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Costs of avian incubation

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The energetic cost of foraging versus incubation in female great tits *Parus major*

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ABSTRACT

The idea that the incubation phase is an energetically demanding period for parental birds is getting more accepted. It remains, however, unclear from what activity these high energetic demands during incubation originate (maintaining egg temperature, rewarming the clutch after each recess or foraging). We constructed a time and energy budget of free-living female great tits (*Parus major*) over a 24-h period during the incubation phase to estimate the energetic demands for the time on the nest and the time away from the nest separately during the active day. To achieve this, we used estimates of energy expenditure during 24-h period of incubation and estimates of expenditure during nocturnal incubation in combination with time budgets of incubating females over 24-h. The high energetic costs of incubation originated during the day. Both the expenditure during the whole period of the active day (active day 55.8 versus night 23.2 kJ) and energy spent per time unit (active day 1.14 versus night 0.63 J s⁻¹) were higher than during the night, even though mean ambient temperatures were higher during the active day. The energy spent during the active day decreased with an increase in the fraction of time the female spent on the nest implying that the energy spent during time away from the nest was higher than that during time spent on the nest (1.58 vs 0.85 J s⁻¹). Uniparental incubating birds have limited time to forage given their requirements to incubate the eggs. For female great tits the calculated intake rate to maintain energy balance (19.9 kJ h⁻¹) amounts to twice that calculated for the nestling phase (9.8 kJ h⁻¹). To answer the interesting question how incubating females manage to obtain this intake rate, more detailed observations are needed on the foraging efficiency of the incubating birds and to the role of the partner in case of uniparental incubation.

INTRODUCTION

Life-history theory predicts that parents allocate their resources in such a way to produce the number of offspring that maximises their fitness (Stearns 1992; Roff 1992). In birds, the peak of energy demand is thought to occur during the nestling phase when parents need to provision their offspring with food, which led to the idea that selection on clutch size primarily takes place during this phase (Lack 1947; Drent & Daan 1980; Walsberg 1983; Daan *et al.* 1990). In contrast, the incubation phase was often viewed as a period when energy expenditure was low (King 1973; Walsberg & King 1978), and consequently, this phase was largely ignored in studies on clutch size decisions in avian life history (Williams 1996; Monaghan & Nager 1997; Visser & Lessells 2001).

The idea that the incubation phase is an energetically demanding period, however, is getting more support (Williams 1996; Monaghan & Nager 1997; Tinbergen & Williams 2002; Reid *et al.* 2002a). Accumulating data show that the metabolic rate (energy spent per time unit) of a bird during contact incubation is higher than that of a non-incubating bird at rest, at least when ambient temperatures are below thermoneutrality (Thomson *et al.* 1998; Tinbergen & Williams 2002). Since at temperate latitudes, incubation generally takes place early in spring when ambient temperatures are low and unpredictable (Perrins 1970), the energetic costs during incubation may be substantial. In a review, Tinbergen and Williams (2002) compare the existing body of data on daily energy expenditure for birds incubating eggs and for birds provisioning nestlings with food. They show that birds expend about the same amount of energy during both phases, thereby confirming previous predictions of the model by Yom-tov & Hilborn (1981). Particularly, for small species of passerines, and for uniparental incubators the daily energetic cost of incubation is equivalent to that of females rearing nestlings. Besides the energetic cost, food availability to balance the energetic requirements is thought to be less abundant during the incubation phase: food is generally assumed to peak during the nestling phase (Perrins 1970; Nager & van Noordwijk 1995). For incubating birds, the low food availability may specifically be demanding, since they have limited time available for foraging (e.g. self-maintenance) due to the requirement to be present on the eggs.

Several studies have attempted to determine the energetic costs of different activities to determine where the high energy costs during the incubation phase originate, using respirometry to determine the energy expenditure per time unit. This technique requires periods of relative inactivity, such as during contact incubation, and is not suitable to measure all types of activities. Studies that measured the metabolic rate during nocturnal incubation for several species of passerines revealed that the costs of incubation during night time are higher than that of a non-incubating female at rest, at least when ambient temperatures are low (Biebach 1981; Biebach 1984; Haftorn & Reinertsen 1985; Weathers 1985; chapter 6).

Biebach (1984) also measured the metabolic rate of contact incubation during the day for female starlings *Sturnus vulgaris*. He discovered that, although the costs of rewarming the clutch were excluded from the measurement, the metabolic rate of incubating birds was 50 – 60% higher during the day than during the night. He attributes this difference in metabolic rate of contact incubation between day and night to energy needed for digestion (i.e. the heat increment of feeding) of food that was gathered during recesses during the day. Two studies measured the costs of rewarming the clutch using different approaches (Vleck 1981; Biebach 1986), either by calculating the instantaneous O₂ consumption (Biebach 1986) or by measuring the metabolic rate of females incubating continuously cooled eggs (Vleck 1981). Both studies revealed that rewarming is energetically more demanding than that of contact incubation. In addition, Biebach report that the energetic costs of rewarming the eggs depend on ambient temperature and the length of the inattentive period.

As an alternative to measuring the energetic costs of a specific behaviour, two studies have tried to get insight in what the most demanding activity during the incubation phase is by relating daily energy expenditure during incubation (DLW-technique) with the activity pattern of incubating birds. Piersma *et al.* (2003) studied the daily energy expenditure of radiomarked red knots *Calidris canutus* in the High Arctic and found that birds that spent part or all of their time on foraging had higher values of daily energy expenditure than those that spent all their time on incubation. These results imply that foraging is more costly than incubating a clutch. In a study on energy expenditure of incubating pectoral sandpipers *Calidris melanotos* in relation to experimentally heated nests, Cresswell *et al.* (2004) also conclude that the energetic costs away from the nest must far exceed that of sitting on the nest, even though relatively little time is spent away from the nest.

To gain more insight in where the high energetic demands of incubation originate, we constructed a time and energy budget of free-living female great tits (*Parus major*) over a 24-h period during the incubation phase. The great tit is used as model species, because it is an uniparental incubator: the female incubates the eggs. Thus, during the day, the female is faced with a trade-off between spending time on the nest to maintain egg temperature and spending time away from the nest for self-maintenance (i.e. foraging). This trade-off, and thereby the consequences of this trade-off, is likely to be pronounced in small passerines, since they cannot store large amount of energy and thus need to forage daily to balance their expenditure. In case of the great tit, the male may at the most assist their mate by providing food or information where to find food.

We used the results from two studies that focussed on the clutch size related energetic costs of incubation: one measured during the night using respirometry (chapter 6) and one over a 24-h period using the doubly labelled water (DLW) - technique (chapter 7). We combined these data with the time budgets of incubating females measured over 24-h period during the DLW-measurement. We derive

an estimate of day time expenditure, which we contrast to our previous measurements of the energy expenditure during nocturnal incubation. Furthermore, we derive an estimate of energy expenditure away from the nest. Besides, an estimate of energy expenditure incubation activities on the nest, such as rewarming of the eggs and contact incubation during the day is derived.

METHODS

Study population

We conducted this study in the woodlots of the Lauwersmeer, in the northern Netherlands (53°20' N – 6°12' E) during the breeding season of 2004. In this population, great tits have been studied since 1993. In part of the area, a limited number of nest-boxes was available since 1980. Since 1994, 200 nest-boxes are available in the study area, located over 8 woodlots of different sizes (6 -106 ha) interspersed with non-breeding habitat. For more details see Tinbergen (2005).

Energy expenditure

Metabolic rate during nocturnal incubation

We measured the oxygen consumption of 20 females during nocturnal incubation using respirometry as early as possible in the incubation period (between 1st - 6th day of incubation; chapter 6). We measured females twice on consecutive nights while incubating either control or experimentally enlarged clutches; the experimental treatment was provided in random order. We enlarged clutches with three eggs (chapter 6) during day time, while measuring the oxygen consumption later that day during night time. Control clutches contained on average 8.8 ± 1.4 eggs. We measured the oxygen consumption using mobile oxygen analysers, the nest-box was used as metabolic chamber. By comparing the oxygen concentration and flow of air drawn from the nest-box with the oxygen concentration and flow of air entering the nest-box, we determined the oxygen consumption of the incubating female. The metabolic rate of nocturnal incubation (MR_{night} , $J s^{-1}$) was calculated using equation 6 of Hill (1972), assuming a respiration quotient (RQ) of 0.75 and an energy equivalent of 19.9 kJ per litre oxygen consumed (Tinbergen & Dietz 1994). Per night of measurement, we used an average value of MR_{night} in the analysis. More details about the experimental set-up and method used are published elsewhere (chapter 6).

Daily energy expenditure

At three quarters of the incubation period - assumed to be 12 days- we used the doubly labelled water (DLW) technique (Lifson & McClintock 1966) to measure the daily energy expenditure (DEE; chapter 7). We measured the DEE of 35 females that incubating clutches with originally 9.1 ± 1.6 eggs; 19 of these

females were incubating control clutches and 16 of them enlarged clutches (three additional eggs). We used both single-sample protocol (Williams & Dwinell 1990), and two-sample protocol. We caught the females during day-time when they were leaving the nest-box. After weighing them, we injected them with 0.10 ml DLW. Depending on the protocol (single-sample or two-sample), we released the birds immediately (single sample) or we kept them in a cloth bag to take an initial blood sample after one hour (two sample). Twenty-five hours after injection, we recaptured the birds a second time to take a (final) blood sample and to weigh them again. We took blood samples from four uninjected females to determine background values of deuterium and oxygen-18 of the population. Blood samples were analysed for deuterium and oxygen-18 concentration at the Centre for Isotope Research of the University of Groningen (the Netherlands) by mass spectrometry. Mean background isotope enrichments of deuterium and oxygen-18 for non-experimental females were -19.74 ± 5.1 ‰ and -0.79 ± 0.47 ‰ relative to standard mean ocean water (V-SMOW). We calculated the daily energy expenditure (DEE), assuming a body water pool of 66% (Mertens 1987), a RQ of 0.75 and an energy equivalent of 19.9 kJ of oxygen consumed. For a more detailed description of this experiment see (chapter 7).

Time budgeting incubation behaviour

During the DLW-measurement, we used a temperature sensor (HOBO logger, Mulder-Hardenberg B.V., The Netherlands), which we placed between the eggs to monitor the nest temperature; this sensor registered nest temperature every 15 s. We derived the incubation behaviour of females from the nest temperature. The departure of the female from the eggs is revealed by a sudden drop in nest temperature, which is followed by a sharp increase in temperature upon her return.

We recorded the *length of the night* (s), which was defined as the time span between the last entry in the evening and the first exit in the morning, and the *length the active day* (s), which we defined as the time span between the first exit in the morning and the last entry in the evening on the same day. Within the active day, we scored the following behaviours: *latency to return* (s), which we defined as the time span between the release of the bird after injection and the first return to the nest; *time on the nest* (s), which we defined as the time during the active day the bird spent on the nest, which comprises both time spent rewarming the clutch after each recess and time spent on maintaining egg temperature; *the number of recesses* (#), which we defined as the number of times the female went away and returned to the nest during the active day; *time away from the nest* (s), which we defined as the time during the day the bird spent away from the nest, which includes all time spent on behaviours outside the nest-box (although the latency to return is excluded from this measure). Since individuals differ in the length of the active day, the time spent on different activities (latency to return, time on the nest and time away from the nest) are expressed as fractions of the active day.

Ambient temperature

When measuring the metabolic rate of nocturnal incubation, we measured the ambient temperature in the vicinity of the nest-box during the measurements. In the analysis, we used the mean ambient temperature taken over the 24-h measuring period. During the 24-h period of the DLW-measurements, we measured the ambient temperature (Tinytalk II, Gemini Data Loggers, INTAB Benelux) at a central location in the study area. For each individual, we calculated T_{a_24} (°C), which is the mean ambient temperature for the entire 24-h period of the DLW-measurement; T_{a_night} (°C), which is the mean ambient temperature during the night and T_{a_day} (°C), which is the mean ambient temperature during the active day.

Calculations

For each individual, we calculated the metabolic rate during the night (MR_{night}) using the following equation, thereby correcting for factors that we had previously found to affect MR_{night} (chapter 6):

$$MR_{night} \text{ (J s}^{-1}\text{)} = -0.028 \cdot T_{a_night} \text{ (}^\circ\text{C)} + 0.039 \cdot CS_{manip} \text{ (# of eggs)} - 0.004 \cdot N_{cup} \text{ (mm)},$$

whereby T_{a_night} is the mean ambient temperature during the night, CS_{manip} is the clutch size manipulation (0 or 3 eggs added) and N_{cup} is the thickness of the nest cup, which is a measure of nest insulation (Szentirmai *et al.* 2005; chapter 5). We used the metabolic rate during nocturnal incubation and the length of the night to calculate the energy expenditure during the night, EE_{night} :

$$EE_{night} \text{ (kJ per 24-h)} = \frac{MR_{night} \text{ (J s}^{-1}\text{)} \cdot \text{Length}_{night} \text{ (s)}}{1000}$$

Next, we calculated the energy expenditure during the active day (EE_{day}) by subtracting the energy expenditure during the night from the daily energy expenditure (DEE):

$$EE_{day} \text{ (kJ per 24-h)} = \text{DEE (kJ per 24-h)} - EE_{night} \text{ (kJ per 24-h)}$$

We calculated the metabolic rate during daytime (MR_{day}) by dividing the energy expenditure during the active day by the duration of the day:

$$MR_{day} \text{ (J s}^{-1}\text{)} = \left(\frac{EE_{day} \text{ (kJ per 24-h)} \cdot 1000}{\text{Length}_{day} \text{ (s)}} \right)$$

Females were caught for the second time after 25h 15min on average and thus, DEE was overestimated for a short period of time during the active day. Therefore, we calculated DEE_{inc} by subtracting the estimated energy expenditure, using the estimated metabolic rate during the day times the deviation from 25-h period from DEE;

$$DEE_{inc} \text{ (kJ per 24-h)} = \frac{(\text{DEE (kJ)} \cdot 1000) - MR_{day} \text{ (J s}^{-1}\text{)} \cdot t_{deviation \ 25h} \text{ (s)}}{1000}$$

Statistical analysis

We had 6 missing values for the DLW-measurements, because 3 birds deserted the nest, 2 birds could not be caught in time for a proper measurement, and for 1 bird the CO₂ production could not be determine accurately. So we used 29 individuals in the analysis. We had 4 missing values for measures of incubation behaviour during the active day due to malfunctioning of temperature loggers. Therefore, we have data on the time budget of 25 individuals.

We tested whether the activity of the incubating birds was related to energy expenditure (in total or per time unit) over the active day. We included clutch size manipulation in the model as explanatory variable, given the experimental set-up. We also included ambient temperature as explanatory variable, since we previously found strong effects of this factor (chapter 6 and 7).

RESULTS

Time budget

For incubating females, a 24-h period consisted of 13h 40min \pm 35 min active day and of 10h 20min \pm 35 min night (for an overview of these data see Table 8.1). During the active day, the females' latency to return was 2h 15min \pm 1h 42min after injection. The remainder of the active day, females alternated time spent on the nest and time spent away from the nest. Females went 23.1 ± 5.5 times away from the nest for on average 7.8 min, and stayed on average 21.8 min on the nest upon return. In total, females spent 8h 24min \pm 1h 29min on the nest and 3h 01min \pm 51min away from the nest. Expressed as fractions of the active day, the females' latency to return was 0.17 ± 0.13 , the time on the nest 0.61 ± 0.10 , and the time away from the nest 0.22 ± 0.06 .

Table 8.1. Overview of time budget for females during the incubation phase of which daily energy expenditure was measured during a 24-h period with use of the doubly labelled water (DLW) technique.

	behaviour	Duration	Fraction
Latency to return		2h 15min	0.17
Time on the nest	23.1 * 21.8min	8h 24min	0.61
Time away from the nest	23.1 * 7.8min	3h 01min	0.22
Active day		13h 40min	1.00
Night		10h 20min	
		24h 00min	

The length of the active day was not related to the time away from the nest ($\chi^2_1 = 1.60$, $p = 0.21$). As a consequence, the fraction of latency to return was negatively correlated with both the fraction of time on the nest ($\chi^2_1 = 38.7$, $p < 0.001$, $R^2 = 0.79$) and the fraction of time away from the nest ($\chi^2_1 = 13.6$, $p < 0.001$, $R^2 = 0.42$).

Energy budget

Over a 24-h period, incubating females spent on average 79.0 ± 9.1 kJ (DEE_{inc}), of which 23.2 ± 2.3 kJ was spent during the night (EE_{night}) and 55.8 ± 8.7 kJ during the active day (EE_{day}). Thus, females spent more energy during the active day than during the night, but the active day is also longer than the night. The energy expenditure per time unit (metabolic rate) during nocturnal incubation was 0.63 ± 0.07 J s⁻¹ (MR_{night}), while the metabolic rate during daytime incubation was 1.14 ± 0.18 J s⁻¹ (MR_{day}). Thus, the incubating female did spend energy at a higher rate during the active day than during the night, and consequently also spent more energy during the active day (Fig. 8.1). Note that the average ambient temperature was about 5 °C higher during the day than during the night.

Covariation between energy expenditure and time budget

To estimate the energetic costs of the different elements of the time budget separately (Table 8.1), the variation in energy expenditure during the active day was

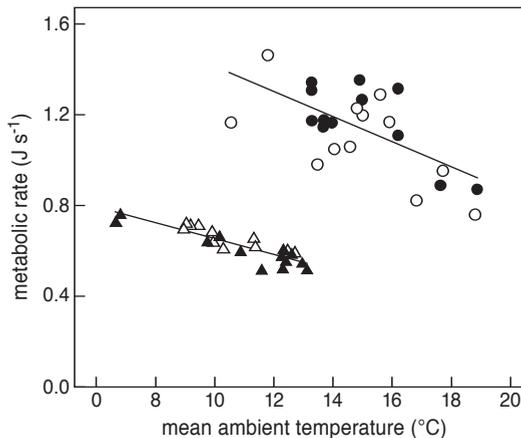


Figure 8.1. Measured values of metabolic rate during night time (MR_{night} (J s⁻¹); see equation in Methods, calculations; triangles) and derived values of metabolic rate during day time (MR_{day} (J s⁻¹) = $2.0 (\pm 0.2) - 0.06 (\pm 0.01) \cdot T_{a_day}$ (mean ambient temperature during the active day; squares) in relation to mean ambient temperature for night and daytime, respectively. For more details about calculations see section in Methods. Closed symbols are control clutches and open symbols are experimentally enlarged clutches.

related to the time budget data. Both the energy spent during the active day (EE_{day} ; $\chi^2_1 = 5.69$, $p = 0.02$; controlled for ambient temperature in the model, $\chi^2_1 = 15.96$, $p < 0.001$) and the metabolic rate during the active day (MR_{day} ; $\chi^2_1 = 8.15$, $p = 0.004$; controlled for ambient temperature in the model, $\chi^2_1 = 14.90$, $p < 0.001$) decreased with an increase in the fraction of time the female spent on the nest (Fig. 8.2).

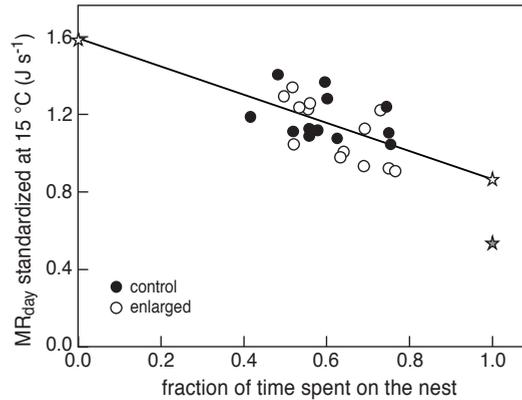


Figure 8.2. Metabolic rate during day-time incubation standardised to the ambient temperature of 15 °C in relation to the fraction of time spent on the nest during the day. The white stars indicate the estimated metabolic rate during the time spent away from the nest and the metabolic rate during the time spent on the nest by extrapolating of the regression line. The grey star indicates the metabolic rate during nocturnal incubation, standardized to 15 °C. For reference BMR for incubating female great tit is 0.34 J s⁻¹. Closed symbols are control clutches and open symbols are experimentally enlarged clutches.

DISCUSSION

We calculated energy expenditure during the day by subtracting estimates of energy expenditure during the night from estimates of energy expenditure over 24-h. We found a strong negative relation between the energy expenditure during the active day and the time spent on the nest that allows us to estimate the energy spent per time unit when time spent on the nest and away from the nest.

In our dataset, females took relatively long to resume normal incubation after being captured for the DLW measurements. This may be a problem because the analysis takes the energy spent per time unit during this latency to return as equal to that during the time spent away from the nest during normal incubation. To give ourselves more confidence that this was the right approach, we looked in

more detail at those females ($n = 5$) that had a short latency (less than 15 minutes). Daily energy expenditure of birds with only short latencies to return followed the same pattern and their mean expenditure was similar to that of the mean of the population (75.0 kJ day^{-1}). These females spent a fraction of 0.72 of the active day on the nest and a fraction of 0.27 away from the nest, fractions also recorded in undisturbed situations (Deeming 2002). We conclude that the energy spent per time unit during the time after injection (and before normal incubation) was equal to the energetic costs per time unit during the time spent away from the nest in normal incubation.

The high energy costs for incubating females over 24-h originates during the active day. Even though mean ambient temperatures were higher during the active day, both the expenditure over the active day (EE_{day} , kJ) and the energy spent per time unit during the active day (MR_{day} , J s^{-1}) were higher than during the night. This means that incubating females not only spent more energy during the active day because it is longer, but also because they spend energy at a higher rate. These findings support the view that it is not contact incubation itself that is energetically the most costly activity during the incubation phase.

We used the regression of MR_{day} on the fraction of time spent on the nest to partition the energetic costs to different activities during the active day; the regression line was extrapolated to either spending all the time away from the nest or spending all the time on the nest. We standardized the expenditure for a mean daily ambient temperature of $15 \text{ }^{\circ}\text{C}$. This was needed, since ambient temperature strongly affects energy expenditure (Biebach 1984; Bryan & Bryant 1999; Weathers *et al.* 2002; chapter 6 and 7). The metabolic rate during time spent away from the nest ($MR_{\text{away from nest}}$) was extrapolated to be 1.58 J s^{-1} , while the metabolic rate during time spent on the nest ($MR_{\text{on the nest}}$) was estimated to be 0.85 J s^{-1} (Fig. 8.3.), meaning that energy spent away from the nest was higher than that while sitting on the nest.

Our measure of energy spent on the nest ($MR_{\text{on the nest}}$) comprises both energy spent rewarming the clutch after each time the female was away from the nest ($MR_{\text{rewarming}}$) and energy spent on maintaining egg temperature ($MR_{\text{inc_day}}$). To get an estimate of the costs of rewarming a clutch to temperature favourable for embryonic development for female great tits, however, we use a calculation by Mertens (1977). We calculated for a clutch containing 9 eggs the energy needed for rewarming it. The mass of a clutch (weight of one egg is 1.77 g) was multiplied with the specific heat of eggs ($3.35 \text{ J g}^{-1} \text{ }^{\circ}\text{C}^{-1}$; Romanoff & Romanoff 1949), the number of times rewarming during the day (23.1 ± 5.5 , $n=25$) and the difference between temperature of the egg at the start of rewarming with the final temperature ($5\text{--}10 \text{ }^{\circ}\text{C}$; derived from data of temperature loggers) over the time spent on the nest. The metabolic rate of rewarming the clutch (MR_{rewarm}) would contribute to $0.20 - 0.41 \text{ J s}^{-1}$ of the energy spent while being on the nest during the active day. This estimate is of similar magnitude as the difference between

$MR_{\text{on the nest}}$ and MR_{night} , when these values were extrapolated to ambient temperature of 15 °C (Fig. 8.2), which would mean that energy spent during contact incubation during the day ($MR_{\text{inc_day}}$) is equivalent to that of contact incubation during the night (MR_{night}). This is a discrepancy with the interpretation of Biebach 1984. He found that $MR_{\text{inc_day}}$ was higher than MR_{night} , which he attributed to the energetic demands of digesting food. Possibly, energy needed for rewarming eggs is reallocated from other processes (such as the heat increment of feeding or flight).

During the active day, females are found to spend most energy during the time away from the nest. The energy is spent on foraging to restore body reserves that have been depleted during incubation (Deeming 2002). Using a measure of DEE and energy expenditure during time on the nest based on data from several species – standardised to 8 °C and expressed as multiples of BMR – in combination with length of the active day and time available for foraging, Tinbergen and Williams (2002) estimated the energetic expenditure during time away from the nest ($MR_{\text{away from nest}}$) during both the incubation phase (female-only incubation) and the nestling phase. They found that females have a higher $MR_{\text{away from nest}}$ during the incubation phase than during the nestling phase. For comparison, we also standardised our values to 8 °C, and found a similar value of 5.7*BMR (compared to 4.2*BMR in nestling phase; Fig. 8.3). $MR_{\text{away from nest}}$ could partly be this

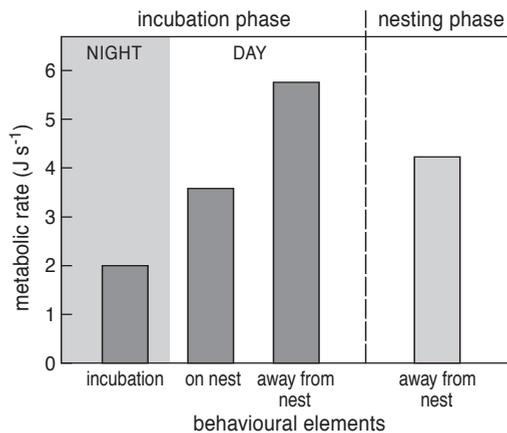


Figure 8.3. Metabolic rate of several behavioural elements; nocturnal incubation (measured), daytime incubation (estimated; value includes energy spent on rewarming the clutch after each recess and that of incubating the eggs) and foraging (estimated; value includes all activities outside the nest-box). For comparison with calculations of Tinbergen and Williams (2002) values are standardised to the ambient temperature of 8 °C and expressed as multiple of basal metabolic rate (BMR). For reference, the calculated value by of the metabolic rate during time spent away from the nest for females provisioning their nestlings is given (calculated by Tinbergen and Williams 2002).

high because of higher flight costs; females are about 3 grams heavier during the incubation phase (20.2 g) than during the nestling phase (17.6, unpublished data of females used in DLW measurement in 2004, $n = 16$). On the other hand, these costs could be high because females need to work hard during the time away from the nest to acquire enough energy within a limited amount of time available.

Given the relatively high DEE_{inc} and the limited time available for foraging, the intake rate per unit time must be high during the time spent away from the nest to meet parental needs during incubation, thereby assuming body mass to be constant. During the time spent away from the nest (on average $316 \text{ min} \pm 79$), females need to obtain on average 78.8 kJ day^{-1} . Assuming an assimilation efficiency of 0.75 % (following Yom-tov and Hilborn 1981), a gross intake rate of 19.9 kJ h^{-1} would be required. This is consistent with the intake rate of a female in uniparental incubation systems calculated by Tinbergen and Williams (2002). These values for intake rate are remarkable high, as compared to the calculated intake rate needed for females feeding nestlings (9.8 kJ h^{-1}). How do these incubating females manage to obtain such a high intake rate in a period that food availability is thought to be less favourable as compared to the nestling phase (Perrins 1970; Nager & van Noordwijk 1995)? A high intake rate may be achieved by an increase in foraging efficiency (energy gain per time spent foraging), which they could achieve by adapting a different foraging strategy (eat less preferred, but easier available prey) or by accepting more risk during foraging (Lima & Dill 1990). Alternatively, the male could have a substantial contribution, either by bringing food to the incubating female or by taking her to food patches. Clutch size manipulations during three years in the same population found that both incubating females as their partners are affected by experimental enlargement of clutches (chapter 2). This hints that the role of the male is more important during the incubation phase than till this far is assumed.

In conclusion, this study reveals that during a 24-h period of incubating, females spent more energy during the active day than during the night. During the active day, the time spent away from the nest is energetically twice as expensive as the time spent on the nest. Daily energy expenditure during incubation is relatively high, and an incubating female must balance her expenditure in her limited time available away from the nest, which would result in a high intake rate. Such a high energy intake can be accomplished by high foraging efficiency of the incubating bird or by the help of their partner in case of the great tit.

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