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CHAPTER 8

COMPENSATION IN RESTING METABOLISM FOR VARIATIONS IN ENERGETIC COSTS OF ACTIVITY

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ABSTRACT

To study the birds' allocation of energy to day and night at two different workloads, we assessed the daily energy budget from 1) metabolizable energy of the food, 2) nocturnal energy expenditure by overnight respirometry, and 3) daily energy expenditure (DEE) measured by turnover of stable isotopes. We imposed two levels of activity on captive Zebra Finches *Taeniopygia guttata*, by applying different computer-controlled workload schedules. A low workload was achieved by requiring 20 hops for 10 sec access time to food; a high workload by requiring 40 hops to obtain 10 sec access to food. Surprisingly, the daily energy budget was on average slightly reduced (3.6-9.5%) when birds were subjected to a high workload schedule. Since hopping activity was higher (43.9%) on the high work schedule, the birds apparently compensated, and even over-compensated for the increased energetic demand due to activity. Nocturnal energy expenditure was indeed reduced (11.7%) on the high workload schedule, which was largely due to a reduction in basal metabolic rate. However, the amount of energy saved during the night could only account for part of the total amount of energy saved. We surmise that the strategy of energetic compensation observed during the night was extended into the inactive hours of the day (34.7-52.9%).

INTRODUCTION

To study the trade-off between current and future reproduction, brood sizes of birds are experimentally manipulated. Parent birds are thereby subjected to an increase in energetic demands (Williams 1987; Dijkstra *et al.* 1990; Deerenberg *et al.* 1995). Animals can respond to this increased demand with two strategies to balance the energetic budget: 1) to adjust the intake of energy, and 2) to compensate, *i.e.*, to reduce other energy intensive activities or processes. Compensation may be achieved by behavioral adaptation in time-budget, or choice of environment, and/or by physiological mechanisms.

Brood size manipulation experiments with Great Tits (*Parus major*, Verhulst 1995) and Starlings (*Sturnus vulgaris*, J.Wright pers. comm.) have demonstrated an increase of parental feeding rates with brood size, but failed to show a positive relation between brood size and parental energy turnover rates as established by stable isotopes. In both studies, raising an experimentally manipulated brood entailed fitness costs due to reduced incidence of second clutches. In a study with captive Zebra Finches (*Taeniopygia guttata*) we demonstrated that parents face a time cost after raising a manipulated brood. This cost of reproduction was associated with energy turnover of females during the nestling phase, which increased with experimental brood size. Energy turnover of male parents, however, was not related to experimental brood size or subsequent costs (Chapter 5). A comparable time cost was observed following episodes of increased activity not related to parental care. At a higher level of activity, daily food intake of experimental birds was reduced, indicating a reduced daily energy budget (Chapter 6). We hypothesize that this reduced level of energy turnover was achieved by energetic compensation. Such compensation of excess energy expenditure during activity may have important consequences. In time-energy-budget approaches in behavioral ecology, it is usually assumed that each behavioral state has a fixed energetic cost, and that time devoted to different behaviours can be directly translated into energy (*e.g.*, Schartz & Zimmerman 1971; Masman *et al.* 1988).

In the same study in which hopping activity of zebra finches was manipulated, we therefore explored the occurrence and the nature of compensation. Here, we report on the overall level of energy expenditure in relation to activity, allocation of energy to day and night, and basal metabolism. We aimed at reconstructing the energy budget, and at assessing contributions of body mass loss and of reallocation of energy to stabilizing the energy budget.

METHODS

Adult zebra finches ($n=26$) with breeding experience were kept individually in cages. Cages were placed in a room with a constant temperature of 25°C, a relative humidity of 60%, and in a LD cycle of 14:10 (lights on at 0800 h). Each cage had two perches 56 cm apart. Hopping activity between the two perches was recorded continuously (DataQuest System III, Data Sciences) as interruptions of an IR beam placed in front of one of the perches. Spontaneous activity was about 2000 hops per day. The birds had drinking water *ad libitum*, and a mixture of dry seeds was supplied according to an experimental protocol (see below). The birds were weighed once a week, and food was weighed daily to assess food intake. Food was provided through an automatic feeder, and access to food was controlled by a central processing unit

(Series III System, GE). We imposed two workload schedules: a low workload consisting of 20 hops for each 10 sec. access to the feeder, a high workload of 40 hops for 10 sec. access to food.

The experimental protocol

The main experiment comprised three four-week episodes of exposure to alternating workloads, each episode followed by breeding. During each workload, nocturnal energy expenditure was measured twice on each bird (see below). Daily gross food intake was assessed continuously on all birds. We measured the food balance of three birds during one of the episodes of work, to assess metabolizable energy of the food (see below). After completion of a workload episode, pairs were reunited, and reproductive behaviour was recorded. A few days after hatching of the eggs, we removed the brood and separated male and female again to expose them to a new episode of work. Results on effectiveness of workloads with respect to daily activity, and effects of workloads on subsequent reproductive decisions are described and discussed in Chapter 6. After three episodes of working and breeding, the birds were again exposed to a workloads to estimate the daily energy budget by means of turnover of stable isotopes (see below), and to assess the energetic costs of activity from the relation between activity and daily energy expenditure (DEE). All birds were measured on both workloads, allowing intra-individual comparisons.

Daily metabolizable energy (DME)

DME was assessed from daily food intake and metabolizable energy per gram of seeds in food balance trials on three birds. We measured energetic content of complete seeds, hulls (not eaten), and faeces using bomb calorimetry. In food balance trials, the amount of seeds taken was measured by daily weighing of the food supply, the remaining hulls and faeces produced were collected and weighed. Hulls accounted for 29% of the weight of seeds. Energetic content of seeds was $19.95 \text{ kJ}\cdot\text{g}^{-1}$, and of hulls $18.09 \text{ kJ}\cdot\text{g}^{-1}$. One gram of seeds thus provided 14.70 kJ. Per gram of seeds taken, 0.05 g (dry weight) of faeces was produced, with an energetic density of $23.8 \text{ kJ}\cdot\text{g}^{-1}$. Metabolizable energy per gram seeds taken amounted to $13.51 \text{ kJ}\cdot\text{g}^{-1}$.

Daily Energy Expenditure (DEE)

DEE was measured with the Doubly Labelled Water (DLW) technique (Lifson & McClintock 1966; Nagy 1980) over 48 h. The birds were injected intraperitoneally with approximately 0.15 ml of a mixture of H_2^{18}O and $^2\text{H}_2\text{O}$. 'Initial' blood samples were taken 1 hour after injection. The zebra finches stayed in their home cages during the interval between injection and initial blood sampling. The isotopic enrichments of the blood samples were

determined by means of mass spectrometry, and corrected for natural isotopic abundance (background) in the body water. Total body water volume was assessed from the dilution space of ^{18}O (Schoeller et al. 1980), using the extrapolation method. Carbon dioxide production was calculated using formulas given by Lifson & McClintock (1966). DEE was then calculated using an RQ of 0.83, and an energetic equivalent of CO_2 of $24.4 \text{ kJ}\cdot\text{L}^{-1}$, based on nutrient catabolism of a typical

Table 1. Descriptives of workloads. Mean values and standard deviations (between brackets) are given. A. Overall averages (see also Chapter 6). B. Values during 48h DEE-measurements.

workload:	LOW	HIGH		
schedule	20	40	T	P
A.				
sample size	13	13		
activity (hops \cdot day $^{-1}$)	5904 (2154)	8497 (2618)	5.60	<.001
body mass (g)	13.84 (1.40)	13.36 (1.34)	3.36	<.01
food intake (g \cdot day $^{-1}$)	3.75 (0.44)	3.39 (0.37)	4.20	=.001
DME (kJ \cdot day $^{-1}$)	50.63 (6.00)	45.81 (5.00)		
DEE (kJ \cdot day $^{-1}$)	53.48 (3.47)	51.55 (4.22)	2.60	=.02
B.				
sample size	11	11		
activity (hops \cdot day $^{-1}$)	5050 (1969)	6506 (2329)	2.22	=.05
body mass (g)	13.54 (1.25)	13.18 (0.85)	1.38	ns
food intake (g \cdot day $^{-1}$)	2.63 (1.05)	2.47 (0.84)	0.46	ns
DEE (kJ \cdot day $^{-1}$)	52.27(9.00)	48.23 (11.56)	1.20	ns

granivorous diet with 15% protein (Gessaman & Nagy 1988). The seed mixture contained 14.4% of dry weight protein (Kjeldahl analysis). For a detailed description of application of the DLW-method to zebra finches, see Chapter 5.

Nocturnal energy expenditure (E_{night}) and Standard Metabolic Rate (SMR)

Nocturnal energy expenditure was measured as oxygen consumption in an open air flow system from 2200 h till 0800 h. Birds were placed in a metabolic chamber of 1.5 L, in darkness, and at 25 °C. Dry air was pumped through the

chamber, with flow rates set at c. 20 L·h⁻¹. Flow rate was measured on the outlet air with a mass-flow controller (type 5850E Brooks) to an accuracy of 1%. Outflowing air was dried over a molecular sieve (3Å, Merck). Gas analysis was done with a zirconium oxide sensor (S3A/II Applied Electrochemistry) to an accuracy of 0.01%, and recorded automatically at 6 min intervals. Oxygen consumption was calculated using equations from Hill (1972), and converted to energy expenditure (kJ) on the basis of a respiratory quotient of 0.83 that is appropriate for granivorous birds (Gessaman & Nagy 1988), and an energy equivalent of 20.24 kJ·L⁻¹ O₂. Standard Metabolic Rate (SMR) was calculated as the lowest value of a 30 min running mean. Because the experiment was conducted at an ambient temperature of 25°C throughout, also during the overnight respirometry, the measurements did not meet the condition of thermoneutrality. Thermoneutrality in

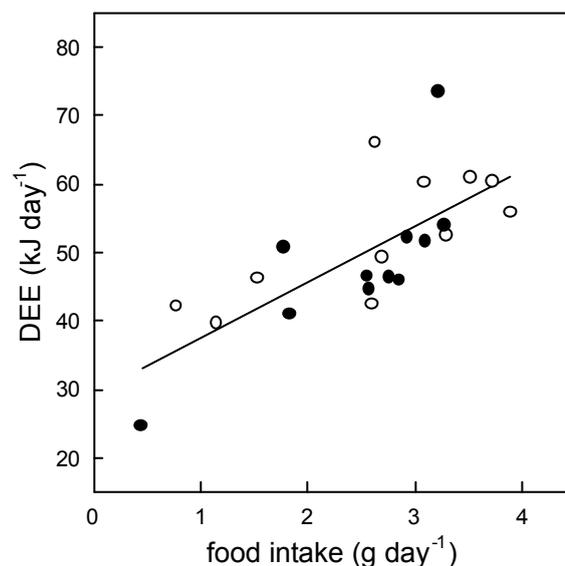


Figure 1. Association of DEE and daily food intake. Open symbols represent birds on the low workload, filled symbols the same birds on the high workload. The linear regression line is described by the equation: $DEE = 29.4 + 8.14 \text{ food}$, $r^2=0.98$, $n=22$, $P<.001$.

zebra finches ranges from 29.5-40°C (Calder 1964). We estimated the additional costs due to thermoregulation as $1.63 \cdot 10^{-3} \text{ W} \cdot \text{g}^{-1} \cdot ^\circ\text{C}^{-1}$ (Calder 1964). BMR was assessed subsequently subtracting these costs of thermoregulation from SMR.

Data analysis

Differences between the two workloads in metabolic rates of the birds, i.e., DEE,

E_{night} , and SMR were tested intra-individually using paired t-tests. We estimated the relations of energy expenditure with food intake using reduced major axis, and of DEE with activity and body mass using multiple linear regression models, with the two workloads included as a factor. The low workload was assigned a value of 1, the high workload a value of 2. The contribution of a variable to the model was examined with an F-ratio test on the difference in deviance (= sum of squares) between models with and without the variable in question (and its interactions). Significance was accepted at $P \leq .05$ (two-tailed).

RESULTS

Daily Metabolizable Energy (DME)

Average hopping activity, body mass and food intake during the workload experiment are listed in table 1A. Activity was increased on the high workload. Concomitant reductions in body mass and food intake were observed, although body mass remained

Table 2. Multiple linear regression model explaining variation in daily energy expenditure (DEE), measured over 48h, of zebra finches working for food on two different workloads. DEE was measured on 11 birds on both workloads. Final model: $r^2=0.41$, $n=22$, $P < .01$.

	(increase in) deviance	(increase in) df	P	coefficient	se
null model	2235.8	21			
final model	1315.9	19			
constant		1		45.56	6.41
workload	343.5	1	=.04	- 8.38	3.76
activity ($\cdot 10^{-3}$)	830.4	1	<.01	2.99	0.86
rejected terms:					
body mass (g)	12.15	1	ns		
activity-workload	83.18	1	ns		

stable during each workload episode. Food intake was reduced on the high workload by 9.5%, in spite of a 43.9% increase in activity. Daily metabolizable

energy intake (DME) was calculated from data on daily food intake. Daily energy expenditure (DEE) was estimated from the regression of DEE on activity, workload, and mass change during the DEE-measurements (see below). Daily energy budgets as assessed by DEE were slightly higher than daily budgets based on DME.

Daily energy expenditure (DEE)

We successfully obtained data from 11 birds on turnover of isotopes on both workloads, and we could calculate their DEE. During the 48h of the DEE measurements, we also recorded food intake, body mass, and activity of the birds (Table 1B). As expected, DEE was closely related to daily food intake (Figure 1), the income part of the energy budget ($DEE = 29.4 + 8.14 \text{ food}$, $r^2=0.98$, $n=22$, $P<.001$). DEE during these measurements may have led to an overestimation of the daily budget, because most birds lost weight during the DEE measurement (-0.54 g , $sd=0.58$, $n=22$), thus deriving additional energy from body reserves.

Energetic costs of activity

Hopping activity increased with workload (Table 1A). We examined the contribution of hopping activity (experimentally manipulated) and body mass to DEE. DEE increased with number of hops per day, but with different levels as a result of the current workload (Table 2). The marginal cost of activity was estimated from the slope of the regression of DEE on the number of hops per day, and amounted to $3 \cdot 10^{-3} \text{ kJ}$ per hop on both workloads. Activity costs did not differ significantly between the low and the high workloads, because the slope of the regressions of DEE on number of hoppings did not differ between the workloads (interaction between hoppings and workload, ns; Table 2).

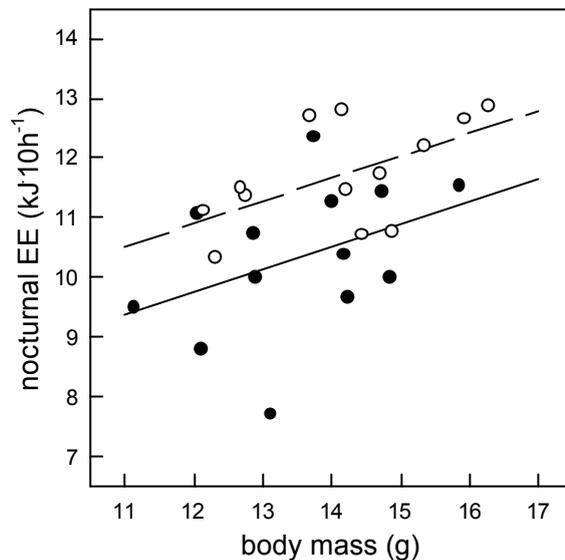


Figure 2. Variation in nocturnal energy expenditure (E_{night}) as a function of body mass and workload. The relation is described by the following equation: E_{night} ($\text{kJ}\cdot 10\text{h}^{-1}$) = 7.51 - 1.15 workload + 0.38 mass (g), $r^2=0.46$, $n=26$, $P<.001$.

There was no further association of DEE with body mass (Table 2).

Energetic costs of hopping activity, calculated from the number of hops per day and the marginal cost of hopping, was $17.71 \text{ kJ}\cdot\text{day}^{-1}$ ($\text{sd}=6.46$) on the low workload, and $25.49 \text{ kJ}\cdot\text{day}^{-1}$ ($\text{sd}=7.86$) on the high workload. The average difference amounted to $7.78 \text{ kJ}\cdot\text{day}^{-1}$ ($\text{sd}=5.00$).

Nocturnal energy expenditure (E_{night}) and Basal Metabolic Rate (BMR) Average E_{night} was 11.70 kJ ($\text{sd}=0.87$, $n=13$) on the low workload, and 10.33 kJ ($\text{sd}=1.25$, $n=13$) for the same birds while working on the high workload. Nocturnal energy expenditure was significantly reduced during the high workload ($t=3.74$, $P<.01$). E_{night} increased linearly with body mass ($F_{1,23}=6.38$, $P=.02$), but with different levels for each workload (slope= 1.15 , $F_{1,23}=8.54$, $P<.01$; Figure 2). The observed average reduction in E_{night} on the high workload compared to the low workload (1.37 kJ) was apparently achieved by a reduction due to workload, in combination with a reduction due to average body mass loss of 0.48 g (Table 1A).

The contribution of reduced body mass to reduction of nocturnal energy expenditure was further examined by assessing basal metabolic rate (BMR). Average SMR during work, and average BMR (corrected for costs of thermoregulation; see methods) are listed in Table 3. BMR was significantly reduced on the high workload ($t=5.02$, $P<.001$).

Table 3. Average standard (SMR) and basal metabolic rate (BMR) of workloads. E_t was calculated for each individual, based on average body mass during the workloads.

workload:	LOW	HIGH
mass (g)	13.84 (1.40)	13.36 (1.34)
SMR (W)	0.315 (0.03)	0.261 (0.04)
BMR (W)		
this study	0.215 (0.02)	0.164 (0.03)
Aschoff & Pohl (1970a)	0.252	0.244
Calder (1964)	0.260	0.249

Allocation of energy

On the basis of the data in Tables 1-3, we reconstructed energy budgets of the low and the high workloads. Allocation of energy to night and day, and, for diurnal energy expenditure, to hopping activity ($E_{\text{day,a}}$) and maintenance ($E_{\text{day,m}}$) are depicted in Figure 3 for both the DEE and the DME budgets. E_{night} was measured, $E_{\text{day,a}}$ was calculated from the number of hops per day using the marginal cost of activity, and $E_{\text{day,m}}$ was calculated as the difference between DEE (or DME) and E_{night} plus $E_{\text{day,a}}$. Although E_{night} was significantly reduced on the high workload, this could only account for a small part of the energy that was compensated for. While the reduction in E_{night} amounted to 11.7%, $E_{\text{day,m}}$ was reduced with 34.7% (DEE budget) or 52.9% (DME budget). Because body mass was reduced on the high workload, and, consequently, the costs of maintenance, we filtered differences due to mass by also expressing energy expenditure as mass-specific rates (Figure 4, right panel). Mass-specific rates of $E_{\text{day,m}}$ were reduced on the high workload with rather similar percentages as observed in the total budgets (DEE budget: 32.0%; DME budget: 51.1%).

DISCUSSION

Nocturnal and diurnal compensation?

We experimentally manipulated workload in order to increase activity costs of zebra finches. Hopping activity on the high workload was indeed higher than on the low workload. The increase in energetic costs of hopping activity between the two workloads was on average $7.78 \text{ kJ}\cdot\text{d}^{-1}$, which represents c. 15% of the

daily budget. In spite of this increase in energetic costs of activity, the daily energy budget was not increased on the high workload. On the contrary, calculation of the daily metabolizable energy intake (DME) based on daily food intake, and estimation of daily energy expenditure (DEE) from daily activity rates both showed significantly reduced energy budgets on the high workload. The birds apparently overcompensated for the experimentally manipulated increase in energy expended on activity. The range of DEE

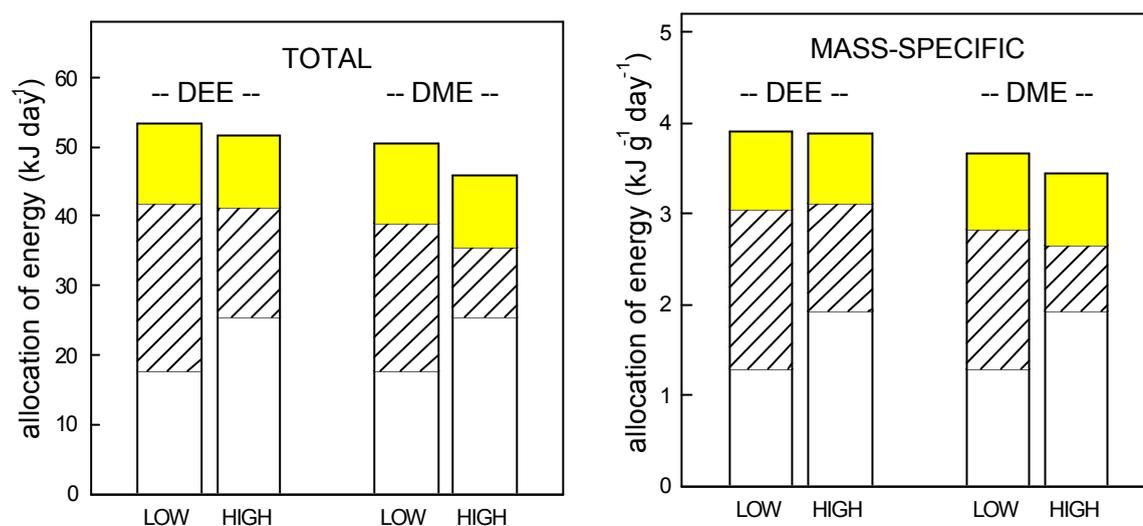


Figure 3. Allocation of daily energy to night (E_{night} , shaded area), hopping activity ($E_{\text{day,a}}$, open area) and diurnal inactive behaviour ($E_{\text{day,m}}$, hatched area). Total budgets (left panel) were assessed from daily food intake and converted to 1) DEE, using the association between DEE and food intake, and 2) DME, using metabolizable energy from food balance trials. Mass-specific budgets (right panel) were obtained by dividing all values by body mass.

induced, manipulated through activity, was 25 to 73 $\text{kJ}\cdot\text{d}^{-1}$ (mean 50.3, $\text{sd}=10.3$, $n=22$). This range of DEE overlap with values of DEE of parents raising the control brood size, ranging from 27 to 85 $\text{kJ}\cdot\text{d}^{-1}$ (mean 58.4, $\text{sd}=15.4$, $n=12$) measured in a brood size manipulation experiment with zebra finches from the same stock (Chapter 5).

It is unlikely that the birds in this experiment compensated by a change in time budget (= behavioural compensation). An increase in hopping activity requires more time, leaving less time for energetically cheaper types of behaviour. Alternatively, reducing the costs of inactive behaviour may serve to arrive at a reduced energetic budget given experimentally increased costs of activity. Several possibilities exist.

The first possibility is that the observed reduction in body mass on the high workload (see also Chapter 6) is a major source of energy savings. Because body mass was stable during each workload episode, no additional energy was derived from stored resources. A reduction in body mass is likely to reduce maintenance costs, and may also reduce activity costs (Freed 1981; Norberg 1981). Is this sufficient to account for the reduced energy budget? We found no evidence for a reduction in costs per unit activity. The effect of intra-individual changes in body mass on overall DEE are difficult to predict. Intra-specific relations of energy expenditure and body mass have been shown to be highly variable, and may deviate considerably from the inter-specific mass exponent of $\frac{2}{3}$ - $\frac{3}{4}$ (parental DEE: Bryant & Tatner 1991; Tinbergen & Dietz 1994). The same argument applies to intra-individual compared to inter-individual associations of energy expenditure and (change in) body mass within one species. The exponent of the dependence of intra-individual change in DEE and body mass in this study was 2.65. The only intra-individual dependence of energy expenditure (i.c. BMR) has been reported for the Kestrel, with exponents of 1.8 for males, and 1.5 for females. In addition to a reduction in mass, these energy savings in BMR coincided with hypothermia and profound differences in body composition (Daan et al. 1989). It thus seems unlikely that such large amounts of energy saved are accomplished by the reduction in mass alone.

A second possibility is that birds compensate for increased activity costs by economizing on energy expenditure of processes during inactive behaviour, e.g., maintenance, and/or nocturnal energy expenditure. Accounting for increased activity costs (43.9%) and a reduced total energy budget (3.6-9.5%) on the high workload, there was an overall reduction in metabolic rate during inactivity of 17.2-38.3%. Nighttime reduction of inactive costs (assessed by respirometry) was 11.7%. A major aspect of the reduction in nocturnal energy expenditure was a reduction in BMR. BMR assessed in this study is compared to literature data on BMR, based on respirometry measurements on zebra finches (Calder 1964), and on allometric relations for passeriformes (Aschoff & Pohl 1970a), to estimate the effect of experimental levels of hopping activity on BMR (Table 2). Increased levels of activity due to either a low or a high workload apparently led to a reduction of BMR of c. 16% and 33%, respectively. However, nocturnal compensation ($1.37 \text{ kJ}\cdot\text{day}^{-1}$) apparently accounted for a small part for the reduced daily energy budget ($7.78 \text{ kJ}\cdot\text{day}^{-1}$) at high workloads.

Estimated duration of activity (based on the maximum number of 200 hops per two-minute interval) was c. 1h (low workload) or 1.5h (high workload), thus leaving 13h, and 12.5h respectively for 'inactive' behaviour during the daytime. Additional compensation, and in fact the major part, must have been achieved by extension of reduced metabolic rate (MR) during the inactive hours of the day of $8.3\text{-}11.2 \text{ kJ}\cdot\text{h}^{-1}$, or 34.7-52.9% (Figure 3). Due to

circadian variation in MR, with higher rates during α than during ρ (Aschoff & Pohl 1970b), there is more potential for energy saving during α . This still leaves us with the intriguing question of how birds achieve a reduced metabolic rate during inactivity.

Potential costs of compensation strategy

Why would birds apply a strategy of compensation? Why do they not simply increase their intake of energy to balance the energetic budget? Compensation may be profitable if the environment does not allow an increase in energy intake beyond a certain level due to, e.g., insufficient food availability. Alternatively, there may be high risks associated with an increase in intake of energy, e.g., exposure to predators, pathogens, or parasites during foraging. Or, costs of high rates of energy turnover, e.g., an increase in free radicals causing cellular or tissue damage, and metabolic dysfunction (Sjödín et al. 1990) may be larger than costs of reallocation of energy.

A strategy of energetic compensation is accompanied by symptoms of physiological and/or behavioral curtailments. The observation that these components are variable within an individual suggests that they are subject to a cost-benefit trade-off. Why would these components otherwise not always be at a minimum level? Various potential cost factors are anticipated. A reduction in body mass may involve a change in body composition, thus affecting body reserves that usually serve as an insurance against starvation (Lima 1986; Houston & McNamara 1993). Reduction in (standard or basal) metabolic rates are often associated with hypothermia (Daan et al. 1989; Rashotte et al. 1995), i.e., a reduction in body temperature. Hypothermia on the one hand may increase the risk of predation, and on the other hand it may reduce body temperature below the optimal T for enzymatic activity, thereby decelerating protein turnover. Also, a reduced allocation of energy to maintenance may decelerate cellular turnover in general, causing arrears in repair of cellular damage. Or it may affect other aspects of maintenance processes, e.g., immunological defense mechanisms (Chapter 7).

The plasticity of metabolic rate described in this paper compares - be it to a lesser extent - to energy saving strategies as exhibited by torpid animals. As such, a reduction in metabolic rate at some times in reaction to high or increased energetic demands at other times thus seems a more general phenomenon. Life history costs, e.g., costs of reproduction, associated with altered patterns of activity may well be due to compensation, e.g., economisation on maintenance processes, instead of a result of increased rates of overall energy expenditure.

We have shown here that energetic consequences of behaviour are not constant under changing energetic demands. This finding has important implications for time-energy budgets (TEB). Validation studies often reveal

deviations of the daily energy budget when assessed by TEB in comparison with estimations from turnover of stable isotopes (Nagy 1989). TEB assumes constancy, thus additivity of energetic costs (Schartz & Zimmerman 1971), and little attention has been paid to the possibility of physiological compensation beyond the effects of a reduction in body mass.

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