Mismatched reproduction is energetically costly for chick feeding female great tits

Luc te Marvelde[1],*, Simone L. Webber[2], Harro A. J. Meijer[3] and Marcel E. Visser[1]

[1]*Department of Animal Ecology, Netherlands Institute of Ecology (NIOO-KNAW), PO Box 50, 6700 AB Wageningen, The Netherlands;* [2]*Centre for Ornithology, University of Birmingham, Birmingham B15 2TT, UK; and* [3]*Centre for Isotope Research, Faculty of Mathematics and Natural Sciences, University of Groningen, Groningen, The Netherlands*

Summary

1. Climate change has caused a phenological mismatch between the timing of reproduction and the local food peak in many bird species. Late breeding birds therefore experience reduced food availability during chick rearing and are thus predicted to have an increased energy expenditure. Observational studies, however, show mixed results, perhaps because they compare energy expenditure across rather than within individuals at different levels of food availability.

2. In a cross foster experiment, we measured daily energy expenditure (DEE) twice within individuals during chick feeding (when chicks were 6 and 14 days old) for 28 free-living female great tits (*Parus major*). To avoid confounding effects of chick age, these females reared on both occasions a standardized foster brood of eight 10-day-old chicks during the 24-h measuring period. For all birds, food availability declined between the two measurements.

3. We show that DEE during chick feeding increased within females when food availability decreased. Variation in DEE within females is partly explained by brood visit rates, food availability and temperature.

4. DEE during chick feeding could be affected by the investment in previous stages of the reproductive attempt. However, energy expenditure during chick feeding was not correlated to energy expenditure during egg laying, measured in these same females.

5. Understanding of energetic costs during all phases of the reproductive cycle is important to forecast the consequences of climate warming on timing of reproduction.

Key-words: chick rearing, cost of reproduction, daily energy expenditure, match-mismatch, timing of breeding

Introduction

Many insectivorous passerines in temperate forests feed their young with caterpillars that occur only in a short period of time during spring (the caterpillar food peak). Breeding success strongly depends on the timing of breeding relative to the timing of the caterpillar food peak (Van Noordwijk, McCleery & Perrins 1995; Verboven & Visser 1998; Blondel *et al*. 2006). When reproduction is well-matched, the occurrence of (large) nestlings in the nest coincides with high levels of food abundance. Being mismatched with the food peak can have negative consequences for both parents and offspring. Nestlings of mismatched nests often fledge in lower body condition, which has negative consequences on their survival and recruitment probability (Perrins 1965; Tinbergen & Boerlijst 1990; Linden, Gustafsson & Part

1992; Verboven & Visser 1998; Visser & Verboven 1999). Parents feeding nestlings also pay higher costs when their reproduction is mismatched with the caterpillar peak. When caterpillar abundance decreases, search time for prey increases (Naef-Daenzer & Keller 1999; Mols *et al*. 2004) and as a consequence, parents of mismatched nests have to work harder to bring the same amount of energy to the nestlings. Working harder can be costly in terms of adult future reproduction and adult survival, as shown by experimental brood enlargements (Nur 1984; Dijkstra *et al*. 1990; Daan, Deerenberg & Dijkstra 1996).

The doubly labelled water (DLW) technique (Speakman 1997) allows us to measure the energetic costs of free-living parents during chick feeding (see Methods). Although it seems logical that energy expenditure increases when the quality of foraging conditions decreases, previous studies have shown mixed results. In a review, Bryant & Tatner (1991) show that energy expenditure can be negatively,

*Correspondence author. l.temarvelde@nioo.knaw.nl

positively or not associated with food availability (respectively, in 4/6, 1/6 and 1/6 species). More recently, Thomas *et al.* (2001) showed that mismatched blue tit (*Cyanistes caeruleus*) parents had higher energy expenditure compared with well-timed parents. A similar result could not be demonstrated in a larger data set of two Dutch populations of great tits (*Parus major*), potentially because food availability is overall higher in the Dutch population compared with the Corsican population masking the negative effect of mismatched reproduction (Verhulst & Tinbergen 2001). However, Verhulst & Tinbergen (2001) also state that if they had found a correlation between energy expenditure and date relative to the food peak, this could be caused by factors other than the timing relative to the food peak. Seasonal differences in energy expenditure could be caused by late breeders being low quality birds or birds in low quality habitats, potentially causing their energetic budgets to be different from earlier breeding birds. Also, late breeding pairs often have a lower clutch size and thus brood size (Kluijver 1951) compared with early breeders; food availability and brood size are thus confounded as late breeders raise their nestlings in a period of low food availability. Because parental energy expenditure is correlated to brood size (Sanz & Tinbergen 1999), energetic measurements between early and late breeders are difficult to compare. Finally, females might differ in their reproductive effort that could increase variation in daily energy expenditure (DEE) when females do not fully compensate for low food availability, resulting in compromised fledgling growth, or loss of their own body mass. Therefore, variation between females in energy expenditure might mask the relationship between food availability and energy expenditure, perhaps causing the mixed results found in previous studies.

An alternative approach is to measure the effect of food availability on energy expenditure *within* individuals. Measures of energy expenditure within individuals dismiss differences in habitat quality and other between individual differences (although differences in female quality can only be accounted for when timing of breeding is manipulated) and focuses on changes between two measurements. Within females, there are a number of changes over the season that can affect energy expenditure; (i) food availability, (ii) nestling age and (iii) temperature. Nestling food requirements and parental feeding rates increase when nestlings get older (to an asymptote around day 10; Royama 1966). Age (and thus mass) of the nestlings can affect parental energy expenditure (Hails & Bryant 1979; Deerenberg *et al.* 1995), but this is not always the case (Sanz & Tinbergen 1999). Nestling age can be easily manipulated with a cross fostering experiment. Temperature is likely to affect energy expenditure because costs for thermoregulation go up under cold conditions (William & Calder 1974), and foraging efficiency for spiders (10–60% of great tit nestling diet depending on caterpillar availability; Naef-Daenzer, Naef-Daenzer & Nager 2000) decreases under cold conditions (Avery & Krebs 1984). Although territory temperature can not be manipulated in the field, its effects can be corrected for using statistical modelling. Thus measuring energy expenditure within individuals

in combination with a temporal cross fostering of nestlings is a good way to study the effects of food availability on energy expenditure.

The aim of this study is to compare variation in energy expenditure within females feeding nestlings in relation to varying caterpillar availability. We experimentally manipulated brood size (when the original nestlings were 6 and 14 days old) by providing a standardized brood in terms of number and nestling age and measured energy expenditure of the female over 24 h using the DLW technique. We predicted that energy expenditure of females differs between the first and the second measurement, and that these differences depended on the timing of breeding; early females might experience sufficient food availability during both measurements, whereas late females are expected to be measured under (very) low caterpillar availability resulting in high energy expenditure. Also, under low food availability, we predict that females compromise weight gain of the foster nestlings and/or their own body weight.

Materials and methods

In 2008, DEE was measured twice in the nestling phase for 28 female great tits (*Parus major*) of the Hoge Veluwe study site (52°02′07″N 5°51′32″E; The Netherlands). The Hoge Veluwe study area consists of 171-ha mixed woodland on poor sandy soils, dominated by oak and pine with about 400 nest boxes.

MEASURING DAILY ENERGY EXPENDITURE

Doubly labelled water technique

The double labelled water technique (Speakman 1997), which enables us to measure DEE in free-living animals, makes use of two isotopes (^{2}H and ^{18}O) that are injected in the body water of the animal (as a mixture of ^{2}H$_2$^{16}O and ^{1}H$_2$^{18}O). Oxygen isotopes in body water are in complete and rapid exchange equilibrium with the oxygen in dissolved CO_2. As a result ^{18}O injected into the body water will be eliminated by the flux of water through the body, the uptake of unlabelled oxygen when breathing in and the elimination of labelled CO_2 when breathing out. Because ^{2}H is only be washed out by the flux of water, a measure of CO_2 production and hence energy expenditure is made possible by the differential elimination of the two labels. DEE includes costs for thermoregulation, foraging and body maintenance.

Field methods

Nest boxes were checked twice a week from the beginning of April to monitor nest building. Once the bottom of the box was covered with nest material, nests were checked daily to determine exact laying dates. Nests were visited from 2 days before the expected hatching date to ensure that the exact hatching date (the date at which at least one chick had hatched) was recorded. Both parents were caught using a spring trap when nestlings were 6 days old. They were ringed with a unique numbered aluminium ring on one leg and three colour rings with a PIT tag glued to it (*c.* 0·25 g; allowing us to record visit rates) on the other leg.

When nestlings were 6 and 14 days old (day of hatching = 0), females were caught in the nest box using a spring trap. Immediately after catching, each female was injected intraperitoneally with 100 µL

DLW using a 0·3 mL 0·33 × 12 mm syringe and then weighed to the nearest 0·1 g and kept in a cotton bird bag for an hour. During this hour, the original nestlings were weighed and swapped for eight (weighed) chicks of 10 days old from a non-experimental nest. One hour after the injection, when the DLW is in equilibrium with the body water, an initial blood sample was taken from a brachial vein (2 × 15 μL) and stored in non-heparinized 25 μL capillaries (Fig. 1). The capillaries were flame-sealed immediately to prevent gas exchange. Each female was recaptured 24 h after the initial DLW blood sample (mean ± SE = 24 h 15 ± 5 min; range = 23 h 12 min–26 h 54 min). A final blood sample was taken from a brachial vein (3 × 15 μL), and body mass was recorded before the female was released. All nestlings were swapped back to the original nest boxes after being weighed. Never was a nest left without nestlings.

Measuring isotope ratios in the samples

Isotopes were analysed at the Centre for Isotope Research using methods described in detail elsewhere (Visser & Schekkerman 1999; Visser, Boon & Meijer 2000; Van Trigt *et al.* 2002). The blood in the capillary tubes was distilled in a vacuum line and brought into a standard vial for automatic injection into the isotope ratio mass spectrometer system. Local water standards (gravimetrically prepared from pure ^{2}H- and ^{18}O-water), which cover the entire enrichment range of the plasma samples, were applied for calibration purposes. The actual ^{18}O and ^{2}H measurements were performed in automatic batches using a High Temperature pyrolysis unit (Hekatech, Wegberg, Germany) coupled to a GVI Isoprime Isotope Ratio Mass Spectrometer for the actual isotope analysis.

Calculating daily energy expenditure

The rate of CO_2 production was calculated according to formula 7·17 of Speakman (1997):

$$rCO_2 = (N/2·078) \cdot (k_{18O} - k_{2H}) - 0·0062 \cdot k_{2H} \cdot N$$

where N is the total body water (TBW) and k_{18O} and k_{2H} are the rates at which ^{18}O and ^{2}H are eliminated from the body per hour (log decay

Fig. 1. Blood sampling a female great tit (*Parus major*) for isotope analysis. A brachial vein is punctured from which the blood is collected in capillary tubes. Bleeding is stopped with a piece of cotton wool (photo SLW).

divided by time interval between the initial and final sample). Because the amount of TBW can differ between the initial and the final capture (24 h apart) because of body mass variation, we used the average pool size (average body mass multiplied by the percentage TBW) as suggested by Lifson & McClintock (1966). We assume a constant TBW% of 66% based on dried great tits (Mertens 1987). An energy equivalent of 27·8 kJ L^{-1} CO_2 produced was used to transform CO_2 production into energy expenditure after which it is multiplied by 24 to get DEE.

ESTIMATING CATERPILLAR BIOMASS

From May 1st to May 30th, caterpillar droppings were collected under 12 oak trees (*Quercus robur*) on 11 locations spread throughout the study site using frass nets; a cheese cloth of 0·25 m^2 in a metal frame, with a weight hung from the centre of the net; two frass nets per tree; about 1–1·5 m from the stem (Visser, Holleman & Gienapp 2006). Caterpillar droppings were collected two times per week, dried at 60 °C for 24 h, sorted (i.e. all debris is removed) and weighted to the nearest 0·001 g. Caterpillar biomass was calculated using the temperature-dependent formula of Tinbergen & Dietz (1994). Temperature data from Royal Netherlands Meteorological Institute (KNMI), location 'Deelen' were used (*c.* 2 km from the study site). We used average caterpillar biomass over the 12 trees.

VISIT RATES

When nestlings were 4 days of age, each nest box was equipped with a transponder plate around the entrance hole containing a metal coil to record nest box visits of the tagged parents. Visit rates were recorded for the 28 nests of during both 24-h periods over which the females' DEE was measured. Because of technical failure, we lost visit rate data for one of the two observations for four nests and visit rate information from one nest completely. For a subset of nests, we also collected visit rates on the day after the first measurement ($n = 21$) or the day before the second measurement ($n = 14$). For these nests, we could thus see how visit rates changed as a result of the cross fostering experiment.

Each visit should have two recordings of the PIT tag (once of the parent going in and once going out of the nest box). However, readings are not always accurate depending on the position of the birds' legs when entering/leaving the box. It can also happen that a bird will sit in the nest box opening, resulting in many 'recordings' in a short period. Therefore, we counted the number of minutes during which at least one reading was recorded. This visit rate was highly correlated with the visit rate scored from video recordings of the nest when the nestlings where 10 days old (linear regression: $P < 0·0001$, $R^2 = 0·72$). When nestlings were 15 day old, parents were caught again and PIT tags were replaced by a unique combination of colour rings.

STATISTICS

For all analyses (unless stated otherwise), we used linear mixed models with Gaussian error structure and female identity as a random effect to account for the fact that each female was measured twice. We first analysed the variation of DEE as a function of date. We expected that DEE measures differ between the first and the second measurement, but that these differences depend on the timing of breeding (because early breeding pairs are better synchronized with the food peak). Thus, we expected a significant measurement × date interaction.

Because we hypothesized that a potential date effect would have been caused by changes in food availability during the season, we then substituted 'date' by 'caterpillar biomass'. Least significant terms were removed from the model, starting with the interaction, resulting in a final model with only significant variables. Parameter estimates and *P*-values of non-significant variables come from model comparisons between the final model and a model in which the non-significant variable was added to the final model (Table 1). In these models, temperature and female body mass were included as a covariate. Hourly temperatures were averaged over the 24-h period over which DEE was measured.

The amount of energy expended is likely to be a function of provisioning rate and search time. Therefore, we ran an additional mixed model with DEE as response variable, female ID as random effect and temperature, visit rate and caterpillar biomass as explanatory variables.

All statistics were carried out using R version 2.9.2 (R Development Core Team 2009) (package 'nlme'). All tests were two tailed and an alpha level of 0·05 was applied throughout.

Results

The difference in DEE of female great tits feeding a foster brood of eight young of 10 days old between the first (day 6) and second (day 14) measurement depended on the timing of breeding (measurement × date interaction; Table 1a; Fig. 2). Early breeding females expended less energy during the day 14 measurement compared with the day 6 measurement, whereas the amount of energy expended by later breeding females is higher for the day 14 measurements as compared

Table 1. Results of the statistical analysis explaining variation in daily energy expenditure (DEE) of female great tits (*Parus major*) provisioning a standardized foster brood using linear mixed models with female as a random effect. We first modelled the effects of date on DEE (a) and then substituted date by actual estimates of caterpillar biomass (b). The first measurement was performed when original nestlings where 6 days old, the second when original nestlings where 14 days old

Linear mixed model; $n = 28$ females, 56 observations

Variable	Estimate	SE	d.f.	*L*-ratio	*P*-value
(a)					
Temperature	−1·04	0·35	1	8·07	0·005
Measurement 1	113·95	20·43			
Measurement 2	52·19	23·32			
Measurement 1 × date	−0·092	0·40	1	6·19	0·013
Measurement 2 × date	1·039	0·44			
Original brood size	0·77	0·46	1	2·90	0·089
Female body mass	1·93	1·13	1	2·86	0·091
(b)					
Temperature	−1·01	0·39	1	6·82	0·009
Measurement 1	107·89	6·18	1		
Measurement 2	113·38	7·23	1		
Measurement 1 × caterpillar biomass	0·40	1·04	1	5·17	0·023
Measurement 2 × caterpillar biomass	−4·23	2·16			
Female body mass	1·31	1·16	1	1·30	0·25

with the day 6 measurements. Temperature affected DEE negatively. DEE was not affected by female body mass (which did not differ between the two measurements (paired *T*-test: $t_{1, 27} = 0.01$, $P = 0.99$)) or original brood size. Although the *P*-values for original brood size and female body mass were rather low, the main result (measurement × date interaction) remained significant independent of the inclusion/exclusion of these variables in the model.

The clearest change in environmental variables between the first and the second measurement was the decline in food availability (Fig. 2). Caterpillar biomass dropped fast after peaking around day 44 (April 1st = day 1) and was zero at day 58. However, many great tit breeding pairs (including the females measured) still had nestlings to feed. By replacing 'date' with 'caterpillar biomass' in the model (Table 1b), we found that the difference in DEE between the two measurements depended on the caterpillar biomass (significant measurement × caterpillar biomass interaction; Fig. 3). This difference was mainly caused by the fast increase in DEE with
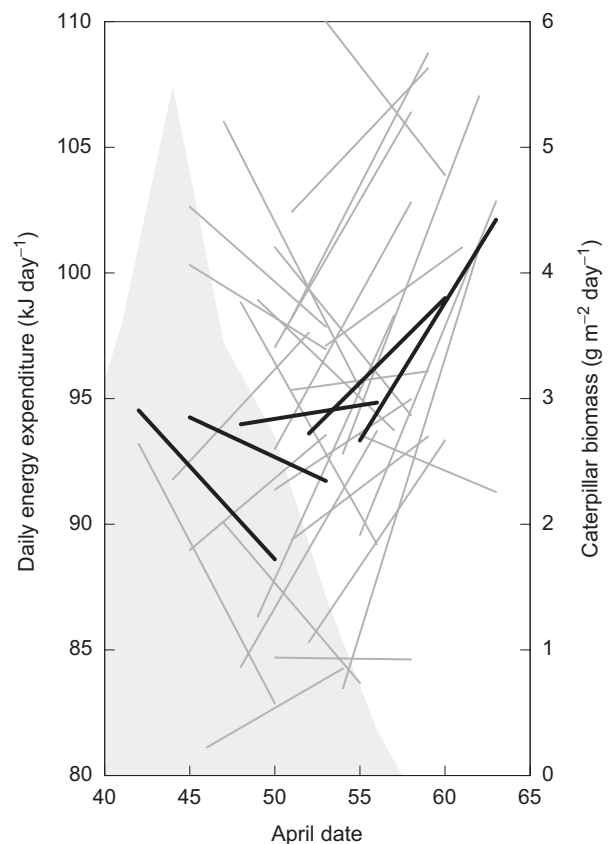

Fig. 2. Timing of the caterpillar food peak (light grey surface) and daily energy expenditure measured for 28 chick feeding female great tits (*Parus major*) of the Hoge Veluwe study population. Grey lines connect the two measurements (corrected for temperature; 15 °C) of each of the 28 females (measured when nestlings were 6 and 14 days old; corrected for a temperature effect of −1·04 kJ day⁻¹ °C⁻¹). Model estimates (black solid lines) come from model DEE ∼ temperature + measurement × date (Table 1a), with female identity as a random effect (temperature at 15 °C). Date is expressed as April dates (April 1st = 1).
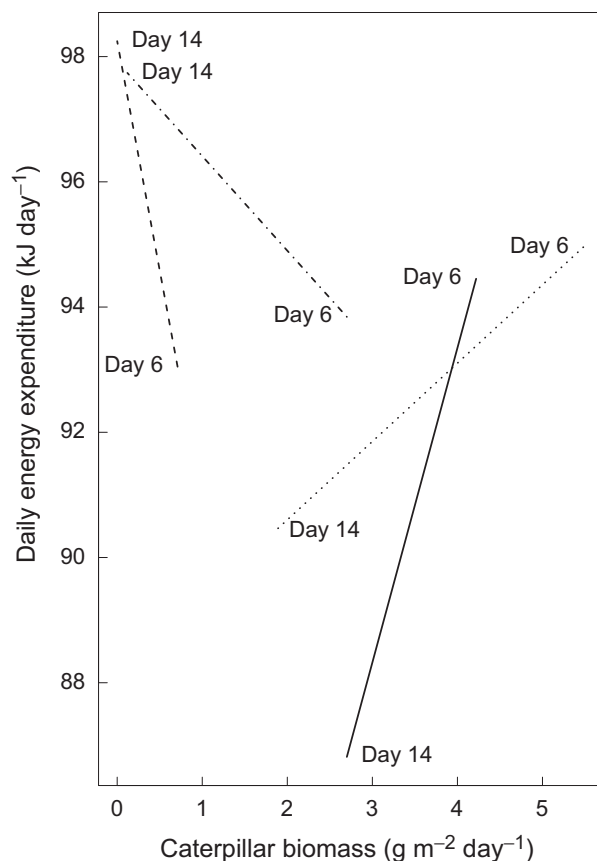
Fig. 3. Model predictions of daily energy expenditure (DEE) as a function of caterpillar biomass, based on the model in Table 1b, shown for four females with different timing of reproduction relative to the caterpillar food peak (lines connects the two DEE measurements (corrected for temperature) per female); latest female measured (----), a female where the first measurement (day 6) was halfway in the caterpillar decline (–·–), a female where the day 6 measurement was at the food peak (·····) and the earliest female measured (——).

Table 2. Variables affecting daily energy expenditure (DEE) of female great tits (*Parus major*) provisioning a standardized foster brood using linear mixed models with female as a random effect

Linear mixed model; $n = 27$ females, 50 observations

Variable	Estimate	SE	d.f.	L-ratio	P-value
Temperature	−1·03	0·35	1	8·85	0·003
Visit rate	0·039	0·015	1	7·18	0·007
Caterpillar biomass	−1·41	0·70	1	4·18	0·041

Variation in DEE within females was partly explained by variation in visit rates; high visit rates were associated with high DEE (Table 2). We also found an additional negative effect of caterpillar biomass showing that, independent of visit rate and temperature, the energy expended increased when food availability decreased.

Visit rates during the first DEE measurement were higher compared with visit rates the following (non-experimental) day in most cases (increase for 17 of 21 cases, Wilcox Signed Rank $P = 0·004$). For 9 of 14 females, visit rates during the 24-h period of the second DEE measurement were low compared with visit rates the preceding (non-experimental) day (Wilcox Signed Rank $P = 0·13$).

Discussion

In this paper, we present the first example of a within-individual study on the effects of food availability on DEE of female birds feeding nestlings. We measured DEE of 28 female great tits twice (8 days apart) while they were feeding a standardized brood and showed that the DEE during the second measurement was lower for early breeding birds, which bred when food was still abundant, but considerably higher for late breeding birds, which bred when food abundance rapidly declined.

As search time for prey decreases exponentially with food availability (Naef-Daenzer & Keller 1999), a decrease in food availability at high densities of food will not have a strong effect on search time, whereas search time will strongly increase when food availability decreases when it was already low. We therefore expected that most first DEE measurements (when original nestlings were 6 days old) would be low compared with the second measurement, especially because the food peak in 2008 appeared to be one of the highest in the last 30 years. While this prediction was met for later breeding females, this was not so for early females: their energy expenditure during the first measurement was higher than their energy expenditure during the second measurement (when original nestlings were 14 days old and food conditions had deteriorated). A possible explanation for this comes from the change in visit rates as a result of the cross fostering experiment. Provisioning rate naturally increases when nestlings get older (Royama 1966; Perrins 1979) probably because of increased nutritional needs (Mols, van Noordwijk & Visser 2005). However, in our study, visit rates during the first measurement period (when the 6-day-old original nestlings were

decreasing caterpillar availability of the second measurements (Fig. 3).

We also evaluated the weight changes of the foster brood and the female during the measurement period. Weight gain of the 10-day-old foster broods over the 24-h measuring period was higher for the first measurements (day 6) than for the second measurements (day 14; 7·2 and 2·8 gram per 24 h, respectively, d.f. = 1 L-ratio = 5·45 $P = 0·020$) and did not change through the season (date × measurement: d.f. = 1 L-ratio = 0·14 $P = 0·71$; date (corrected for measurement): d.f. = 1 L-ratio = 1·11 $P = 0·29$). Female body mass at the start of the 24-h measurement period did not differ between the first and second measurement (paired *t*-test: $t = 0·01$, d.f. = 27, $P = 0·99$). Female body mass did not change over 24 h during the first measurement of DEE (paired *t*-test: $t = 0·81$, d.f. = 27, $P = 0·42$); however, female body mass decreased during the second DEE measurement (paired *t*-test: $t = 4·09$, d.f. = 27, $P = 0·0003$). Neither female body mass nor the change in body mass over the 24-h measurement period changed throughout the season.

replaced by a 10-day-old foster brood) were higher compared with visit rates the following (non-experimental) day. For nine of 14 females, visit rates during the second measurement were low compared with visit rates on the preceding day. During the first measurement, small nestlings are replaced by older larger nestlings, which likely resulted in a sudden increase in food demand. During the second measurement, the older nestlings were replaced by younger smaller nestlings, therefore possibly relaxing food provisioning for the parents. Because most first measurements were performed in a period with high food availability, parents were able to meet the nutritional needs of the nestlings. Weight gain of the foster brood during the first measurement was similar to that reported in Van Balen (1973), and female body mass did not decrease over the 24-h measuring period for the first measurement. Therefore, we believe that the sudden increase in food demand (in combination with high food availability) increased visit rates during the first measurement which in turn increased the DEE.

When food availability decreases, females should work harder to bring the same amount of food to the nestlings, which may affect the body mass of the female. However, females might not work as hard as needed to fully compensate low food availability and thus might compromise chick growth to prevent the costs associated with working hard. Indeed, average weight gain of the foster brood was lower during the second measurement period compared with the first. Even with the increased DEE during the second measurement, chick growth was compromised. Also female body mass decreased over the 24-h period of the second measurement, but not during the first measurement. This might reflect an increased work rate during low food conditions.

Daily energy expenditure of the measurements when the original nestlings were 6 days old did not change over date between females, whereas DEE measurements at day 14 increased with date (and food shortage). This is not caused by a lack of variation in caterpillar biomass, but probably because of a threshold level of food availability under which work rate (and DEE) is not affected by food availability. This parallels results of Tremblay *et al.* (2003) who showed that fledgling success increased with food availability, but levelled off when food availability exceeds a threshold. Therefore, not only the timing of the food peak but also its width is important in understanding consequences of mismatched reproduction on energy expenditure.

Our results show that there is ample variation in DEE measures among females. Indeed, model comparison between a model with and without the female identity as a random effect shows that female differences explain a significant part of the variation in DEE (d.f. = 1, L-ratio = 6·84, P = 0·009). The strength of our study is that we studied the relationship between food availability and energy expenditure within females, therefore excluding differences between females, although we can not exclude subtle differences between individuals in their response to changing food conditions. If we would only have used the measurement on day 6 or day 14, and thus compare DEE among females, we would not have found a relationship between DEE and food availability (P = 0·83 and P = 0·10, respectively) like in many other studies (see introduction).

The amount of energy expended is likely to be a function of provisioning rate and search time (Table 2). We found that females that had high visit rates also had high DEE. We also found an additional negative effect of caterpillar biomass, showing that independent of visit rate and temperature the energy expended increases when food availability decreases. This most likely resembles an increase in search time for prey, which not necessarily shows up in the feeding rates. Our interpretation is that the energetic costs of searching for prey increased when caterpillar biomass decreased.

The ability to work hard (and expend energy) during chick rearing might be affected by the workload (or energy expended) in earlier phases of the breeding cycle. For example, Monaghan, Nager & Houston (1998) have shown that female lesser black-backed gulls (*Larus fuscus*) that had experimentally increased costs during egg laying (by producing more eggs) had reduced offspring rearing capacity in the nestling stage. For 27 of the 28 females of which we measured DEE during chick feeding, we also measured DEE during egg laying (te Marvelde *et al.* 2011). DEE during egg laying is mainly affected by temperature, which is increasing throughout the laying period. So, early females lay eggs under colder conditions and at higher energetic costs. We can use these data to test whether these costs at eggs laying have on effect during chick rearing, either as a carry over effect or because early laying females will have high DEE during egg laying but will be better matched during chick feeding and hence have lower DEE during chick feeding. In our data set however, DEE during chick feeding was not correlated to DEE during egg laying (d.f. = 1, L-ratio = 0·069, P = 0·79).

Understanding the energetic consequences of mismatched timing of reproduction is important as climate warming is still increasing the mismatch between the timing of maximum food availability (timing of the food peak) with the timing of maximum food requirements (nestlings of 10 days and older; Visser *et al.* 1998; Visser, Holleman & Gienapp 2006). Therefore, parents will have to spend increasing amounts of energy to rear their offspring. Ultimately, this has to come at a fitness cost, either in terms of future reproductive success of the parents or in fitness of their offspring, as their fledging weight decreases. Even in recent years, virtually all birds have been breeding during the decline in the food abundance (Fig. 2) and if the rate of adaptation in the timing of reproduction keeps lagging behind the rate of climate change these increased energetic costs are likely to have consequences for population viability (Visser 2008).

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