

# Heating nest-boxes reveals an energetic constraint on incubation behaviour in great tits, *Parus major*

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According to the 'energetic-bottleneck' hypothesis, incubation in birds is constrained by the availability of energy. Hence, uniparental incubators are predicted to respond to a change in energy supply by adjusting, positively or negatively, the time spent warming the clutch. Energetic constraints on incubation in the great tit (*Parus major*) were demonstrated by heating nests, so that the night-time thermostatic component of daily energy expenditure in females was reduced by comparison with a control group. Birds in heated nests increased the time allocated to incubation during the day by 55 minutes, consistent with the predictions of the energetic-bottleneck hypothesis. Daily energy expenditure of all birds was inversely related to night-time ambient temperature, and did not differ between warmed and control birds on mild nights. When temperatures were low, however, escalation of daily costs was less for birds in heated nests. It is suggested that the balance of the energy budget may effect a proximate control on the constancy of incubation, with likely implications for reproductive success.

**Keywords:** doubly labelled water; energy expenditure; great tit; incubation; incubation rhythm;  
*Parus major*

## 1. INTRODUCTION

The formation of a clutch and the rearing of nestlings are frequently identified as periods of energetic constraint (Bryant & Westerterp 1983; Drent & Daan 1980; Yom Tov & Wright 1993). Associated fitness costs are likely to affect clutch sizes (Daan *et al.* 1996; Monaghan & Nager 1997). Several lines of evidence suggest, however, that incubating birds may also experience difficulties in maintaining a positive energy balance (Hainsworth *et al.* 1998; Yom Tov & Hilborn 1981) and incubating eggs to hatching (Moreno 1989).

Despite earlier debate (Kendeigh 1973; King 1973), it now appears that maintaining eggs at temperatures suitable for embryonic development under field conditions (Webb 1987) requires an expenditure of energy above the resting metabolic requirement of the parent (Mertens 1980; Vleck 1981; Williams 1996). Indeed, studies using the doubly labelled water (DLW) technique to measure energy use by free-living birds have found daily energy expenditure during incubation to be comparable with that of parents feeding a brood (Bryant 1997; Tatner & Bryant 1993; Williams 1991, 1996). Clearly, a perception that incubation is invariably an energetically low-cost stage in the annual cycle is not appropriate.

In many species, provisioning at the nest by a mate is infrequent or lacking, and incubation duties limit foraging time (Jones 1987; Skutch 1962). If energy balance is to be

maintained, average foraging success during periods off the nest (and possibly its costs) must increase when compared with other stages in the annual cycle (Bryant & Tatner 1988; Tatner & Bryant 1993; Walsberg & King 1978). Therefore, energetic considerations, involving increases in foraging efficiency or reductions in energetic costs, may be important determinants of success during incubation (Jones 1987; Lifjeld & Slagsvold 1986; Lyon & Montgomerie 1985; Moreno 1989; Sanz & Moreno 1995; Siikamaki 1995; Smith 1989; Smith *et al.* 1989; Székely *et al.* 1994).

In this study, we tested the hypothesis that female great tits (*Parus major*), which incubate alone but are provisioned to some extent by their mates (Kluyver 1950), are constrained in their constancy of incubation by the availability of energy. In theory, the responses of incubators should not be sensitive to the form of energy available, whether food or heat, for example, but rather to the amount supplied or removed. In practice, energy provided as food is likely to be taken during daytime and will therefore modify the period required for foraging. In the time-limited context of uniparental incubation, this is likely to reduce the time spent on foraging. Hence, although a resultant increase in the period spent on the nest, and most probably hatching success, would be consistent with energetic limitations (Moreno 1989; Nilsson & Smith 1988), it would also be consistent with other interpretations: for example, that time on the nest is favoured over time off, because of a greater risk of predation or accident in the open.

Accordingly, we chose to manipulate energy supplies by heating the nest at night. With no direct impact on foraging time, this permitted a variety of responses (see

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below) to the reduction in overnight thermostatic costs. Responses were monitored for 'heated' birds and for a 'control' group by recording incubation behaviour at the nest, daily energy expenditure and mass change.

### (a) *Predicted responses to heating treatments*

The female great tit normally incubates continuously during the hours of darkness ('night-time session'), whereas the 'active day' (the period between the first exit in the morning and the last entry in the evening (Haftorn 1981)) is divided between periods of attentiveness ('sessions') and periods out of the nest ('recesses'). The daily energy expenditure (DEE,  $\text{kJ d}^{-1}$ ) of incubating birds therefore includes components arising from both on-nest and off-nest activity:

$$\text{DEE} = (I s_d n) + (Fr(n+1)) + (R(n+1)) + (I s_n), \quad (1)$$

where  $I$  is the hourly cost of incubation;  $F$  is the cost of foraging and other activity during recesses (both in  $\text{kJ h}^{-1}$ );  $R$  is the cost of reheating the clutch (Biebach 1986) after recesses ( $\text{kJ}$ );  $s_d$ ,  $r$  and  $s_n$  are, respectively, the mean durations (h) of daytime incubation sessions, recesses and night sessions. The number of sessions in the active day,  $n$  is related to  $s_d$ ,  $r$  and  $s_n$  by equation (2):

$$n s_d + r(n+1) = 24 - s_n. \quad (2)$$

For energy balance to be maintained, energy gain from foraging (EG,  $\text{kJ h}^{-1}$ ) during the active day must equal this expenditure. Thus

$$\text{EG}r(n+1) = (I s_d n) + (Fr(n+1)) + (R(n+1)) + (I s_n). \quad (3)$$

The cost of incubation ( $I$ ) includes a thermostatic component and is therefore dependent on nest-box temperature (Haftorn & Reinertsen 1985); so heating the nest-box overnight imposes a reduction in overnight expenditure and allows for a lowering of DEE. Four possible responses to nest-box heating (hypotheses  $H_1$ – $H_4$ ) were envisaged. First, birds could maintain energy inputs (left-hand side of equation (3)), leading to an inequality, where energy gains were greater than expenditure. Under these conditions, birds could either remain in positive energy balance (resulting in a gain in body mass,  $H_1$ ) or they could increase their off-nest activity and the value of  $Fr(n+1)$ , such that energy balance is maintained owing to the greater costs during recesses ( $H_2$ ). Alternatively, daily energy inputs could fall to match a reduced expenditure, either by lowering the rate of energy gain, EG ( $H_3$ ) or by reducing the time spent foraging ( $r(n+1)$ ), and thereby increase incubation constancy ( $H_4$ ). Incubation constancy (IC) is defined as the proportion of the 24-h day spent on the nest.

The 'energetic-bottleneck' hypothesis (Yom Tov & Hilborn 1981) predicts that birds in heated boxes should respond by increasing IC, enabled by the reduction in thermostatic demands (consistent only with the fourth hypothesis,  $H_4$ ). In contrast, no adjustment in IC by heated birds would imply that natural incubation patterns are already those that maximize fitness and are not normally constrained energetically. Therefore, IC would not be expected to change as a result of changing energy fluxes ( $H_1$ – $H_3$ ). With regard to energy expenditure,

heating nest-boxes was predicted to lower DEE owing to thermostatic savings alone ( $H_1$ ,  $H_3$ ) or in combination with reduced activity during recesses ( $H_4$ ). Alternatively, it may effect no change in DEE ( $H_2$ ).

## 2. MATERIALS AND METHODS

An established box-nesting population of great tits, sited in parkland and mixed woodland near Stirling, Scotland ( $3^{\circ}54' \text{W}$ ,  $56^{\circ}8' \text{N}$ ), was studied in April–June 1994–1995. Nests were checked every 1–5 days to determine clutch sizes, and experimental nests were assigned alternately, by clutch initiation date, to control or treatment groups.

Nest-box heating apparatus, consisting of a night-light in a tin can below the nest-box (Yom-Tov & Wright 1993) was assembled at all nests over a period of 2–3 days to reduce the risk of disturbance. Nests in the 'heated' group were then warmed for three consecutive nights in the period 5–10 days after clutch completion. Heating commenced 1–2 h before dusk. Control nests were subjected to similar disturbance, but with no heating. Nest-temperature loggers were employed to provide a continuous temperature record by sampling every minute within each nest and in the shade of each box. The temperature in the nest-box overnight was determined from hourly mean temperatures measured in nest-air about 1 cm above and behind the nest-cup, for eight heated and eight control nests.

Energy expenditure was measured over a 48-h period by means of the doubly labelled water (DLW) technique (Lifson & McClintock 1966). Females from 28 nests were caught at 14.00–16.00 on the day after the first night of heating or 'control' disturbance. Where possible, experiments were paired, whereby one control and one experimental female were captured on the same day (ten pairs), or within two days (three pairs). The other two nests were not paired. Field protocols (Tatner & Bryant 1989) involved dosing females with  $15 \mu\text{l g}^{-1}$  of doubly labelled water ( $0.524 \text{ g}$  of 99%  $\text{D}_2\text{O}$  in  $10 \text{ ml}$   $14\text{APE H}_2^{18}\text{O}$ ) by intraperitoneal injection, then holding birds in a cloth bag for 1 h to allow for isotopic equilibration before taking ten blood samples of  $5 \mu\text{l}$  from the femoral or brachial vein. Birds were then released. Records of nest temperature (see below) after release enabled identification of aberrant behaviour. Although most females (17) resumed normal patterns of incubation within 1 h of release, five did not return to their nests until the following dawn, and six (four controls and two heated birds) deserted. Twenty-two females were recaptured at the nest 48 h after release to take a second blood sample, but the data from the five birds that spent a night off the nest were excluded from all analyses. Birds were weighed at first capture and on recapture. Blood samples from a further five incubating females were taken to establish background concentrations of deuterium and oxygen-18 in the population. All blood samples were analysed with isotope ratio mass spectrometry (Tatner & Bryant 1989).

Average daily metabolic rate (ADMR) in  $\text{cm}^3 \text{CO}_2 \text{g}^{-1} \text{h}^{-1}$  was calculated from the equations of Lifson & McClintock (1966), where the body water pool averaged 66% of total body mass (Mertens 1987). Daily energy expenditure (DEE,  $\text{kJ d}^{-1}$ ) was calculated by taking a respiratory quotient (RQ) of 0.75 and  $26.44 \text{ J cm}^{-3} \text{CO}_2$ . Metabolic intensity ( $M$ ) expresses DEE as a multiple of basal metabolic rate (BMR), the latter estimated from the equation of Aschoff & Pohl (1970) for passerines (resting phase).

Nest temperatures over a continuous period of *ca.* 24 h were extracted from the 2-day experimental period to determine incubation constancy. The duration of recesses was indicated by

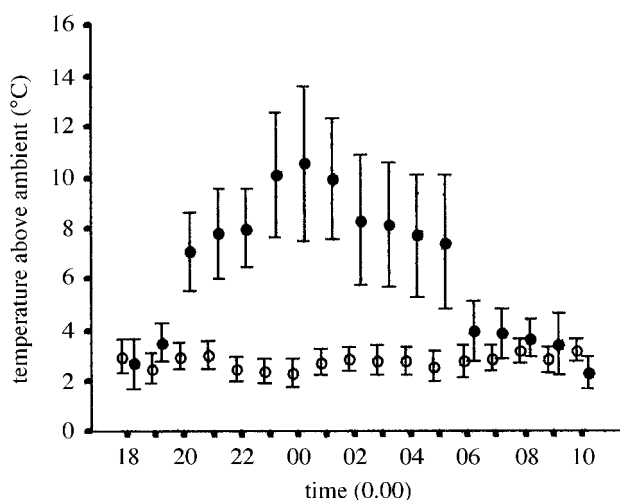


Figure 1. The effects of nest-box heating apparatus on the elevation of nest-air temperature above ambient ( $^{\circ}\text{C}$ , hourly mean values) for the period of nocturnal incubation, from 18.00 (approximate time of candle lighting) to 10.00, for eight heated nests (closed symbols) and eight control nests (open symbols). Error bars indicate  $\pm 1$  s.e.

a rapid fall and subsequent rise in the temperature recorded by three probes placed amongst the eggs, as the female left the nest and later resumed incubation.

Daily weather records were available from the Parkhead Meteorological Station, situated within the study site.

### 3. RESULTS

#### (a) *Effects of the heating treatment*

Although the effectiveness of night-lights as heat sources was variable, mean nest-air temperature between 19.00 and 06.00 (covering the night-time session for most birds) was significantly higher in heated nests ( $6.15 \pm 0.92$   $^{\circ}\text{C}$  (mean  $\pm$  s.d.) above ambient,  $n=8$ ) than in the controls ( $2.78 \pm 0.75$   $^{\circ}\text{C}$  above ambient,  $n=8$ ,  $t$ -test,  $t_{14}=7.99$ ,  $p < 0.001$ ) (figure 1).

To estimate the magnitude of the energetic savings induced by heating, we used the heat-transfer coefficients (slopes) of linear regressions from Haftorn & Reinertsen (1985), which relate energy expenditure to temperature for incubating blue tits (*Parus caeruleus*, mean value =  $0.58 \text{ ml O}_2 \text{ }^{\circ}\text{C}^{-1} \text{ g}^{-1} \text{ h}^{-1}$ ). After scaling to allow for the greater mass of an incubating great tit ( $21.5 \text{ g} \pm 1.04$  s.d. in this study,  $n=28$ ) compared with a blue tit (Herreid & Kessel 1967), the heating treatment was expected to reduce thermostatic demands by 6.8 kJ overnight.

#### (b) *Incubation constancy*

Patterns of nest attendance were monitored for 22 (11 control and 11 heated) birds in 1994–95. The durations of incubation sessions, recesses and night-time sessions did not differ between the two years ( $t$ -tests,  $p > 0.2$  in all cases), so data for 1994 and 1995 were pooled for subsequent analysis.

Birds that had spent the night in a heated nest-box displayed modified incubation schedules (table 1). The combined effect of longer night-time sessions and of longer incubation sessions throughout the following day increased incubation constancy (IC) from 86.3% (95%

Table 1. *Effects of temperature manipulation on patterns of nest attendance for incubating great tits*

(Duration (in minutes, mean  $\pm$  s.d., sample size in parentheses) of incubation sessions, recesses and night-time sessions, measured over a period of ca. 24 h for each of 22 females. Incubation constancy (IC) represents the proportion of each 24-h period spent on the nest, calculated from the mean session and recess duration for each bird. Analysis of variance was performed with angular-transformed values of IC, as this improved normality (Kolmogorov–Smirnov goodness-of-fit,  $p > 0.89$ ). Three covariates were not significant: mass ( $p=0.901$ ), maximum ( $p=0.285$ ) and minimum ( $p=0.695$ ) temperature.)

	'control'	'heated'	
session	29.6 $\pm$ 8.9 (11)	39.2 $\pm$ 9.3 (11)	
recess	8.1 $\pm$ 1.5 (11)	7.8 $\pm$ 2.4 (11)	
night session	590.2 $\pm$ 56.5 (11)	647.0 $\pm$ 68.3 (11)	
IC (%)	86.3 (95% CI 84.1–88.6)	90.1 (95% CI 88.1–92.2)	ANOVA $F_{1,21}=7.749$ , $p=0.011$

confidence limits (CL) 84.1–88.6%) among 'controls' to 90.1% (CL 88.1–92.2%) among 'heated' birds; this increase is equivalent to, on average, an additional 55 minutes of incubation per day (ANOVA of angular-transformed values of IC, main effect of treatment group  $F_{1,21}=7.749$ ,  $p=0.011$ ; covariates mass, maximum and minimum temperature were not significant).

#### (c) *Daily energy expenditure*

Of the 28 females dosed with doubly labelled water (nine in 1994, 19 in 1995), 17 birds yielded useful data on energy expenditure (see § 2). Among these,  $\text{ADMR} = 7.53 \pm 2.22 \text{ cm}^3 \text{ CO}_2 \text{ g}^{-1} \text{ h}^{-1}$ ;  $\text{DEE} = 103.00 \pm 28.63 \text{ kJ d}^{-1}$  or  $M = 3.47 \times \text{BMR}$ . Weather conditions, particularly ambient temperatures, may have influenced energy use over the study period (Mertens 1987). To examine this, partial correlation coefficients, controlling for 'metabolic mass', calculated as  $\text{mass}^{0.726}$  (g) (Aschoff & Pohl 1970), were computed between DEE and mean temperature maxima and minima (calculated over the 48-h study period). Energy expenditure was inversely related to minimum temperature, which occurred overnight ( $r_{14} = -0.586$ ,  $p=0.017$ ), whereas the correlation with maximum temperature (occurring during the day) was not significant ( $r_{14} = 0.328$ ,  $p=0.215$ ). To test for the effects of the heating treatment on DEE, mean minimum temperature was therefore included as a covariate in the analysis of variance (table 2). The slopes of the regressions of DEE against minimum temperature differed between groups (group  $\times$  temperature interaction,  $F_{1,13}=4.82$ ,  $p=0.047$ ); the escalation of costs at low temperatures was more pronounced among control than among heated birds (figure 2).

#### (d) *Body mass*

Body mass changed little over the experimental period (final mass, measured after the 48-h study period,

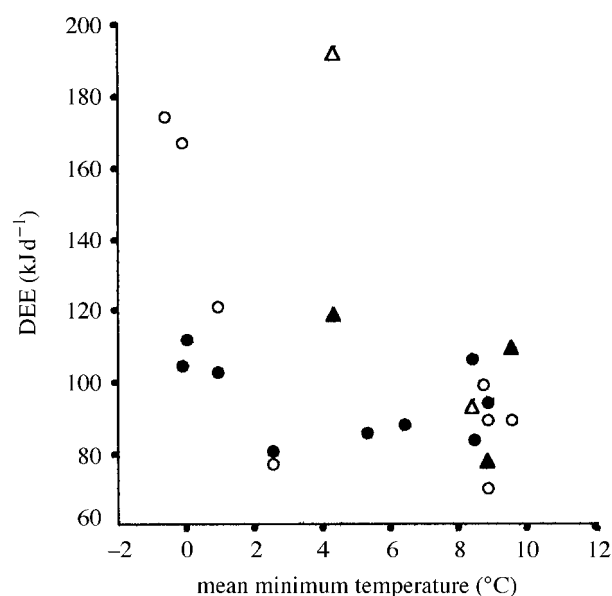


Figure 2. Daily energy expenditure (DEE,  $\text{kJ d}^{-1}$ ) of 22 incubating great tits in relation to mean minimum temperature ( $^{\circ}\text{C}$ ) over the 48-h measurement period. The marker indicates whether the nest-box was heated (closed symbols) or 'control' (open symbols) and also whether the female resumed incubation after labelling before nightfall (circles) or spent the first night of the study period away from the nest (triangles).

differed from initial mass by  $-0.34 \pm 0.63$  g). Mass change did not differ between control and heated birds (ANCOVA of mass change ( $\text{gd}^{-1}$ ) by treatment group  $F_{1,14}=2.55$ ,  $p=0.215$ , covariate initial mass,  $F_{1,14}=0.730$ ,  $p=0.406$ ).

#### 4. DISCUSSION

By reducing thermostatic costs overnight, our heating treatment would have caused female great tits to retain at dawn more of their stored energy. It was this more favourable body state, we suggest, that led to more time being spent warming the eggs, in comparison with the control group. Effects of heating treatments on daily energy expenditure were also detected and were particularly marked after cold nights. These responses to an enhanced energy supply are more easily understood if incubation is an inherently costly stage in the annual cycle of birds. Recent evidence indeed suggests, in contrast to earlier assumptions (Walsberg & King 1978), that the costs associated with incubation are not negligible, at least among uniparental incubators (Tatner & Bryant 1993; Williams 1991; Thomson *et al.* 1998).

Although the great tit has been intensively studied, including estimation of the cost of warming eggs (Mertens in Drent 1972; Mertens 1977, 1980), this is the first report of incubation costs obtained by using the DLW technique for this species. The validity of the application of DLW studies to incubating birds has been discussed elsewhere (Bryan 1996). The present value ( $3.8 \times \text{BMR}$ , range 2.4–6.1, for 'control' birds under natural conditions) exceeds previous estimates for this species ( $1.75$ – $2.95 \times \text{BMR}$ , during periods of continuous incubation), mainly because, as an integrated measure of daily energy expenditure, it includes the effects of activity

off the nest. This result is consistent with evidence that incubation represents an approximate threefold increase above basal levels of metabolism for hole-nesting passerines (Bryant 1997; Moreno & Carlson 1989; Moreno *et al.* 1991; Moreno & Sanz 1994; Westerterp & Drent 1985; Williams 1987) and also, in uniparental incubators, that energy expenditure during incubation is comparable to that during nestling rearing (Bryant 1997; Tatner & Bryant 1993; Weathers & Sullivan 1989; Williams 1991) (cf.  $95.1 \pm 14.8 \text{ kJ d}^{-1}$ ,  $n=32$ , for female great tits feeding nestlings (Tinbergen & Dietz 1994)). This makes incubation liable to constraints that simply act on high rates of energy expenditure (Drent & Daan 1980; Hammond & Diamond 1997).

Heating nest-boxes raised the mean nightly temperature by an average of  $3.4^{\circ}\text{C}$  for the 11 h covering the period of continuous incubation, yielding an estimated saving of around 7 kJ per individual per night (*ca.* 6% of DEE for a female incubating under normal conditions). Only hypothesis  $H_4$ , the 'energetic-bottleneck' hypothesis, is consistent with the reduced time spent off the nest on self-maintenance, which permitted, on average, an additional 55 minutes of incubation per day.

Hypothesis  $H_4$  predicted a reduction in total DEE arising from the combination of reduced thermostatic demands and a greater efficiency of energy use, as the number of recesses, and hence clutch re-heating costs, were reduced (Drent 1972). Even so, no difference in DEE of incubating birds in the two groups was detected under mild conditions. When ambient temperatures fell, however, the rate of increase was reduced among heated birds compared with the controls. Because there was no evidence that the adjustment in incubation behaviour occurred only at low temperatures (ANCOVA of angular transformed values of IC, group  $\times$  temperature interaction  $F_{1,18} < 0.01$ ,  $p=0.950$ ), other factors presumably accounted for the greater energetic savings associated with the heating treatment when it was colder. These might include a reduced foraging success on cooler days (Avery & Krebs 1984), elevated thermostatic demands or foraging costs while off the nest, or rapid cooling rates of eggs, and could explain the greater energetic economies arising when more time was spent on the nest under cool conditions.

Other studies manipulating nest temperature have similarly reduced thermostatic demands and facilitated an increase in the allocation of time and energy to reproduction. In response to heating boxes between nest-building and clutch completion, for example, the frequency of interruptions in the laying sequence of the blue tit was reduced (Yom Tov & Wright 1993), and a modification in nest-building behaviour and egg size was recorded in the great tit (Nager & van Noordwijk 1992).

The results of this study imply a proximate energetic control on nest attendance. Relaxation of this control, by reducing overnight thermostatic demands and thereby sustaining energy stores, allowed an increase in nest attendance, which is likely to be fitness-enhancing. Reduction in the total time spent away from the nest would not only reduce the risk of eggs chilling (Webb 1987) and of nest predation (Clark & Wilson 1981) but would also increase the average egg temperature during the active day. The duration of the incubation period is



Table 2. *Effects of temperature manipulation on energy expenditure*

(Mass (mean  $\pm$  s.d., in g at first capture), clutch size (eggs) and energy expenditure (ADMR,  $M$  and DEE, see text) of incubating great tits, grouped according to nest-box treatment. Independent samples  $t$ -tests and analysis of covariance were used to test the difference between groups.)

	control	heated	
mass in g	21.49 $\pm$ 1.00 (8)	22.13 $\pm$ 1.22 (9)	$t_{15} = 1.18, p = 0.258$
clutch size	7.88 $\pm$ 0.9 (8)	7.56 $\pm$ 1.33 (9)	$t_{15} = 0.55, p = 0.588$
ADMR in cm <sup>3</sup> CO <sub>2</sub> g <sup>-1</sup> h <sup>-1</sup>	8.21 $\pm$ 3.06 (8)	6.92 $\pm$ 0.89 (9)	
$M$	3.78 $\pm$ 1.39 (8)	3.20 $\pm$ 0.40 (9)	
DEE in kJ d <sup>-1</sup>	111.2 $\pm$ 39.77 (8)	95.71 $\pm$ 11.31 (9)	ANCOVA treatment group: $F_{1,13} = 7.81; p = 0.015$ min. temp(cov): $F_{1,13} = 10.43; p = 0.007$ group $\times$ temp.: $F_{1,13} = 4.82; p = 0.047$

inversely related to average egg temperature (Haftorn 1983), so individuals that succeed in maintaining clutch temperatures by more persistent incubation are likely to reap the benefits of elevated postfledging survival associated with early hatch dates (Perrins & McCleery 1989). In addition, egg temperatures are maintained above the level at which developmental anomalies are likely to arise (Webb 1987). Finally, a reduction in DEE arising from the increased energy efficiency of high incubation constancy could reduce any physiological costs associated with high work rates (Daan *et al.* 1996).

The hypothesis that incubation may represent an energetic bottleneck in the reproductive cycle (Williams 1996; Yom Tov & Hilborn 1981) is supported by the results of this study, in contrast to earlier hypotheses, which often viewed incubation as a low-cost activity, and particularly emphasized parental ability to feed the young as the ultimate control on avian clutch size (Lack 1947). The present study implicates current energy balance as a proximate constraint, which, via its control over patterns of incubation behaviour, may underlie the link between incubation effort and reproductive success (Lyon & Montgomerie 1985; Moreno & Carlson 1989; Moreno *et al.* 1991; Siikamaki 1995; Smith 1989; Székely *et al.* 1994; Tombre & Erikstad 1996). In the quantification of daily energy expenditure during incubation in the great tit, and by detecting behavioural and energetic responses to manipulation of the energy budget, this study provides both observational and experimental evidence for an energetic constraint on incubation behaviour.

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