DAILY ENERGY EXPENDITURE DURING BROOD REARING OF GREATEST TITS PARUS MAJOR IN NORTHERN FINLAND

J.J. SANZ1,2, J.M. TINBERGEN2, M. ORELL3 & S. RYTKÖNEN3


We present data on the natural variation in daily energy expenditure (DEE, measured by the doubly labelled water technique) of individual female Great Tits Parus major tending their brood near the northern border of the species' distribution. We expected that longer foraging days would result in a higher energy expenditure. Female DEE, visitation rate and the duration of the active period were measured at the nestling age of 12 days. There was a positive relationship between the duration of activity period and brood size. Female DEE was positively associated with the duration of the activity period and the number of young in the nest. Energy expenditure was not related to temperature or feeding rates. Despite the longer foraging day and lower ambient temperatures, female DEE did not differ from the values obtained in central Europe. This result suggests that there are differences in foraging cost and/or mode with latitude.

Key words: Parus major - parental effort - latitude - daily energy expenditure

1Depto. de Ecología Evolutiva, Museo Nacional de Ciencias Naturales (CSIC), José Gutierrez Abascal 2, E-28006 Madrid, Spain, E-mail: MCNS111@MNCN.csic.es; 2Zoological Laboratory, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands; 3Dept of Biology, University of Oulu, Linnanmaa, 90570 Oulu, Finland

INTRODUCTION

Reproductive effort, defined as the amount of resources that an individual allocates to reproductive functions (Tuomi et al. 1983), is one of the central concepts of life history theory (Roff 1992; Stearns 1992). Energy expenditure estimates have been used as a measure of reproductive effort, since they integrate various aspects of parental care (Drent & Daan 1980). The doubly labelled water technique (DLW; Lifson & McClintock 1966; Nagy 1980; Bryant 1989) has offered the possibility to measure energy expenditure under natural conditions. In recent years, estimates of daily energy expenditure (DEE) of free-living birds tending their young based on the DLW technique have been measured for an increasing number of species (Bryant & Tatner 1991; Tinbergen & Dietz 1994).

Interspecific allometric predictions of energy expenditure on the basis of body mass are available (Bennet & Harvey 1987; Nagy 1987; Bryant & Tatner 1988; Masman et al. 1989; Daan et al. 1990a; Daan et al. 1991; Tinbergen & Dietz 1994), but data on the within-species population variation in energy expenditure are scarce. Hypotheses on factors that limit clutch size in birds centre around limits in available foraging time (Lack 1948) or maximal sustained levels of energy expenditure while provisioning offspring (Drent & Daan 1980). But, if there are fitness costs associated to energy expenditure, life history theory would predict that parental energy expenditure of iteroparous organisms is optimized and not maximized (Williams 1966; Charnov & Krebs 1974; Drent & Daan 1980; Daan et al. 1990b). Parental energy expenditure should then be adapted to the environmental conditions of the individual.
Analysis of daily energy expenditure in a Dutch Great Tit *Parus major* population suggested that a limit in the available daylight period might determine parental energy expenditure. Therefore it became of interest to us to study variation in energy expenditure of a population breeding in Finland. As day length increases with latitude, the activity period may increase (Sanz in press), while temperature may decrease and both factors are expected to increase parental energy expenditure. Ambient temperature explained 15% of the variation in parental energy expenditure of female Great Tits feeding nestling in a population in The Netherlands (Tinbergen & Dietz 1994). In the northern part of the species' distribution, the lower temperatures during the breeding season (Sanz in press) may be a cost of breeding there.

In this study, we present data on the level of energy expenditure and its natural variation for individual female Great Tits tending a brood near the northern border of the species' distribution (Orell & Ojanen 1983). We examine the association between female DEE during the peak demand by the nestlings, measured by the DLW technique, and potential factors governing individual variation (body mass, working day, visitation rate and temperature) with the expectation that longer foraging days lead to higher energy expenditure.

**METHODS**

The study was conducted in 1995 in a mixed forest in the Oulu area, northern Finland (65°00'N, 25°30'E). A detailed description of the study area is presented elsewhere (Orell & Ojanen 1983). Nestboxes were checked for occupation by Great Tits, and the dates of clutch initiation, clutch sizes and number of fledged young were determined. Mean (± SD) laying date and clutch size of the breeding pairs were 26 May ± 2.2 days (*n* = 10) and 10.90 ± 0.87 (*n* = 10), respectively.

**Energy expenditure**

Females were caught in the nestboxes between 22.00h and 24.30h when their chicks were 11 days old. After weighing, to the nearest 0.1 g, with a spring balance and measuring the tarsi, to the nearest 0.5 mm, with a caliper, they were injected with 0.10 ml DLW (2.69 g H$_2$O, 90.1 atom%, 1.22 g D$_2$O, 99.9 atom%) and returned to the nest. After equilibration of the isotopes in their body fluids (one hour), blood samples were taken from a brachial vein and kept in flame-sealed, heparinized capillary tubes. After bleeding was arrested, the birds were returned to the brood. The next night, the females were caught again and the final blood samples were taken from the brachial vein in the opposite wing. The females were reweighed and returned to the brood. Blood samples were also obtained from 4 un.injected birds to determine background isotope concentrations. Background values expressed in %o relative to standard mean ocean water (V-SMOW; Ehleringer & Rundel 1988) for both $^{18}$O and D were $\delta_{18}$: -1.84 ± 3.36 (mean ± SD) and $\delta_{2}$: -73.48 ± 17.47, respectively.

From the initial and final body mass estimates, the daily mass change of females Great Tits was calculated as: (Final body mass - Initial body mass) x (24 h$^{-1}$ between the two captures). Blood samples were analysed for $^{18}$O and D concentrations at the Centre for Isotope Physics of the University of Groningen (The Netherlands) by mass spectrometry. Estimation of body water via isotopes was not feasible because of lack of precision of injection, and we assumed the water content to be 66% of body mass (Mertens 1987). Daily CO$_2$ production (from which the average daily metabolic rate, ADMR, in ml CO$_2$ g$^{-1}$ h$^{-1}$ is derived) was determined from fractional turnovers of the two isotopes using the equations by Lifson & McClintock (1966). CO$_2$ production was converted to daily energy expenditure (DEE, kJ day$^{-1}$) assuming a respiratory quotient of 0.75 and an energetic equivalent of 19.9 kJ l$^{-1}$ of oxygen consumed. CO$_2$ production is directly proportional to body water content and we assumed no differences between populations in this respect.
Additional measurements

Data on ambient temperature on the day of energy expenditure measurements were obtained from the meteorological station of Oulu airport, which was 18 km from the study area. The length of the daily activity period and the total number of visits during the day was determined by using an Automatic Visits Recorder (CortexT GM, Hungary). To measure the sex-specific provisioning rates, nestboxes were monitored for 3 h using a video-camera (3-5 m from the nest). These data were averaged to periods of 1 hour. Feeding rates were recorded between 8.00h and 16.00h, which corresponds to the high activity period of the parents and when no differences occur in their hourly feeding activity (see Fig. 1a). From the share of the sexes and the total number of visits we calculated the female feeding visits per day. Using the Automatic Visits Recorder we got data from 8 nests, and with video-cameras from 10 nests. We present data only for pairs that female DEE measurements were obtained.

Statistical procedures

Parametric statistical analyses were used because the different variables did not differ from a normal distribution (Kolgomorov-Smirnov test). Frequency measures such as feeding rates were subjected to square root transformations before parametric statistical analysis. Statistics are presented as mean ± one standard deviation (SD).

RESULTS

Behavioural measurements

Birds started bringing food to the nest at around 04.00h (03.56 ± 0.68 h) and finished at 21.30h (21.19 ± 0.84 h; Fig. 1a). The activity period was estimated as 17.62 ± 0.79 h (range 16.5 - 19.0, n = 8). Birds did not bring food at a constant rate throughout the day; feeding rate increased during the first 2 h of the activity period, and decreased during the last 4-5 h. The activity period was positively correlated with the number of young in the nest (Table 1). The total number of feeding visits per day was 493.6 ± 74.8 (range 380 - 629, n = 8). Feeding rate did not differ between sexes (female: 20.55 ± 10.26, n = 10; male: 19.30 ± 10.57, n = 10). Paired t-test: t9 = 0.45, n.s.). Female and male feeding rates did not correlate with the number of young in the nest (female: Table 1; male: r9 = 0.16, n.s.).

Individual variation in daily energy expenditure

Female ADMR was 9.50 ± 1.51 ml CO2 g-1 h-1 (n = 10), and female DEE was 103.21 ± 17.32 kJ day-1 (n = 10; Table 2). Mean daily mass change was estimated as -0.24 ± 0.25 g day-1 (range -0.59 - 0.10, n = 10). Female DEE was not correlated with initial body mass (r9 = 0.27, n.s.), final body mass (r9 = 0.31, n.s.) or daily mass change (r9 = 0.09, n.s.). Female DEE was significantly positively correlated with the activity period (Table 1, Fig. 2), while no significant correlation was found with ambient temperature between blood sam-

<table>
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<tr>
<th>Parameters</th>
<th>n</th>
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<th>Ambient temperature</th>
<th>Brood size</th>
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<td>8</td>
<td>0.74*</td>
<td>-0.08</td>
<td>0.81**</td>
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<tr>
<td>Feeding rate</td>
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<td>0.12</td>
<td>0.39</td>
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<tr>
<td>Brood size</td>
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<td>Ambient temperature</td>
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Table 1. Correlation coefficients of various parameters in relation to female daily energy expenditure (DEE, kJ day-1), ambient temperature (°C) and brood size on the day of energy expenditure measurements. n = sample size. * P < 0.05, ** P < 0.01 (To control for type-I errors, adjusted significance levels were obtained by the Bonferroni Sequential procedure).
Table 2. Brood size, initial and final body masses (g), feeding visits per h, activity period (h), ADMR (ml CO₂ g⁻¹ h⁻¹) and DEE (kJ day⁻¹) of female Great Tits tending a brood with nestlings of 12 days old.

<table>
<thead>
<tr>
<th>Nest</th>
<th>Brood size</th>
<th>initial mass</th>
<th>final mass</th>
<th>feeding rate</th>
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<tr>
<td>16</td>
<td>5</td>
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<tr>
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<td>18.6</td>
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<td>24.6</td>
<td>17.0</td>
<td>9.58</td>
<td>108.37</td>
</tr>
<tr>
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<td>18.0</td>
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<td>3.5</td>
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<tr>
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<td>7</td>
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<td>17.7</td>
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<td>23.8</td>
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<td>10.09</td>
<td>108.15</td>
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<tr>
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Mean ± SD 17.8 ± 1.2 17.5 ± 1.1 20.6 ± 10.3 17.6 ± 0.8 9.5 ± 1.5 103.2 ± 17.3

Fig. 1. Hourly profile of daily nest visits (mean ± SE) of sex-combined data when the young were 12 days old in (a) Oulu (Finland, n = 8 nests) and (b) Hoge Veluwe (The Netherlands, n = 4 nests).

Fig. 2. Daily energy expenditure of female Great Tits as a function of activity period. The regression equation is Female DEE = -179.19 + 16.23 Activity period; F₁,6 = 7.16, P = 0.04, r = 0.74 (Test of significance of coefficients: constant t = 1.67, P = 0.14; x t = 2.68, P = 0.04).

lings (Table 1). Furthermore, female DEE was significantly positively correlated with the number of young in the nest, and female DEE was not correlated with female feeding rate (Table 1), nor with female feeding visits per day (r₇ = 0.22, n.s.).
DISCUSSION

The main conclusion of this study is that mean female DEE in Great Tits tending their young in northern Finland (103.2 kJ day\(^{-1}\)) is similar to those measured in two different breeding populations at different latitudes: 100.1 kJ day\(^{-1}\) (52°05'N; Tinbergen & Dietz 1994) and 97.0 kJ day\(^{-1}\) (53°10'N; Verhulst & Tinbergen 1997).

The duration of the activity period was positive related to brood size, females with more young in the nest spent more time feeding their broods. For manipulated brood sizes of Great tits this effect was not found (Verhulst & Tinbergen 1997). However, in their study the parents used almost all (15.3 h) the available daylight hours to collect food for their young (16.6 h daylight, Anon. 1974) while in the present population the activity period was appreciably shorter than the available daylight period (activity period 17.6 h; 22.5 daylight hours). Great Tits breeding near the northern border of their distribution have the option to work longer during the day when brood demands increase. Potentially, the trade-off they are faced with is between activity and sleep, a trade-off that may be equally important in the middle range of the distribution, but the shorter daylight hours available does not allow them any choice. The effect needs experimental verification at northern latitudes.

The distribution of the feeding visits over the day differed between the populations (Fig. 1a, 1b). In Finland feeding rates were lower during the first and last hours than in the middle hours of the day. This may be an effect of lower ambient temperature, lower light intensity, or a combination of both factors. The activity of arthropods increases with ambient temperatures and they then become more vulnerable to the birds (Avery & Krebs 1984). In an experiment with captive Great Tits, Kacelnik (1979) showed that the foraging efficiency is limited by light intensity and that the handling time of prey items was longer at lower light intensity. Thus, reduced foraging yield can potentially explain lower feeding rates at the beginning and end of the activity period. In The Netherlands, the activity period was shorter than in Finland, but pairs fed the young at a constant level throughout the day (Fig. 1b; The Netherlands; Tinbergen unpubl. data).

Whether or not DEE correlates with feeding rate varies between species (Bryant & Tatner 1991). In our study the active period showed a positive correlation with female DEE, but the feeding intensity (feeding rate per hour) did not. Other studies have also failed to show a correlation between DEE and feeding rate: Pied Flycatchers Ficedula hypoleuca (Moreno et al. 1995), Great Tits (Verhulst & Tinbergen 1997) and Kestrels Falco tinnunculus (Jönsson et al. 1996). A possible explanation is that feeding costs may be unrelated to feeding visits, because foraging distance and technique may vary widely between situations. In addition females may have spent considerable amounts of energy on activities unconnected with the delivery of food to the nest, masking the effect of feeding rate on DEE.

Since female body mass and DEE did not differ between Finland (this study) and the Netherlands (Tinbergen & Dietz 1994; Verhulst & Tinbergen 1997), but working day did, lower rates of energy expenditure while foraging at higher latitudes are suggested. The data therefore do not support the time limitation hypothesis in its simplest form. The similarities in energy expenditure between populations are more in line with the idea of maximal sustained energy expenditure (Drent & Daan 1980). However, to distinguish between the hypotheses of time limitation, energy limitation or optimization of energy expenditure we need data of more populations and detailed experimental studies.

That there was a positive correlation between female DEE and the duration of activity period within the Finland population suggests that females with more young in the nest did spend more energy as a consequence of an increased working day. The quantitative relationship found is statistically in agreement with this simple explanation, since the intercept of the regression of DEE on working day did not differ significantly from zero (Fig. 2). Further verification of the rela-
relationship between activity period and parental DEE should be undertaken across the entire range of possible activity periods because it may shed more light on the role of the duration of the working day in the explanation of differences in DEE within and between populations.

ACKNOWLEDGEMENTS

We acknowledge to J. Drent for participation in data collection. This work was supported by the H. Kluyverfonds and the BION grant 436.911 to J.M. Tinbergen and the Research Council for the Environmental and Natural Resources of the Academy of Finland to M. Orell. J.J. Sanz was supported by a postdoctoral grant (Formación de Personal Investigador) from the Ministerio Español de Educación y Cultura. The comments by two anonymous referees on a previous version of the manuscript are greatly appreciated.

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SAMENVATTING

Bij het onderzoek naar de grenzen aan de voortplanting speelt het werk dat ouders verzetten om hun jongen groot te brengen een centrale rol. Het kwantificeren van dit werk is op verschillende manieren te doen. Eén manier is het meten van het energieverbruik van ouders gedurende het verzorgen van de jongen. Energieverbruik is een aantrekkelijke maat omdat het verschillende aspecten van de ouderlijke zorg combineert. Zo kan aanbod, verbruik, opname en opslag allen in dezelfde eenheden uitgedrukt worden. Over de grenzen aan de voortplanting bestaan verschillende hypotheses. Al lang geleden is het idee geopperd dat vogels simpelweg gelimiteerd zouden zijn in de beschikbare tijd (Lack 1948). Een ander idee is dat de dieren een grens aan hun energetische uitgaven zouden hebben (Drent & Daan 1980). Een derde idee is dat we niet met directe grenzen te doen hebben, maar dat ouders hun werkniveau zo kiezen dat hun fitness gemaximaliseerd wordt (Daan et al. 1990b). In deze zienswijze heeft de ouder de keus hoe hard ze werkt, maar heeft harder werken nadelen, in termen van eigen overleving of voortplanting, en voordelen in termen van de kansen van de jongen. De ouder zou de balans zo kiezen dat de totale fitness gemaximaliseerd wordt. Bij onderzoek aan Koolmezen in de Hoge Veluwe leek het er sterk op dat de vrouwen tijdsgelimiteerd waren. Daarom waren we erg nieuwsgierig hoe het energieverbruik van Koolmezen in Finland was omdat daar de daglucht periode veel langer is. We verwachtten daarom een hoger energieverbruik. Dankzij het Huib Kluyver fonds hebben we dat kunnen meten. Binnen Finland werd het verwachte verband tussen de duur van de werkdag en het energieverbruik gevonden (Fig. 2) en vrouwen met meer jongen in het nest hadden een langere werkdag. Mogelijk leveren de dieren wat van hun nachtrust in om beter voor de jongen te zorgen. Tegen onze verwachting in bleek dat het energieverbruik van de Koolmezen in Finland, hoewel ze langere werkdagen hadden (Fig. 1), nauwelijks verschilde van het energieverbruik van de mezen in Nederland. De hypothese dat de energiebesparing van mezen die hun jongen verzorgen puur van de beschikbare tijd afhankt kan geen verklaring bieden voor de (niet aanwezige) verschillen in energiebesparing tussen Finland en Nederland. Mogelijk gebruiken de Koolmezen in Finland andere technieken bij het voedsel zoeken waardoor hun kosten per tijdseenheid van de werkdag lager zijn. Verder, met name experimenteel onderzoek zal nodig zijn om de factoren die de grenzen aan de voortplanting bepalen te doorgronden.

Received 18 July 1997, accepted 6 February 1998
Corresponding editor: Bruno J. Ens