time they had been transported to NIOZ and BMR measurements had started, they weighed on average  $168.5 \pm 13.5$  g. At the end of the experiment they weighed  $130.0 \pm 2.6$  g. Between two and four BMR measurements were made on each of the eight captive knots; 23 measurements were made in total. A similar change in total

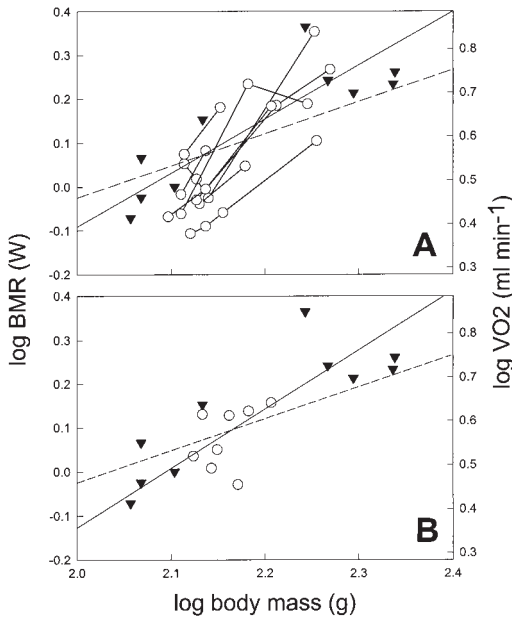


FIGURE 2. The relationship between BMR and body mass in Great Knots. Values are log-transformed. (A) all data points: dark triangles are wild birds and hollow circles joined by lines are captive birds. Solid regression line is for the wild birds only. Dotted regression line gives the predicted BMR based on the interspecific equation for shorebirds of Kersten and Piersma (1987). (B) Regression using mean BMR and mean body mass values for captive birds. Solid line shows the regression for wild and captive birds combined. Dotted line as in (A). Kersten and Piersma (1987) regressions are least-squares; Great Knot regressions are reduced major axis.

BMR was recorded in the captive birds as in the wild birds: the eight birds had a mean BMR of  $1.54 \pm 0.37$  W when heaviest and  $0.97 \pm 0.13$  W when lightest, a reduction of 37%. The average drop in BMR within individuals was  $35 \pm 13\%$ .

#### DEPENDENCE OF BMR ON BODY MASS

Reduced major axis regression of the relationship between log BMR and log body mass for the wild birds gave the relationship  $\log \text{BMR} = -2.57 + 1.24 (\pm 0.16) \log \text{body mass}$  (95% CI = 0.87–1.61,  $n = 10$ , Fig. 2A). The slope for the relationship between log mean BMR and log mean body mass for the captive birds was much higher, though weak ( $\log \text{BMR} = -5.57 + 2.61 (\pm 0.97) \log \text{body mass}$ , CI = 0.26–4.97,  $n = 8$ ). An alternative approach, averaging the individual slopes for birds measured three or four times ( $n = 3$  and 2 respectively), gave a high slope across the individuals (average  $2.23 \pm 0.18$ , range = 1.60–2.70). The interindividual relationship for the wild birds plus mean values for the captive birds combined was  $\log \text{BMR} = -2.84 + 1.36 (\pm 0.17) \log \text{body mass}$  (CI = 1.00–1.71,  $n = 18$ , Fig. 2B). None of the slopes generated by the regression analyses differed from each other.

#### CORRELATES WITH ORGAN CHANGES

To test for the influence of specific organs on BMR we used body composition data for the ten wild birds plus the three sacrificed birds (mean values in Table 1). The four organs we tested were flight muscles, intestine, liver, and kidneys. Residual masses of two of these organs, flight muscles and intestine, were positively related to residual BMR. Neither was significant on its own, but both were significant in multiple regressions with just those two organs ( $F_{2,10} = 6.1$ ,  $P < 0.02$ ; residual flight muscle mass  $P < 0.02$ , residual intestine mass  $P < 0.01$ ) or with liver or kidneys (liver included  $F_{3,9} = 4.6$ ,  $P < 0.04$ ; flight muscle  $P < 0.02$ , intestine  $P < 0.02$ ; kidney included  $F_{3,9} = 5.0$ ,  $P < 0.03$ , flight muscle  $P < 0.02$ , intestine  $P < 0.01$ ). The overall relationship for all four organs was not quite

TABLE 1. Mean  $\pm$  SD body composition of three groups of Great Knots: pre-migration birds caught in Australia ( $n = 5$ ), post-migration birds in China ( $n = 5$ ) and experimentally fasted birds caught in Australia and taken into captivity ( $n = 3$ ). All values are in grams. Total mass refers to fresh undissected mass, all organs and total lean mass are fat-free dry masses, and total fat mass refers to dry extracted fat.

Organ	Pre-migration	Post-migration	Fasted
Total mass	198.4 $\pm$ 19.1	122.2 $\pm$ 9.2	129.7 $\pm$ 0.6
Pectoral muscles	7.87 $\pm$ 0.67	6.36 $\pm$ 1.53	6.71 $\pm$ 0.24
Heart <sup>a</sup>	0.55 $\pm$ 0.05	0.50 $\pm$ 0.15	0.44 $\pm$ 0.07
Lungs	0.83 $\pm$ 0.12	0.62 $\pm$ 0.10	0.40 $\pm$ 0.05
Leg muscles	1.22 $\pm$ 0.04	1.08 $\pm$ 0.13	1.11 $\pm$ 0.14
Stomach <sup>a</sup>	1.83 $\pm$ 0.35	1.93 $\pm$ 0.56	0.89 $\pm$ 0.10
Intestine	1.49 $\pm$ 0.17	0.88 $\pm$ 0.08	0.59 $\pm$ 0.15
Liver	1.33 $\pm$ 0.20	0.86 $\pm$ 0.10	0.62 $\pm$ 0.08
Kidneys	0.59 $\pm$ 0.05	0.40 $\pm$ 0.05	0.28 $\pm$ 0.04
Remainder	12.71 $\pm$ 0.77	12.38 $\pm$ 0.49	11.25 $\pm$ 0.86
Total lean mass	34.26 $\pm$ 1.01	29.14 $\pm$ 2.67	26.26 $\pm$ 1.38
Total fat mass	66.73 $\pm$ 21.64	8.73 $\pm$ 3.10	28.11 $\pm$ 4.25

<sup>a</sup> Heart and stomach lean masses were estimated from fresh mass (Battley et al. 2001).

TABLE 2. Exponents of log-log regressions of BMR on total body mass in birds, in taxonomic order.

Species	Intraspecific <sup>a</sup>	Intra-individual <sup>b</sup>	Source
European Kestrel <i>Falco tinnunculus</i>	0.79	1.38 males 1.20 females	Daan et al. 1989
Redshank <i>Tringa totanus</i>	1.02	1.05 <sup>c</sup> 1.26	Scott et al. 1996
Red Knot <i>Calidris canutus</i>	0.69	1.38	Piersma et al. 1995 Weber and Piersma 1996
Great Knot <sup>d</sup> <i>C. tenuirostris</i>	1.36	2.23 <sup>e</sup>	This study
16 species of wader <sup>d</sup> Charadriidae	1.82	1.19	Kvist and Lindström 2001
Tree Swallow <i>Tachycineta bicolor</i>	1.03		Burness et al. 1998
Thrush Nightingale <i>Luscinia luscinia</i>		0.92 <sup>f</sup> 1.48	Lindström et al. 1999
House Sparrow <i>Passer domesticus</i>	0.84 adults 0.80 juveniles		Chappell et al. 1999

<sup>a</sup>Values from single measurements on individuals, or means of several measurements on different individuals.

<sup>b</sup>Values are not strictly intra-individual; Daan et al. (1989) and Scott et al. (1996) combined multiple measurements from different individuals in single analyses. Other studies used mean values from individuals.

<sup>c</sup>First value is for all birds studied; second value is for a subset of birds with a large range in total body mass.

<sup>d</sup>Reduced major axis regression slopes.

<sup>e</sup>Average slope of individual regressions based on three or four measurements.

<sup>f</sup>Each value represents the relationship for a single individual.

significant ( $F_{4,8} = 3.5$ ,  $P = 0.06$ ), though again only flight muscles and intestine showed significance ( $P < 0.02$  for both). The same patterns of significance held with an apparently nutrient-stressed bird from China (which had especially small flight muscles, Battley et al. 2001) omitted.

## DISCUSSION

The 42% reduction in total BMR documented here for the wild birds is one of the largest we know of in birds not undergoing torpor. Reductions of a similar magnitude are known from long-term fasting birds: a 38% decrease in resting metabolic rate (RMR; equaling an 18.5% drop in mass-specific RMR) in fasting Greater Snow Geese (*Chen caerulescens atlantica*, Boismenu et al. 1992); and a 28–38% drop in RMR of fasting Emperor Penguins (*Aptenodytes forsteri*; Dewasmes et al. 1980).

Seasonal (rather than fasting) variation in BMR is known from a variety of bird species, though changes are usually not as large as in these migrating Great Knots, at least in wild animals (Weathers and Caccamise 1978, Mortensen and Blix 1986, Swanson 1991, Cooper and Swanson 1994). Miller (1939), however, claimed a mass-specific oxygen consumption 43–49% lower in summer than in winter in the House Sparrow (*Passer domesticus*).

The flight of Great Knots from Australia to China probably takes around four days, and the decrease in BMR across individuals that we found in the field presumably occurs within individuals over that same period, if the change is a direct result of migratory flight. A reduction of over 40% in BMR in only three or four days would be one of the more rapid and dramatic

metabolic changes known in wild birds, although we have not demonstrated this directly. We have been unable to find other studies demonstrating changes in such a short period, though we expect that other long-distance migrant birds will show similar changes, especially those performing extremely long individual flights. A Thrush Nightingale (*Luscinia luscinia*) recovering from 12-hr flights or fasts increased BMR by 23% over three days, suggesting that the decrease during the flight or fast was of an equal magnitude (Lindström et al. 1999).

## SLOPE OF INTRASPECIFIC CHANGE

Recent studies have made it clear that while BMR scales with body mass interspecifically with an exponent of around 0.72–0.76 in birds (Aschoff and Pohl 1970, Daan et al. 1990), the slope of the relationship within a species or within individuals is much steeper, often being well above 1.0 (Table 2). Note that the studies in Table 2 refer to animals under a wide range of conditions (some during starvation or exercise, others during breeding; during decreasing or increasing body mass), and include wild and captive (both long and short-term) animals.

It is not surprising that analyses involving repeated measurements on individuals at different body masses, or even of different individuals that differ greatly in body mass, do not conform to interspecific relationships. An individual does not simply “scale up” as it becomes heavier. Because the structural portion of the body is fixed (by skeleton size), any change in body mass will necessarily involve a change in composition as well. In birds with large changes in body mass and composition, individuals will have very different phe-

notypes during fueling or fasting. An exponent of around 0.75 might be expected if birds varied in size (we use size here to denote the structural dimensions of the skeleton, rather than the volume; see Piersma and Davidson 1991) but not composition (which is flexible). Intraspecific comparisons of shorebirds during migration, however, will typically vary more in composition than structural size; intra-individual comparisons will not vary in structural size at all. There is no intuitive expectation of how steep the BMR-body mass slope will be in intraspecific or intra-individual comparisons such as ours. Across a large number of shorebird species, BMR of juvenile birds scaled with exponents of 1.82 for intraspecific and 1.19 for intra-individual comparisons (reduced major axis exponents; Kvist and Lindstrom 2001).

In this study, the slope of the regression of mean BMR on mean body mass for all eight captive birds was much lower than the average slope from individuals measured three or four times. This is partly because the BMR values for some individual birds ran parallel to each other (similar slopes but different probable intercepts; Fig. 2A). Birds with similar rates of change (slopes) but different absolute BMR levels (intercepts), when measured across the same body masses, would have different mean BMR values but the same mean body mass. Regression analyses using mean values may therefore not reflect the true individual rates of change. The average slope for the repeatedly measured individuals may be more realistic, and indicates that the BMR-body mass slope was apparently higher for the birds fasted in captivity than for the birds measured in the wild. Such a high intra-individual slope in the birds fasted in captivity is consistent with their having catabolized more protein during the fast than the wild birds did. At the end of the fast, despite having similar body masses to the wild birds, they had lower lean tissue contents (Table 1; Battley et al. 2001).

A very high exponent suggests that organs that contribute greatly to BMR have been disproportionately reduced in light animals (Daan et al. 1989), or that the mass-specific metabolic intensity of certain tissues varied during the study (Kersten et al. 1998). Several studies have shown correlations between various organs and BMR in a variety of animals (particularly intestine, liver, kidneys, heart, flight muscles, and lungs; Daan et al. 1990, Speakman and McQueenie 1996, Meerlo et al. 1997, Burness et al. 1998, Chappell et al. 1999). Despite this study's limited statistical power, the flight muscles and intestine clearly were influential. The flight muscles are large and especially metabolically active during migration (Marsh 1981, Lundgren 1988), while the intestine also has high metabolic activity and shows large changes in mass (Blaxter 1989, Piersma et al. 1999).

Another possible (partial) explanation for changes in BMR in migrants could be that elevated corticosterone before migration causes an increase in metabolic rate. Fasting decreases in BMR could then partly be caused by a drop in corticosterone concentrations. If captive birds became less stressed through repeated measurement, then metabolic rates might also drop accordingly. Since similar metabolic-rate

decreases were recorded in birds measured two, three, or four times, we do not think stress influenced the results much. Furthermore, corticosterone was higher in Bar-tailed Godwits (*Limosa lapponica*) arriving after a flight in The Netherlands than in birds about to depart on migration (M. M. Landys et al., unpubl. data), so corticosterone concentrations should not have systematically affected BMR measurements in the wild birds.

We have demonstrated that Great Knots show great metabolic and compositional flexibility in the wild and in captivity. Individual captive birds fasting without hard work showed the same metabolic reductions as found in the migrated groups. It is therefore plausible for individuals to seasonally adjust their body mass, composition, and metabolism depending on the energetic demands at different times. Studies at nonbreeding sites when migrants return are needed to determine whether reduced demands result in a lowering of BMR via changes in body composition. One factor that complicates this is if birds arrive in a nutrient-depleted state after a long flight and merely "recover" to a lower level than held at other times of the year.

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