Maximum energy intake rate is proportional to basal metabolic rate in passerine birds

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SUMMARY

A high energy intake rate may be important for many animals, but little is known of factors that determine intake capacity. Birds in migratory disposition presumably eat at their maximum capacity and therefore form a good model for studying the energy intake capacity of animals. We measured the maximum daily gross energy intake (GEI_{max}) and basal metabolic rates (BMR) in 22 species of migrant passerines during autumn. Both GEI_{max} and BMR scaled to body mass (w) close to $w^{0.70}$. More importantly, species with high GEI_{max} for their body mass also had relatively high BMR. BMR may reflect the size of the metabolic machinery involved in energy uptake. The maximum daily metabolizable energy intake (DME_{max}) was estimated from our GEI_{max} data. The average ratio DME_{max}/BMR was 4.6. In comparison, daily energy expenditure of reproducing passerines have been reported in the literature to be 3.6 times BMR. This suggests that energy intake rates may not normally limit breeding performance in passerines. Earlier studies have shown that BMR of homoeotherms reflect the rate of energy expenditure during reproduction. Our study shows that the energy intake capacity also correlates with BMR, which gives new perspectives on the ecological significance of BMR.

1. INTRODUCTION

Rates of energy intake and expenditure, and the balance between them, are pivotal to an animal's fitness during many phases of the annual cycle. Some animals may have evolved a comparatively large metabolic machinery in response to periodically high levels of energy expenditure (Kersten & Piersma 1987; Daan *et al.* 1990, 1991). Daan *et al.* (1990, 1991) found, for both birds and mammals, that animals with relatively high levels of daily energy expenditure during reproduction (DEE_{par}), also had relatively high basal metabolic rates (BMR). They concluded that natural selection has operated on DEE_{par}, and that BMR reflects the size of the metabolic machinery needed to sustain the optimal DEE_{par}.

Has natural selection operated in a similar way on energy intake rates? The capacity for energy acquisition may be reflected in the BMR of animals for at least two reasons. First, natural selection may operate primarily on upper levels of DEE when shaping an animal's metabolic machinery (Daan *et al.* 1990). The capacity for energy acquisition may then simply be adjusted to support these levels of DEE (symmorphosis). For this reason only, energy acquisition capacity and BMR could be correlated. Second, natural selection may operate separately on upper levels of energy intake, independently of DEE. BMR then reflects the capacity of the energy acquisition machinery.

Many organs with high metabolic activity (for example, heart, liver, kidney), which probably make up a significant part of BMR (Blaxter 1989; Daan *et al.* 1989; Scott & Evans 1992; Konarzewski & Diamond 1994), are involved both in energy acquisition and

energy expenditure. Therefore, it may be difficult to disentangle the importance of the two systems in contributing to BMR. However, the possibility that natural selection has operated independently on energy intake rates deserves attention. For example, high energy intake rates, enabling high fuel deposition rates, may be advantageous during migration (Alerstam & Lindström 1990), or when replenishing reserves that have temporarily been exhausted during reproduction or on cold winter days. In these cases, the most favourable energy intake rates may be far higher than the corresponding energy expenditure rates during, for example, reproduction.

Several studies have reported DME_{max} (the maximum daily metabolizable energy intake) of 3–6 times BMR (Kleiber 1933; Kirkwood 1983; Kersten & Piersma 1987; Karasov 1990). It is important to recognize that animals are known to reach their DME_{max} also in the wild (Diamond *et al.* 1986; Masman *et al.* 1989; Lindström 1990; Zwarts & Dirksen 1990). Also, Lindström (1991) showed that the maximum fuel deposition rates of migratory birds in the wild reach the upper levels to be expected if the birds reach their DME_{max}. Thus, DME_{max} is a potentially important parameter for wild-living animals, on which natural selection may operate. Although DME_{max} and BMR vary in parallel in inter-specific allometric comparisons, a direct relation between them remains to be shown, because DME_{max} and BMR are not normally measured in the same animals, populations or species. In addition, the parallel allometric relations may not reflect a causal link between DME_{max} and BMR, they may simply scale similarly to body mass (Harvey & Pagel 1991).

We have measured energy intake rates and BMR in

Proc. R. Soc. Lond. B (1995) **261**, 337–343
Printed in Great Britain

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passerine birds during migration. Many migratory birds probably try to maximize their migration speed, that is, to minimize the time spent on migration (Carpenter *et al.* 1983; Alerstam & Lindström 1990; Gudmundsson *et al.* 1991; Lindström & Alerstam 1992). The time spent on migration will mainly depend on how fast migrants can build up fuel reserves for the migratory flights. A time-minimizing migrant should accordingly maximize its fuel deposition rate. It is well known that migrants in captivity gain substantial fat loads, often at rates comparable to the highest rates found in nature (Klaassen & Biebach 1994). We would therefore expect caged migrants given food *ad libitum* to maximize their daily energy intake, and therefore to be suitable objects for studying the relation between maximum energy intake rates and BMR in homoeotherms.

2. METHODS

Migrating passerines were trapped at Falsterbo Bird Observatory (55° 12′ N, 12° 23′ E) in August–October 1993 and 1994. A few birds were caught at Ottenby Ornithological Research Centre (56° 12′ N, 16° 24′ E) and at Stensoffa ecological station, 18 km east of Lund (55° 42′ N, 12° 27′ E). Bluethroats *Luscinia svecica* were captured between 25–27 August 1993 in Norrtälje in east central Sweden (59° 46′ N, 18° 45′ E). The trapping of birds at bird observatories ensured that most individuals studied were in 'migratory mood'. The experiments were done at Stensoffa ecological station in 1993, and in Lund in 1994, under licence from the Swedish Environmental Protection Board and the Lund–Malmö Ethical Board for Animal Experiments.

Only first-year birds that had completed their post-fledgling moult were included in this study. The birds were kept indoors in separate cages at an ambient temperature of +20–24 °C under the natural light regime of Lund, including the period of civil twilight. This meant a light period of 16 h and 4 min on 19 August, and 10 h and 30 min on 1 November, the earliest and latest dates, respectively, in our study. Birds were given mealworms *ad libitum*, as well as fresh water and vitamins daily. The birds were allowed one to several days to get used to the cages and the food. Birds that did not eat during the first day in captivity were released.

Birds that did eat were subsequently deprived of food until they reached a low level of stored fat (fat score 1–2, Petterson & Hasselquist 1985). On average food deprivation lasted less than two days and normally not more than three days. The following night BMR was measured (see below). During the following days the birds were fed *ad libitum*. Birds were weighed to the nearest 0.1 g (thrushes to nearest 0.5 g) on a Pesola spring balance every evening, no more than 3 h before dark. Both the new and remaining food were weighed to the nearest 0.1 g. The birds were released when their mass increased no further.

Maximum gross energy intake rates (GEI$_{max}$, in kJ d^{-1}) were calculated as the highest average daily amount of mealworms eaten during three consecutive days, multiplied by the energetic density of mealworms. The three-day period was chosen for several reasons. First, any measurement error in the amount of food eaten is likely to diminish with an increasing number of days. Second, we do not know to what extent energy intake on a given day influences energy intake the next day. Thus, longer periods may give more realistic values. However, we knew before-hand that many birds reach a plateau in mass already after four or five days of

fattening, precluding the use of longer periods. Third, a common length-of-stay at migratory stopover sites is three days (Lindström 1986). Nevertheless, corresponding values for periods of one and two days have also been analysed.

The energy content of the mealworms was measured by bomb calorimetry to 12.0 kJ g^{-1} wet mass (s.d. = 0.22, n = 6, M. Klaassen, Å. Lindström & R. Zijlstra, in preparation), the value used when estimating GEI$_{max}$. When estimating DME$_{max}$ from values of GEI$_{max}$ we assumed an assimilation efficiency of 0.84 for all species, as measured on fattening thrush nightingales *Luscinia luscinia* the same autumn (M. Klaassen, Å. Lindström & R. Zijlstra, in preparation). This value is close to other estimates for full-grown passerines eating fresh mealworms (0.84–0.86, Castro *et al.* 1989).

Many birds did not increase in mass although they did eat, while some birds increased in mass at very moderate rates. As we were interested in maximum rates, we excluded GEI estimates if, during the three GEI$_{max}$ days the minimum one-day GEI was less than 50 % of the maximum one-day GEI. Also, the average daily mass increase over the three GEI-days had to be at least half the maximum found in birds of similar size in nature (0.164 w$^{0.75}$ g d^{-1}, w in g; recalculated from Lindström 1991). As a last requirement the bird had to have increased in mass all three days of the GEI$_{max}$ estimate. As we do not know how rapidly a bird can adapt its metabolic machinery to changing circumstances (Piersma *et al.* 1995a), we excluded GEI estimates based on starting dates more than ten days apart from the BMR measurement.

Metabolic rates were calculated from measurements of oxygen consumption in an open-circuit system. Birds were measured in 1.6 l metabolic chambers (6.5 l for thrushes) in total darkness. Measurements started around 18h00 local time. Temperature was controlled at +23 °C. Indoor air was led through the system in the following order: bird, dryers (silica gel), pumps, mass flow controllers (Brooks 5850E), valves, oxygen analyser (Servomex 1100 A). Air flow rates of 13.0–30.0 l h^{-1} were used depending on the size of the bird. IR-sensors were used during most nights to detect locomotory activity. Two birds were measured alternately for periods of 25 min throughout the night. Reference air was measured for 15 min every 90 min. Data on oxygen concentration, temperature, and activity were registered on a data logger (Grant SQ1202-40K). Oxygen consumption was calculated according to Hill (1972), and recalculated to energy metabolism assuming an RQ of 0.72 and an energetic equivalent of 19.8 kJ l^{-1} oxygen consumed.

By definition BMR should be measured on post-absorptive birds. However, measuring night-migrating passerines, often showing strong night-time activity ('Zugunruhe'), creates particular problems. Zugunruhe have been shown to be low if the birds are lean and have a good supply of food (Biebach 1985; Gwinner *et al.* 1988). To suppress Zugunruhe, we gave the birds food *ad libitum* for 3 h or more, until measurements started. No food was given during measurements. This may cause oxygen consumption to reflect heat increment of feeding, in addition to BMR. However, digesta retention times of arthropod-eating passerines (Karasov 1990), and changes in RQ in Garden Warblers *Sylvia borin* after foraging has ceased (Klaassen & Biebach 1994), imply that even the largest birds in our experiment reached a post-absorptive state already within 4 h of their last meal. Moreover, because most of our analyses refer to comparisons between our own measurements, any effect of heat increment of feeding on the BMR measurements should be of little importance to our conclusions. Birds that showed Zugunruhe during the first measurement, were measured again a second time, after being brought back to low fat levels. When estimating BMR (kJ d^{-1}) we used the lowest ten-minute average rate of oxygen consumption.

Table 1. *Average body mass, basal metabolic rate* (BMR), *and maximum gross energy intake rate* (GEI_{max}), *of passerine migrants during autumn migration*

(Maximum daily metabolizable energy intake (DME_{max}) was calculated from GEI_{max} assuming an assimilation efficiency of 0.84. The ratio DME_{max}/BMR is also presented.)

no	species	n	mass/g	range	$BMR/(kJ\ d^{-1})$	range	$GEI_{max}/(kJ\ d^{-1})$	range	$DME_{max}/(kJ\ d^{-1})$	range	DME_{max}/BMR	range
1	*Phylloscopus collybita*	4	6.7	6.4–7.1	13.0	11.7–14.2	72.8	67.6–76.0	61.2	56.8–63.8	4.73	4.01–5.48
2	*Phylloscopus trochilus*	2	8.0	8.0–8.1	14.8	13.6–16.2	86.9	73.4–102.8	73.0	61.7–86.4	4.93	4.54–5.33
3	*Troglodytes troglodytes*	1	8.9	—	14.3	—	65.2	—	54.8	—	3.84	—
4	*Parus ater*	1	9.0	—	17.6	—	78.0	—	65.5	—	3.71	—
5	*Parus caeruleus*	2	9.6	9.6–9.7	14.3	13.5–15.2	95.0	88.4–102.0	79.8	74.3–85.7	5.56	5.51–5.62
6	*Sylvia curruca*	1	10.1	—	16.7	—	96.4	—	81.0	—	4.86	—
7	*Acrocephalus schoenobaenus*	3	10.5	9.9–11.1	20.2	19.1–21.8	121.0	107.6–136.8	101.7	90.4–114.9	5.09	4.15–6.01
8	*Acrocephalus palustris*	1	10.7	—	21.4	—	96.8	—	81.3	—	3.80	—
9	*Ficedula hypoleuca*	2	10.7	9.5–12.0	18.1	16.2–20.4	97.6	80.5–118.4	82.0	67.6–99.4	4.53	4.19–4.88
10	*Muscicapa striata*	2	13.9	13.9–13.9	24.5	23.3–25.7	145.4	132.4–159.6	122.1	111.2–134.1	4.99	4.76–5.21
11	*Motacilla flava*	1	14.0	—	24.1	—	143.6	—	120.6	—	5.01	—
12	*Parus major*	1	14.9	—	22.3	—	136.8	—	114.9	—	5.16	—
13	*Luscinia svecica*	11	15.5	13.9–17.7	23.9	20.4–27.2	144.1	114.8–170.4	121.0	96.4–143.1	5.11	3.93–5.81
14	*Erithacus rubecula*	3	16.2	15.9–16.4	22.4	20.5–25.1	113.7	109.2–116.8	95.5	91.7–98.1	4.28	3.86–4.79
15	*Sylvia atricapilla*	4	16.9	16.1–17.8	23.8	21.2–25.6	153.4	136.4–166.0	128.8	114.6–139.4	5.46	4.64–6.36
16	*Emberiza schoeniclus*	1	18.2	—	26.6	—	132.8	—	111.6	—	4.19	—
17	*Prunella modularis*	3	18.6	16.9–19.8	30.5	26.9–34.9	130.7	122.4–141.6	109.8	102.8–118.9	3.64	2.94–4.03
18	*Sylvia nisoria*	1	20.9	—	24.7	—	143.2	—	120.3	—	4.88	—
19	*Fringilla montifringilla*	6	21.4	20.2–23.3	30.9	27.9–34.4	171.4	137.2–215.2	144.0	115.2–180.8	4.72	3.76–6.22
20	*Lanius collurio*	3	26.1	24.5–27.7	30.6	29.4–31.3	158.6	135.5–177.3	133.2	113.8–149.0	4.37	3.87–4.80
21	*Turdus iliacus*	2	57.9	54.0–62.1	61.6	56.5–67.1	365.3	319.6–417.6	306.9	268.5–350.8	4.99	4.76–5.22
22	*Turdus philomelos*	4	62.4	58.0–68.0	61.6	56.9–66.3	315.7	265.6–341.2	265.2	223.1–286.6	4.32	3.92–4.83

We considered several of the BMR estimates unreliable. The following selection criteria where used: (i) birds that reached fat score 0 were excluded as there was a risk of hypothermia (Reinertsen & Haftorn 1986; Daan *et al*. 1989); (ii) birds that showed clear activity throughout the night (as recorded by the IR-sensors) were also excluded; and (iii) because birds were measured in small boxes and flow rates were high, oxygen consumption readings changed rapidly in response to activity. As a result there were distinct differences in the shape of the oxygen consumption curves of inactive and active birds, and active birds could be excluded with high certainty.

For statistical evaluation of the results we used ANCOVA, ANOVA and Pearson correlation. We relate all metabolic measurements to the body mass the birds had just before the metabolic measurements. All data on body mass, GEI_{max} and BMR were $\log_{10}$-transformed before calculations. Therefore geometric means are presented for the different species. Residuals were calculated from model I regressions. Because numbers are small we give no other statistic of dispersion than range for each species. Statistical analyses were performed using Systat 5.0 (Wilkinson 1990).

Species may (for evolutionary reasons) not be considered independent values. Therefore we also estimated the allometric relation on independent contrasts between nodes in a phylogenetic tree according to Harvey & Pagel (1991). This method assumes that rates of evolutionary change may not be uniform throughout the phylogenetic tree and uses a punctuational model under the assumption that it yields acceptable properties for statistical tests. The regression slope derived from independent contrasts can be proven to estimate the true slope based on traditional across taxa analyses (Harvey & Pagel 1991). A disadvantage of phylogenetic contrasts is that only the slope is estimated and not the elevation of the regression line. We used a phylogeny and taxonomy based on DNA–DNA hybridization studies to construct our phylogenetic tree (Sibley & Alquist 1990; Sibley & Monroe 1990).

3. RESULTS

In total 132 individuals belonging to 34 species fed voluntarily and entered our test protocols. Of these, 59 individuals of 22 species fulfilled our selection criteria on both GEI_{max} and BMR (see table 1 and figure 1). The

allometric relations of BMR, and GEI_{max}, respectively (in kJ d^{-1}) on body mass (w, in g) in the 22 species, are:

$$BMR = 3.53\ w^{0.69} \quad r^2 = 0.947, \tag{1}$$

$$GEI_{max} = 19.16\ w^{0.70} \quad r^2 = 0.902. \tag{2}$$

The slopes of the two regressions are statistically indistinguishable ($F_{1,20} = 0.0029$, $p = 0.958$). Species-specific residuals from the allometrically predicted $\log GEI_{max}$ and $\log BMR$ were significantly positively correlated ($r = 0.425$, $p = 0.048$, see figure 2). Thus, when the effect of body mass is excluded, species with high GEI_{max} also have a relatively high BMR. GEI_{max} was also calculated as two-day and one-day averages, showing a similar relation between residuals of $\log GEI_{max}$ and $\log BMR$ (two-day, $r = 0.370$, $p = 0.058$, $n = 27$ species; one-day, $r = 0.279$, $p = 0.177$, $n = 25$ species). Residuals from regressions of phylogenetically independent contrast of $\log GEI_{max}$ and $\log BMR$ also show a significant positive correlation ($r = 0.558$, $p = 0.013$, $n = 19$).

After estimating DME_{max} from GEI_{max} (assuming an assimilation quotient of 0.84), the average DME_{max}/BMR ratio was calculated to be 4.6 (s.d. = 0.56, $n = 22$). The equation describing DME_{max} in relation to body mass in migrating passerines is:

$$DME_{max} = 16.09\ w^{0.70}. \tag{3}$$

4. DISCUSSION

Data on maximum energy intake rates are scarce and difficult to obtain (Kirkwood 1983; Blaxter 1989; Karasov 1990; Weiner 1992). Those available for interspecific comparisons have been collected under varying conditions: often during cold stress or high work load, that may give rise to unreliable values (Ricklefs 1974; Karasov 1990). In addition, data on energy intake rates and BMR have not normally been investigated in the same animals, or even the same species, precluding detailed comparisons (Blaxter 1989; but see Konarzewski & Diamond 1994).
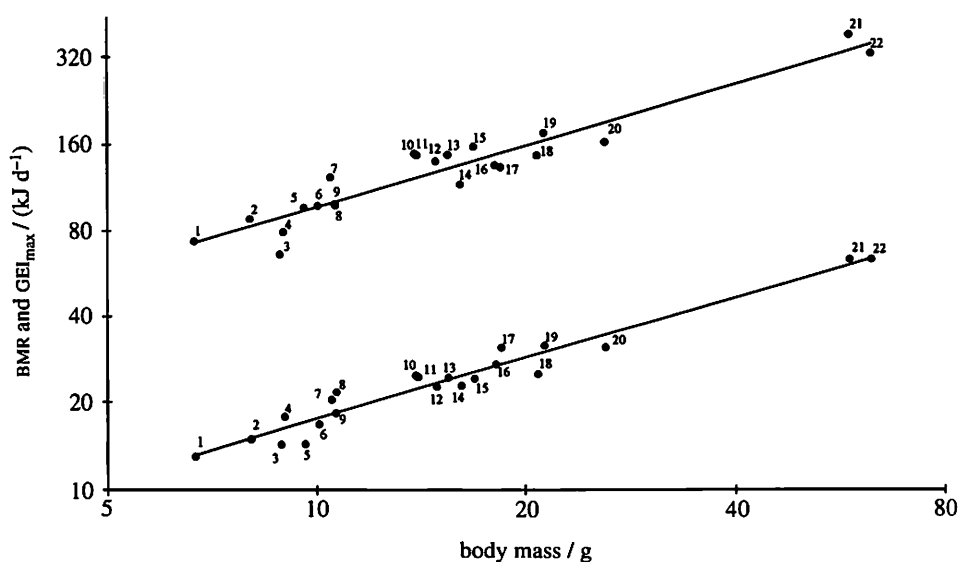

Figure 1. Basal metabolic rate (BMR) and maximum daily gross energy intake rate (GEI_{max}) in relation to body mass in 22 passerine migrant species in autumn. Numbers refer to species listed in table 1.
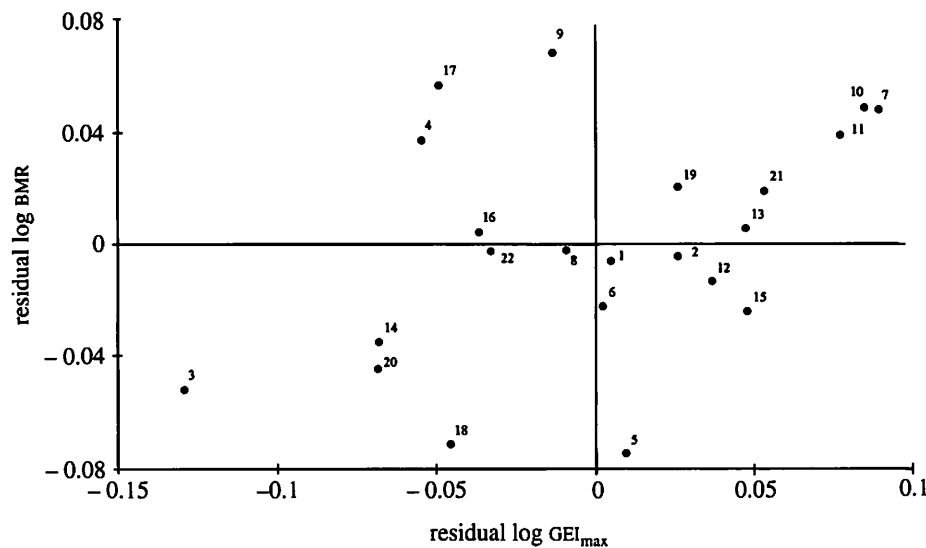
Figure 2. The association between residuals of log BMR and log GEI_{max} in 22 passerine migrant species in autumn. Numbers refer to species listed in table 1.

We measured energy intake rates of birds that have a natural urge to feed at high rates, and we measured BMR in the same individuals. Of basic importance for our interpretations is that the migrants did eat at, or close to, their maximum capacity. A parallel study on thrush nightingales, feeding for migratory fattening, showed that they did not increase GEI when exposed to cold stress (increasing energetic demands), indicating that they were already feeding at their maximum capacity (Klaassen, M. *et al.* in preparation). In addition, Kirkwood (1983) listed data on DME_{max} in 21 species of birds and mammals and suggested that an absolute ceiling to DME_{max} in homoeotherms lies at $2200 \ w^{0.72} \ kJ \ d^{-1}$ (w in kg). Out of 22 species in our study 12 had DME_{max} higher than this level; the highest being $2699 \ w^{0.72} \ kJ \ d^{-1}$ (*Acrocephalus schoenobaenus*). Therefore we feel confident that our data set on migrating passerines provides a good opportunity to analyse the association between BMR and maximum energy intake rates in a uniform group of homoeotherms.

We found a significant positive correlation between GEI_{max} and BMR, after correcting for body mass. The phylogenetic-contrasts method supported and even strengthened this result. This suggests a direct relation between the ability to digest food and BMR. To our knowledge, this is the first time such a correlation has been demonstrated. The physiological explanation is likely to be the high metabolic activity of organs involved in the digestion of food, and the uptake and transportation of energy (Blaxter 1989; Daan *et al.* 1989; Scott & Evans 1992; Konarzewski & Diamond 1994). The metabolic activity of these organs probably contribute significantly to BMR. Konarzewski & Diamond (1994), studying cold-stressed mice, found a correlation between energy intake rates and the size of kidneys and small intestines, as well as a correlation between resting metabolic rate (RMR) and the size of heart, kidneys and intestines. However, they did not find the expected correlation between DME_{max} and RMR.

A corresponding relation between DEE and BMR has been demonstrated before, both for birds (Daan *et al.*

1990) and mammals (Daan *et al.* 1991; Koteja 1991). Daan *et al.* (1990, 1991) suggested that natural selection has operated on upper levels of DEE in animals, and that BMR simply reflects the size of the metabolic machinery evolved to sustain these levels of DEE. Support for this hypothesis has come from recent work on intra-specific variation in BMR and body composition in long-distance migrant Knots *Calidris canutus* (Piersma *et al.* 1995a).

For the moment it is not possible to decide whether the correlation we find between GEI_{max} and BMR simply reflects that the energy intake rate is adjusted to sustaining optimal DEE levels, for example during reproduction, or if selection has operated on the energy acquisition system independently of the energy expenditure system. Daan *et al.* (1990) listed DEE_{par}/BMR ratios for eight species of passerines and found them to be on average 3.6 (s.d. = 0.84, range 2.64–4.59, calculated from table 3 in Daan *et al.* 1990). Our estimated DME_{max}/BMR ratio (4.6) is significantly higher than the average DEE_{par}/BMR ratio reported by Daan *et al.* ($t_{28} = 3.25$, $p = 0.010$). Thus, given that our estimate of assimilation quotient (0.84) is not too high (any value down to 0.78 would still make the difference significant), it is likely that DME_{max} does not normally set proximate limits to parental effort in passerines. However, because organ sizes and metabolic rates may vary intra-specifically over the year (Piersma *et al.* 1995a, b), our DME_{max}/BMR ratio may not be applicable to the breeding season. Preferably, DME_{max} and DEE_{par} should be measured in parallel before strong conclusions regarding the relation between DME_{max} and energy turnover during reproduction can be drawn.

The discrepancy between DME_{max} and DEE_{par} indicates that selection may operate independently, at least partly, on the energy intake system. However, the relative importance of the energy acquisition machinery (digestion and assimilation), as studied by us, and the energy expenditure machinery (muscles etc., reflected in DEE), in contributing to BMR, remains to be explored.

Variation in components of body mass that con-

tribute little to metabolism, for example fat (Scott & Evans 1992), will produce a correlated variation in residuals of DME_{max} and BMR. However, to account for all the residual variation found in our study, the metabolically inactive tissues would have to show a variation of up to 35 % of the total body mass, and an average variation of 13 % of total body mass. The mass we used in our calculations was for virtually lean birds (fat score 1–2), which corresponds to 3–7 % fat of total mass (Pettersson & Hasselquist 1985; Åkesson *et al.* 1992). Therefore, any effect of metabolically inactive tissues on our results should be minor.

Ricklefs *et al.* (1995) have argued that all association between DEE and BMR in birds may arise from the fact that DEE actually includes the same metabolic turnover which continues during BMR-measurements. The same argument cannot be applied to GEI because this is simply a measure of total energy intake before it enters any metabolic pathway.

If we accept that BMR is directly related to DME_{max}, and that natural selection may operate directly on DME_{max}, new perspectives arise on the ecological significance of BMR. This possibility seems largely unexplored in the literature. A rapid intake of energy may regularly, or occasionally, be advantageous and important for an animal's fitness. For example, birds at higher latitudes often have relatively high BMR, and small passerines are known to have higher BMR in winter than in summer (Weathers 1980). This is interpreted as an adaptation to cold, the thermogenic capacity varying in parallel with BMR (Cooper & Swanson 1994). Alternatively, or additionally, the high BMR of birds adapted to cold conditions may reflect an increased capacity to metabolize food at high rates. If energy stores are depleted as a result of inclement weather, and foraging becomes impossible, it may be of utmost importance to be able to store new reserves when weather and food availability permits. Even under more stable winter conditions, the daily need to gain large reserves for long cold nights may put a premium on high DME.

Another possible case where selection may operate directly on DME_{max} is birds on migration. If time-minimization during migration is important (Alerstam & Lindström 1990; Gudmundsson *et al.* 1991; Lindström & Alerstam 1992), we may expect strong selection on high DME_{max}, so BMR should be high. The significance and importance of a high BMR during migration is suggested by Piersma *et al.* (1995*b*). They found that the BMR of captive Knots varied over the year and was highest during the migratory seasons when energy is deposited at high rates, although the BMR increase was paralleled by an increase in lean body mass.

Mass-independent variation in BMR has previously been demonstrated between taxonomic groups (Lasiewski & Dawson 1967), between phases of the circadian rhythm (Aschoff & Pohl 1970), and in relation to ecological parameters such as latitude (Weathers 1980), season (Weathers 1980), food habits (McNab 1988), plane of nutrition (Daan *et al.* 1989), phase of moult (Dietz *et al.* 1992; Lindström *et al.* 1993) and natural DEE (Daan *et al.* 1990, 1991). We add a

further parameter to this list: the maximum level of energy intake rate.

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