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Maximum Daily Energy Intake: It Takes Time to Lift the Metabolic Ceiling

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ABSTRACT

Conventionally, maximum capacities for energy assimilation are presented as daily averages. However, maximum daily energy intake is determined by the maximum metabolizable energy intake rate and the time available for assimilation of food energy. Thrush nightingales (*Luscinia luscinia*) in migratory disposition were given limited food rations for 3 d to reduce their energy stores. Subsequently, groups of birds were fed ad lib. during fixed time periods varying between 7 and 23 h per day. Metabolizable energy intake rate, averaged over the available feeding time, was 1.9 W and showed no difference between groups on the first day of refueling. Total daily metabolizable energy intake increased linearly with available feeding time, and for the 23-h group, it was well above suggested maximum levels for animals. We conclude that both intake rate and available feeding time must be taken into account when interpreting potential constraints acting on animals' energy budgets. In the 7-h group, energy intake rates increased from 1.9 W on the first day to 3.1 W on the seventh day. This supports the idea that small birds can adaptively increase their energy intake rates on a short timescale.

Introduction

Energy intake rates in wild animals are sometimes limited by the rate at which food can be processed by the digestive tract rather than by food availability (Diamond et al. 1986; Saarikko and Hanski 1990; Zwarts and Dirksen 1990; Kersten and Visser 1996). Kirkwood (1983) reviewed estimates of metabolizable energy intake in homeotherms, presumed to process food at their maximum capacity, and constructed an allometric equation describing the limit to metabolizable energy intake. The review included birds and mammals ranging in size from <20 g to >600 kg and covered a wide selection of feeding habits, including insectivores, carnivores, piscivores, granivores, omnivores, and herbivores. This allometric equation has been used widely as a measuring stock for maximum energy intake. Kirkwood (1983) built his analysis on daily averages and did not present the amount of time the animals had available for ingestion, digestion, and absorption of food per day. The aim of this article is to show that available feeding time can influence daily energy intake strongly and that failure to recognize this influence may lead to erroneous conclusions about limits and constraints on animals' energy budgets.

We define daily metabolizable energy intake (DME, in J) as the product of the rate at which energy is absorbed by the digestive tract (metabolizable energy intake rate [MER, in W]) and time available for absorption of food energy. This definition applies when MER is constant throughout the time over which MER is calculated. In some animals and under some circumstances, MER may vary with time. DME will then still be a result of MER and time available for absorption of food energy, but the calculation will be more complex because MER has to be integrated over time.

Whether wild animals in different natural circumstances are limited by the rate at which food can be digested has important ecological implications (Karasov 1996). Therefore, it is of great interest to compare energy budgets measured in wild animals with the maximum rates at which food energy can be assimilated (e.g., Daan et al. 1991; Lindström 1991). Maximum DME, such as that reported in Kirkwood's (1983) review, rather than MER, has often been used as reference in these comparisons (Masman et al. 1989; Karasov 1990; Daan et al. 1991; Lindström 1991; Weiner 1992; Lindström and Kvist 1995). A better approach would be to use MER and the actual time available for assimilation of food energy. For example, if animals acquire energy at maximum capacity only during daytime, they can most likely reach a higher daily energy intake during summer at high latitudes than they can in winter, when only a few hours each day are available for feeding. Other factors may also restrict the time available for feeding (e.g., tidal regime and requirement for sleep). Using maximum DME, estimated under a different daily cycle, to assess digestive limitations in these circumstances may lead to erroneous conclusions.

In this article, we present maximum MER and DME for thrush nightingales (*Luscinia luscinia*) depositing fuel stores in

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preparation for autumn migration. It has become increasingly clear that many migrants try to maximize speed of migration (distance covered per day, including time spent on both flying and fueling; Alerstam and Lindström 1990). To achieve this speed, the birds should maximize fuel deposition rates, which is normally best accomplished by maximizing energy intake. Klaassen et al. (1997) presented convincing evidence that thrush nightingales that deposit fuel stores for migration do indeed maximize energy intake. We investigated the effect that duration of food availability has on MER and DME. This study shows that thrush nightingales, given enough time to feed per day, have daily energy intake rates well above previously suggested maximum levels in animals (Kirkwood 1983).

Material and Methods

Birds and Housing Conditions

Thrush nightingales were caught near Ottenby (56°12′N, 16°24′E) and Revinge (55°22′N, 12°27′E) in southern Sweden in August 1994 and 1995. The birds were transported to Stensoffa Ecological Station in 1994 and to the ecology building of Lund University in 1995. Birds were held individually in cages measuring 35 × 35 × 35 cm. Air temperature was 22° ± 2°C. Lights were controlled by a timer to simulate the natural photoperiodic conditions of Lund. This means a light period varying between 14 h 40 min and 13 h 50 min on the experimental days. Lights were switched on between 0545 and 0610 hours local time. All birds were fed mealworms (*Tenebrio* sp.) ad lib. from capture until the start of the experiments. To enable the birds to eat at night without disturbing their normal seasonal photoperiodicity, a dimmed "night lamp" (3 lux) was placed above each feeding tray. A few observations were done at different times during the nights of the experiments, and we could affirm that the birds did indeed feed in this dimmed light. Water for drinking and bathing was available at all times. At the end of August, the birds spontaneously increased their body mass in preparation for autumn migration. The increase resulted in an elevated and constant body mass before the experiments started on September 7, 1994, and on September 14, 1995.

Experimental Design

In 1994, the 17 thrush nightingales were divided into three experimental groups with food ad lib. available for 7, 10, and 13 h each day. New food was supplied at 1200, 0900, and 0600 hours, respectively. Remaining food for birds in all groups was collected at 1900 hours. The birds were weighed between 0530 and 0600 hours each morning. In 1995, there were 20 birds divided over four experimental groups, and their available feeding times were 14, 17, 20, and 23 h each day. Fresh food was supplied at 2000, 1700, 1400, and 1100 hours, respectively. Remaining food was collected at 1000 hours the following

morning. All birds were weighed between 1030 and 1100 hours. In both years, the experiment started with 3 d of limited food rations (61 kJ d^{-1}, SD = 16.9 kJ d^{-1}), which caused a reduction in body mass and motivated the birds to subsequently maximize their energy intake. In the days that followed, food ad lib. was available for the periods defined for each group. In 1994, the experiment continued for 7 d. In 1995, the experiment continued for only 3 d because the birds had already regained their initial body mass after these 3 d. Free-living thrush nightingales depart on migratory flights when sufficient energy stores have been deposited. The energy is used to fuel the flights. At the next stopover site, new stores are deposited, and the process is repeated until they reach their migratory destination. Captive thrush nightingales, however, are prevented from departing on migratory flights. Once fuel stores of sufficient size for departure are accumulated, they do not add more fuel and just become more restless in the cages. Accordingly, they also stop maximizing energy intake when fuel stores and body mass start to reach "departure" levels.

Data Analysis

Food intake was determined by weighing the supplied food and the remaining food each day. Food intake was converted to DME, assuming a gross energy content of fresh mealworms of 12 kJ g^{-1} (SD = 0.22) and an assimilation efficiency of 83.7% (Klaassen et al. 1997; DME [kJ] = food intake [g] × 12 × 0.837). Klaassen et al. (1997) found the assimilation efficiency for thrush nightingales that were eating mealworms to be constant regardless of energy intake rate (gross energy intake explained 99.98% of the variation in metabolizable energy intake). On the first day with food ad lib., we used linear regression of DME on time available for feeding (T) to estimate MER and the metabolizable food energy remaining in the gut when food intake ceased (E_r). We assumed a constant rate of food processing during the time food was available and thus the slope of the regression line estimates MER (kJ h^{-1}) and the intercept estimates E_r (kJ; Fig. 1). In following days, MER was calculated by dividing DME by T after subtracting E_r estimated on the first day with food ad lib. (MER [kJ h^{-1}]] = [DME − E_r]/T). MER is presented throughout in the SI unit watts (MER [W] = MER [kJ h^{-1}]/3.6).

Differences in MER between treatment groups were tested by using one-way ANOVA. We also tested for differences in initial mass decrease and morning mass on the first day of refueling between years by using one-way ANOVA. Statistics were calculated by using the Analysis Tools package of Microsoft Excel 7.0.
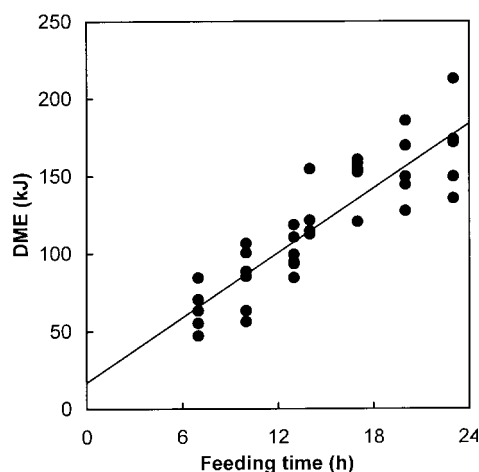
Figure 1. Daily metabolizable energy intake (DME) in thrush nightingales (*Luscinia luscinia*) plotted against available feeding time (T) for the first refueling day after a 3-d period with limited food rations. The line is fitted by ordinary linear regression (DME = 17.0 + 6.95 × T, $r^2 = 0.77$). The slope of the regression line estimates metabolizable energy intake rate (MER). The intercept estimates the metabolizable food energy remaining in the gut after food intake has ceased (E_r, see "Data Analysis").

Results

Body Mass

The average decrease in morning mass over the three initial days with limited food was 5.2 g (SD = 0.95 g). There was no significant difference between years in mass decrease ($F_{1,35} = 2.15$, $P = 0.15$). Morning mass on the first day of refueling was, on average, 21.2 g (SD = 2.2 g) in 1994 and 23.3 g (SD = 3.8 g) in 1995 ($F_{1,35} = 4.21$, $P = 0.048$). On the first day of refueling, body mass gain was positively related to available feeding time (Fig. 2). Birds in the 7-h group regained on average 9% of their initial mass loss, while birds in the 17-, 20-, and 23-h groups regained more than 50% of their mass loss. The 7- and 10-h groups showed an increase in rate of mass gain from the first to the third day of refueling, whereas all of the other groups (13–23 h) showed a decreased rate of mass gain over the period of refueling (Fig. 2).

Energy Intake

On the first refueling day, 77% of the variation in DME can be explained by linear regression of DME on time available for feeding (Fig. 1). A MER of 1.93 W (SE = 0.18 W) is estimated by the slope of the regression. The ordinate is intercepted at 17 kJ (SE = 9.9 kJ), indicating that approximately 17 kJ of metabolizable food energy remains in the digestive tract at the cessation of feeding.

Because the birds in the groups with 17 h or more available

for feeding regained more than 50% of their mass loss on the first day of refueling, these birds were probably not motivated to maximize energy intake on the second and third refueling days. In addition, the 23-h group most likely started the second refueling day with metabolizable food energy from the first day still remaining in the digestive tract. For these reasons, linear regression cannot be used to estimate E_r and MER on the second and following refueling days. Therefore, MER was estimated separately for each group, as described earlier under data analysis. On the second and third refueling days, the groups with longer time available for feeding did indeed show a lower MER (Fig. 3). The differences were significant on day 3 ($F_{6,30} = 6.10$, $P < 0.001$) but not on day 2 ($F_{6,30} = 1.64$, $P = 0.17$).
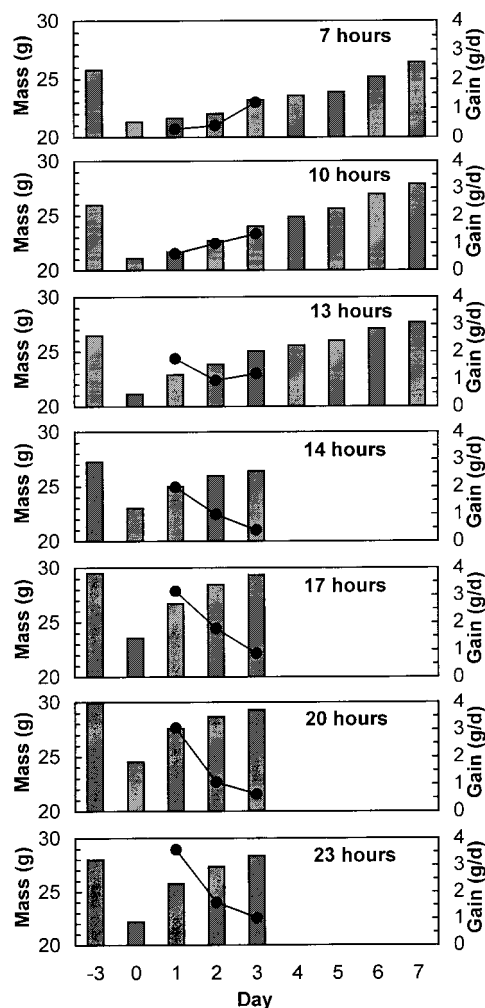

Figure 2. Morning body mass on the first of 3 d with limited food rations (−3) and on subsequent days of refueling (0–7) for groups of thrush nightingales (*Luscinia luscinia*) with different available feeding times per day. The dots connected by lines show the gain in body mass from the previous morning.
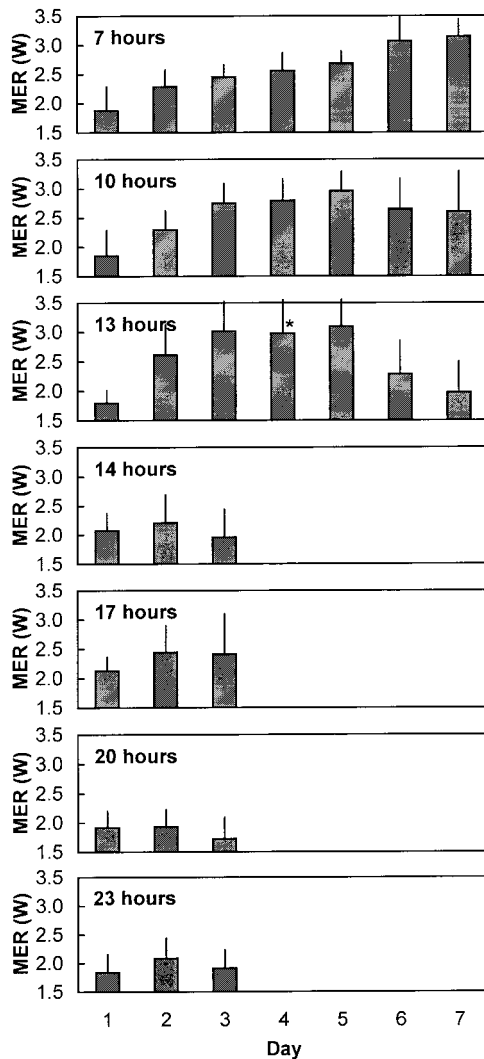
Figure 3. Metabolizable energy intake rate (MER) in thrush nightingales (*Luscinia luscinia*) on the first to seventh refueling days after a 3-d period with limited food rations. The different charts represent groups of birds with different available feeding times per day. Error bars represent 1 SD. On day 4, the birds in the 13-h group were accidentally given food for only 10 h and hence MER is calculated over 10 h.

The birds in the groups with the least time available for feeding are the birds most likely to be motivated to maximize energy intake throughout the experiment. The birds in the 7-h group did not completely regain their body mass until the seventh day of refueling (Fig. 2). In the 7-h group, MER gradually increased on all seven refueling days, from 1.9 W on the first day to 3.1 W on the last day (Fig. 3). The 10- and 13-h groups showed similar increases in MER up to the fifth and third day, respectively, whereas MER decreased on the following days (Fig. 3).

Discussion

It is essential for the interpretation of our results that the thrush nightingales were indeed maximizing energy intake. Klaassen et al. (1997) used a similar experimental procedure to ours but exposed their thrush nightingales to an additional energy demand in the form of cold stress. Cold stress did not increase energy intake, even though fuel deposition decreased, implying that energy intake was already maximized. Our observed increase in DME with available feeding time in itself suggests that the birds were maximizing energy intake. Despite a negligible increase in body mass on the first day of refueling, birds in the 7- and 10-h groups had a similar MER to the birds in groups with longer time available. However, the groups with longer time available recovered more than 50% of their mass loss during the first day and should have been able to recover fully on the second day. The fact that they did not indicates that they did not maximize energy intake on the second day. Motivation to maximize energy intake probably decreased as energy stores were replenished. Hence, most of our experimental birds probably maximized, or came very close to maximizing, energy intake on the first day of refueling. Birds with little available feeding time most likely continued to maximize energy intake on the days that followed. However, the birds with 17 h or more available probably did not maximize energy intake on the second and third days of refueling.

When the thrush nightingales were supplied with food, they generally started eating immediately. We believe that digestion of mealworms is rapid enough to allow absorption of food energy to reach a constant high rate soon after the ingestion of the first food items. In the cages, the thrush nightingales usually spend most of their time resting. At more or less regular intervals, they visit the food bowl and eat a few mealworms in rapid succession. We estimated that 17 kJ of metabolizable energy remains in the digestive tract at cessation of feeding. This corresponds to about 15 mealworms. A thrush nightingale may well eat 15 mealworms when the bird is first supplied with food (A. Kvist and Å. Lindström, personal observations). A reasonable interpretation of these observations is that the birds first fill their digestive tracts with food corresponding to about 17 kJ of metabolizable energy. Then, as food is digested and absorbed, new food is ingested to replace the food that has been processed. At any time, when feeding is interrupted, 17 kJ of metabolizable food energy will remain in the digestive tract.

The thrush nightingales increased DME in proportion to the time available for feeding. Evidently, the time available for feeding is a factor that must be taken into account when studying maximum capacities for energy intake. Kirkwood (1983) suggested an absolute ceiling to mass-specific DME (DME_m) in homeotherms of 2,200 kJ kg$^{-0.72}$ from data in the literature. The thrush nightingales in our 23-h group reached a DME_m of 2,700 kJ kg$^{-0.72}$ on the second day (Fig. 4), clearly higher
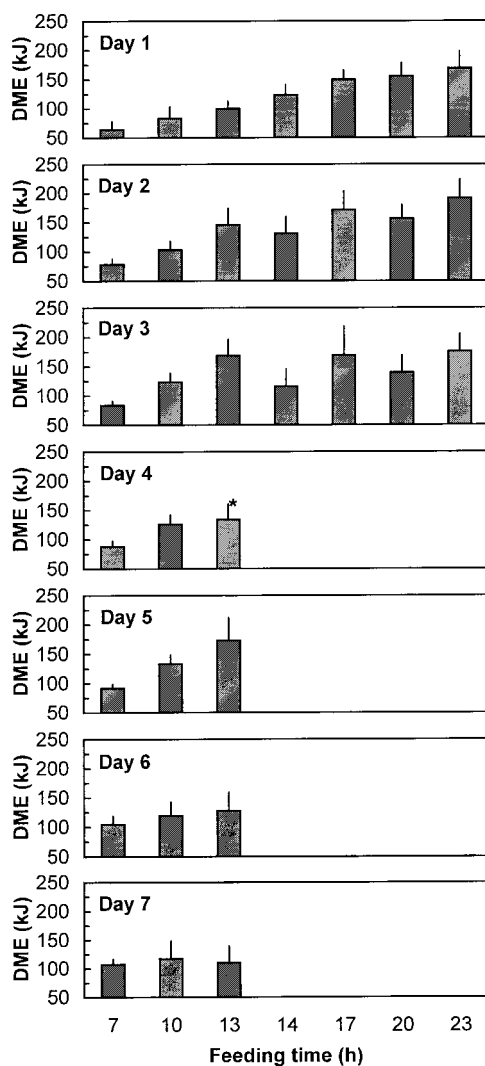
Figure 4. Daily metabolizable energy intake in groups of thrush nightingales (*Luscinia luscinia*) with different available feeding times per day. The different charts represent the first to seventh refueling days after 3 d with limited food rations. Error bars represent 1 SD. Note that on day 4 the birds in the 13-h group were accidentally given food for only 10 h.

than Kirkwood's absolute ceiling. More recently, Karasov (1996) suggested an upper benchmark to DME_m of 1,515 kJ $kg^{-0.655}$ in birds. Our thrush nightingales in the 23-h group were close to 40% above this benchmark on the second refueling day. The 13-h group had a DME_m of 2,200 kJ $kg^{-0.72}$ (Fig. 4) on the second day, which equals Kirkwood's suggested ceiling to DME_m. Maybe 2,200 kJ $kg^{-0.72}$ is the correct region for a ceiling to DME_m in thrush nightingales with 13 h available for feeding. However, when the time available for assimilation of food energy is increased, DME can be increased further. In addition, the amount of metabolizable energy that can be stored

in the digestive tract and processed and absorbed when food is not available will also influence DME. We conclude that maximum DME in animals is set by MER, the time available for assimilation of food energy, and the storage capacity of the digestive tract. All three factors must be taken into account when interpreting potential constraints acting on animals' energy budgets.

Available feeding time in natural situations is likely to vary and to influence the ecology of animals. Obvious constraints on available feeding time are photoperiod and duration of low tide. Other constraints also exist. For example, African bat hawks (*Machaeramphus alcinus*) have to get their entire daily food requirement in 20–30 min each evening when their bat prey emerge from their roosts (Black et al. 1979). Possibly, animals with restricted available feeding time could balance this with a larger storage capacity of the digestive tract.

Maintaining MER at a maximum does not require a continuous high food intake rate. Wood pigeons (*Columba palumbus*) and hummingbirds (*Selasphorus rufus, Calypte anna*) can maintain MER at a maximum despite spending about 50% and 75% of their respective time resting (Kenward and Sibley 1977; Diamond et al. 1986). These birds alternate between bouts of feeding and periods of rest. The same feeding pattern has been observed in several bird species (e.g., Temeles 1989; Worthington 1989; Lindström 1990; Zwarts and Dirksen 1990; Zwarts and Blomert 1992) and also in a shrew (Saarikko and Hanski 1990).

At the onset of autumn migration in southern Scandinavia, a thrush nightingale will have around 16 daylight hours available for feeding. If food availability is unlimited, the thrush nightingale could then reach a DME of 130 kJ or more (Fig. 4). This means a fuel deposition rate of more than 10% of its body mass per day, assuming a daily energy expenditure of about 1 W (2.5 times basal metabolism) and a fuel of 70% fat and 30% protein (Klaassen et al. 1997).

From data presented by Hildén and Saurola (1982), Alerstam and Lindström (1990) showed that the speed of migration of birds in autumn decreased as the season progressed. Given that the speed of migration to a large extent may be governed by the fuel deposition rate (Alerstam and Lindström 1990; Lindström 1991), an important reason for the seasonal decline in migration speed may be the declining time available for feeding.

The birds with a short time available for foraging probably maximized MER for several days; in the 7-h group, this presumably occurred throughout the experiment. These groups showed an increase in MER on successive refueling days (Fig. 3). Several recent studies have shown that animals can adaptively adjust their digestive machinery and thereby adjust their energy intake capacity on a short timescale (Dykstra and Karasov 1992; Klaassen and Biebach 1994; Secor and Diamond 1995; Karasov 1996; Speakman and McQueenie 1996; Klaassen et al. 1997; Piersma and Lindström 1997; Piersma 1998; Lindström et al. 1999). Accordingly, it is likely that the near doubling

of MER by our birds over the 7-d experimental period represents an upregulation of the birds' digestive capacities.

Maximum energy intake rates are often presented as metabolic scope, the ratio of maximum DME to basal metabolic rate (BMR). The reason for this is twofold. First, BMR is often regarded as a reference value in metabolic studies against which other measures of metabolism are compared (Blaxter 1989). Second, a portion of BMR is caused by the metabolism of the energy acquisition machinery, and BMR is therefore thought to reflect the capacity of this energy acquisition machinery (Daan et al. 1990; Konarzewski and Diamond 1995; Speakman and McQueenie 1996). We did not measure basal metabolism during our experiment. However, another experiment with the thrush nightingale showed that the average basal metabolism after a 2-d period of high energy intake was 0.39 W (Lindström et al. 1999). Calculating metabolic scope in the customary manner by using DME and a literature value of BMR, we get metabolic scope values ranging from 1.9 in the 7-h group to 5.0 in the 23-h group on the first day of refueling (Fig. 4). Clearly, metabolic scope calculated in this way has little value without information on the time available for feeding. If we instead calculate metabolic scope by dividing MER by BMR, the values differ less between groups. On the first day of refueling, metabolic scope varied between 4.7 in the 23-h group and 5.5 in the 17-h group (Fig. 3). However, metabolic scope calculated in this way increases on successive days to a maximum of 8.1 on the seventh day of refueling in the 7-h group. However, basal metabolic rate can vary within individuals to a great extent (Daan et al. 1989; Piersma et al. 1995; Scott et al. 1996; Speakman and McQueenie 1996). Lindström et al. (1999) have shown that basal metabolism in thrush nightingale can increase substantially in a matter of days during migratory fuel deposition. Because part of BMR is caused by the metabolism of the energy-acquisition machinery, it is likely that BMR increased in parallel to MER on successive days. If metabolic scope is to accurately describe a causal link between maximum MER and BMR, it is necessary to measure both variables in the same individuals, preferably during the same day (see Speakman and McQueenie 1996 for a good example).

Acknowledgments

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