Parental energy and fitness costs in birds

Deerenberg, Charlotte Maria

PARENTAL ENERGY EXPENDITURE IN RELATION TO MANIPULATED BROOD SIZE IN THE EUROPEAN KESTREL

Charlotte Deerenberg[1], Ido Pen[1], Cor Dijkstra[1], Bart-Jan Arkies[1],
G.Henk Visser[1,2], Serge Daan[1]

[1]Zoological Laboratory, University of Groningen, Haren NL
[2]Centre for Isotope Research (CIO), University of Groningen, Groningen NL

ABSTRACT

Parental daily energy expenditure (DEE) of European kestrels *Falco tinnunculus* with manipulated brood sizes was measured with the doubly labelled water (DLW) method. The reproductive output of the experimental broods increased with brood size. DEE was positively associated with the number of young that were added to the brood, while no association with original brood size could be established. The average level of DEE did not differ between the sexes, but female DEE increased with age of the brood, whereas male DEE was not affected by age of the brood. Other potentially important effects on DEE were examined, such as environmental factors (wind speed, rainfall, and ambient temperature), characteristics of experimental nests (laying date, mortality), and characteristics of experimental individuals (body mass). None of the tested factors contributed significantly to the explained variance in DEE. The negative association of DEE and local survival rate of experimental parent birds is the first observed direct link between parental energy expenditure and fitness costs. We discuss potential causes of fitness costs as a result of hard work.

INTRODUCTION

Parental investment is defined as the reduction in future reproductive output as a result of the effort made by parents in their current reproductive attempt (Williams 1966; Trivers 1974). In altricial birds, this effort can be expressed in terms of the rate of energy expenditure of parents provisioning their offspring. A key role has been attributed to parental daily energy expenditure (DEE) in the trade-off ultimately determining the optimal size and frequency of broods (Masman *et al*. 1989a; Daan *et al*. 1990a). Increased DEE is postulated to lead to an increased reproductive output, albeit at the expense of parental survival, resulting in a reduction in future reproduction.

Experimental manipulations of brood size in birds have become a popular tool to evaluate this theory, and there is an increasing body of data on reduction of parental local survival or future reproduction associated with artificially enhanced brood size (reviews in: Dijkstra *et al*. 1990; Stearns 1992). A prerequisite to study the effects of brood size on parental fitness is that parents indeed adjust their effort to meet the needs of the experimental brood (Lessells 1993). Adjustment of parental effort can be evaluated by the current reproductive output. Brood enlargements usually lead to an increased number of fledglings, in spite of reduced nestling survival rates. However, a concurrent reduction in fledgling body mass, which may reduce the probability of first year survival and thus reproductive prospects (Tinbergen & Boerlijst 1990), is common (reviews in: Dijkstra *et al*. 1990; Stearns 1992). In brood size manipulation experiments it is therefore crucial to examine whether, and how, current reproductive output and parental effort are affected. Manipulation of brood size obviously does not affect the costs of production and incubation of eggs. There is evidence that the nestling provisioning period is the episode of maximum energy turnover in the annual cycle of the European Kestrel *Falco tinnunculus* (Masman *et al*. 1988a), and this is possibly the critical period for most altricial birds (Lack 1947).

Behaviour of parent birds with manipulated broods has often been studied (review in Lessells 1993), and most studies show a change in parental effort in terms of provisioning rates. Dijkstra *et al*. (1990) used time-energy budgets (TEB) to translate observed behaviour of parent kestrels into DEE, and showed that brood size manipulation caused differences in parental hunting activity, and thus in their DEE. The TEB-method does not take into account that birds may compensate energetically for intensive foraging (Masman *et al*. 1988a), *e.g*., by hypothermia.

Direct measurements of parental energy expenditure in relation to brood size manipulation, for example using stable isotopes, are scarce. Bryant & Westerterp (1983b) reported for House Martins (*Delichon urba*) that parental DEE remained unchanged in response to brood size enlargement. In this experiment parental feeding rates of the enlarged brood were insufficient to sustain it (Bryant & Westerterp 1983b). Moreno (1989) was also unable to show changes in the DEE of parents of experimental broods of Wheatears (*Oenanthe oenanthe*), but sample sizes were small (Reduced: n=2, Enlarged: n=4). Williams (1987) reported for parent Savannah Sparrows (*Passerculus sandwichensis*) a linear increase of DEE, corrected for body mass, with experimental brood size. So far, only the work on the Savannah Sparrow (Williams 1987) and the European Kestrel (Dijkstra *et al*. 1990) satisfy the prerequisite of adjustment of parental effort to the current brood size.

Our present aim was to measure DEE of parent kestrels directly, by means of the doubly labelled water (DLW) technique, in relation to experimental brood size. Drent & Daan (1980) postulated that brood size is adjusted to the optimum working capacity of the parent. Thus, we

will test the hypothesis that brood size manipulation affects parental DEE independently of a relationship between original brood size and DEE.

To close the circle of reasoning, we need to take a final step, and show a direct association between DEE and fitness. In the kestrel, local survival in the year following the experiment has been identified previously as the factor of parental fitness that is affected by brood size manipulation experiments (Dijkstra *et al*. 1990). The probability of recovery (about 15%) is usually too low to allow calculation of global survival rates. Estimation of local survival carries the restriction that observed variation in survival may be an effect of variation in dispersal from the study area. However, Daan *et al*. (Chapter 2) estimated global survival rates based on birds found dead, and concluded that differential dispersion accounted for the lower local survival rates of female parents, but emigration did not explain the effects of the experiment on survival rate. Thus, in addition to the hypothesis that manipulation of brood size affects DEE, we will also test the hypothesis of a negative relation between DEE and local survival rates.

METHODS

The data presented here were collected in the Lauwersmeer area (The Netherlands, 53° 20' N, 6° 12' E). The study area comprises extensively managed (by grazing) lowland surrounding the lake, sometimes inundated in winter, a grassland area with newly planted patches of trees (0 to 15 years), used for military manoeuvres, and arable fields.

In this area, a breeding population of the European Kestrel (*Falco tinnunculus*) has been the subject of study since 1976 (Masman 1986; Dijkstra 1988; Meijer 1988). Kestrels breed here almost exclusively in artificial nest boxes mounted on poles. In 1992 about 40 nest boxes were present in the area, of which 33 were occupied by breeding kestrel pairs. In the standard population survey in the reproductive season, we determined for each pair laying date of the first egg, clutch size, hatching date, and the number of hatched chicks by inspecting the nest boxes regularly. Parent birds were identified upon capture from numbered leg rings, or in the field from wing tags. Individual birds were caught using a net or a radio-controlled trap door placed at the nest box entrance, or a *bal-chatri* in the field (Cavé 1968).

Manipulation of brood size
In the Lauwersmeer area, clutch size ranges from 3 to 7 and decreases with laying date (Dijkstra *et al*. 1982; Dijkstra 1988). Nests of similar dates were randomly assigned to one of the categories Reduced, Control, or Enlarged, thereby anticipating a possible effect of date on parental effort (see Dijkstra *et al*. 1990). Manipulation of brood size was carried out about 7 days (range 5 to 10) after the chicks hatched to avoid potentially biased mortality, which is fairly common at those small ages. Two or three nestlings were transferred to create reduced and enlarged broods of similar age. Control broods were left without manipulation.

Measurement of parental daily energy expenditure
Field estimates of the energy expenditure of kestrels raising a brood were obtained with the Doubly Labelled Water (DLW) technique (Lifson and McClintock 1966; Nagy 1980). Validation of this technique and means of application for the kestrel have been described by Masman *et al*. (1988a). The measurements were taken between day 10 and 22 of the nestling period, on average 7 days (minimum 4 d, maximum 11 d) after the manipulation of brood size.

Captured adults were identified and/or marked, and weighed to the nearest gram with a Pesola spring balance. The birds were injected intra-peritoneally with a mixture of $H_2^{18}O$ (90.4 atom %) and ^2H_2O (99.8 atom %). To take sexual size dimorphism into account, males were injected with 0.45 ml and females with 0.50 ml. 'Initial' blood samples were taken after 2.0 h (sd=0.6 h, n=33). During the interval between injection and blood sampling, kestrels were maintained at rest in a dark box to allow complete equilibration of the injected isotopes with body water. The birds were then released close to the nest box after reweighing. They were recaptured after approximately 24 h or 48 h. Upon recapture, body mass and 'final' blood samples were taken. All blood samples were obtained by puncturing the posterial tibial vein or the brachial vein. Blood was collected in 4 to 12 glass microcapillaries of 10 µl each, which were subsequently flame-sealed.

The isotopic enrichments of blood samples were determined at the Centre of Isotope Research, University of Groningen, by means of mass spectrometry. Natural isotopic abundance (background) in body water, determined from blood samples of five kestrels before injection, was $0.200 \pm 1.04 \cdot 10^{-4}$ atom %^{18} O and $0.0153 \pm 0.823 \cdot 10^{-4}$ atom % ^{2} H. The percentage body water of total body mass was estimated from the isotope enrichment of the initial blood samples (Schoeller *et al.* 1980). In eight cases, the percentage body water could not be estimated accurately, owing to spilling of some water while injecting the bird. Because the value of percentage body water greatly affects the DEE estimate, we excluded these eight cases from further calculations and analyses. Carbon dioxide production was calculated with the equations of Lifson and McClintock (1966). DEE was then calculated using an RQ of 0.72, and an energetic equivalent of respired CO_2 of 27.3 kJ per litre, based on nutrient catabolism of 80% protein (Gessaman & Nagy 1988). The actual diet of kestrels in summer contains 76% of dry mass protein (Masman *et al.* 1986). If the birds were in nitrogen balance, catabolism of protein would have been overestimated slightly. However, parent kestrels loose weight during the period of nestling care (see Results; Masman *et al.* 1989a; Dijkstra *et al.* 1990), resulting in a negative N balance. This would mean that more protein was catabolized than was available from the diet.

Meteorological data

Mean daily wind speed and minimum, maximum, and average temperatures were obtained from the KNMI monthly weather reports for Groningen Airport Eelde, about 50 km inland from the study area.

Data analysis

Differences between the manipulation categories (Reduced, Control, and Enlarged) were tested with one-way ANOVA. We investigated the reaction to experimental manipulation using linear regression of the response variables on the number of young manipulated. In the case of multiple covariates we used stepwise multiple regression and the backward elimination method of variable selection. All tests were two-tailed; significance was accepted at $P<.05$. The statistical package used for the analyses was SX (version 4.0, NH Analytical Software Co. 1992).

RESULTS

Reproductive output

Brood size at fledging of the experimental broods increased with manipulation. This was not due to initial differences between the experimental groups, because clutch size, laying date, and original brood size did not differ significantly between the Control, Reduced, and Enlarged broods (Table 1). Also, nestling mortality after manipulation occurred almost equally in all experimental groups (Table 1, ANOVA on arcsine-transformed values of % nestling survival): in one control nest and in one enlarged nest, one nestling died between manipulation and measurement of parental DEE. Thus, we conclude that we successfully manipulated the current reproductive output of the experimental kestrel pairs.

Parental Daily Energy Expenditure (DEE)

We succeeded in capturing, injecting, and recapturing 33 parents from 23 different nests. We restricted the analysis to 25 cases for which reliable estimates of DEE could be obtained (see Methods).

Among the 25 individuals (9 males, 16 females) were eight pairs of which both male and female were successfully sampled. Theoretically, the DEE of partners were not independent measures, as the parents were provisioning the same brood, and might have adjusted their activity to that of their partner. After controlling for experimental manipulation of brood size, there was no significant within-pair correlation between residual DEE of paired individuals (partial correlation: $r^2=0.06$, n=8, ns). In all subsequent analyses, we therefore assumed independence of DEE of partners.

An initial comparison of means showed a significant difference between average DEE of the three experimental groups ($F_{2,22}=3.77$, P<.05). A post-hoc comparison (Tukey HSD) identified two groups: DEE of parents of enlarged broods was higher than DEE of parents of both control and reduced broods. A closer analysis was carried out to identify the relative importance of various factors affecting DEE.

Correlates of DEE

Environmental factors Factors affecting DEE other than parental time budgets, such as environmental conditions, have been suggested to be of greater importance than brood size (solar radiation: Williams 1987; ambient temperature: Weathers *et al.* 1984; Buttemer *et al.* 1986; Moreno 1989, Weathers & Sullivan 1989; temperature and wind: Bryant & Westerterp 1983a; rain and/or wind: Tatner 1990), and should therefore be examined (Nagy 1989). During the period of the DEE measurements, there was virtually no rain. We tested two other potentially important factors: ambient temperature, which affects thermoregulatory costs (Masman *et al.* 1988a), and windspeed, which affects the

Table 1. Descriptives of the experimental broods. Means ± standard deviation, and tes t results of analysis of variance are given.

	Experimental groups			F	P
	Reduced	Control	Enlarged		
Sample size	6	5	7		
Clutch size	5.0±0.6	4.6±0.5	5.1±0.7	1.10	ns
Laying date (day of year)	121.3±7.8	126.2±15.9	122.3±8.5	0.31	ns
Brood size:					
original	4.7±0.5	4.6±0.5	4.7±0.8	0.05	ns
experimental	2.0±0.0	4.6±0.5	7.3±1.0	102.4	<.01
at fledging	1.8±0.4	4.4±0.9	6.7±1.1	50.4	<.01
Nestling survival (%)	91.7±0.2	95.0±0.1	92.3±0.1	0.17	ns
Mass at fledging (g)	247.0±15.0	238±11.2	237.2±14.7	0.89	ns
At DEE-measurement:					
brood size	2.0±0.0	4.4±0.9	7.1±0.9	80.0	<.01
age of young (d)	15.8±2.0	15.8±3.6	17.1±1.1	0.72	ns
parental mass: males	194.4±7.7 (n=4)	190.0±21.2 (2)	195.2±1.6 (3)	0.17	ns
females	242.8±8.6 (5)	244.3±16.5 (5)	228.5±12.8 (6)	2.53	ns
parental DEE: males	383.6±80.9 (4)	415.9±3.5 (2)	453.9±85.2 (3)	0.74	ns
females	355.1±42.7 (5)	433.5±78.9 (5)	447.2±70.0 (6)	2.96	=.09

cost of flight hunting (Masman & Klaassen 1987).

Thermoregulatory costs comprise roughly 10% of the kestrel's energy budget during the nestling phase (Masman *et al.* 1988a). In the warm summer of 1992, mean maximum temperatures (1 June to 9 July: 22.8 ± 3.7°C) were generally above the kestrel's lower critical temperature of 17°C, but mean minimum temperatures (11.0 ± 2.5°C) were not. Extra

overnight (8 h) thermoregulatory costs would amount to an increase of $8.6 \cdot 6 \cdot 0.3$ kJ·d^{-1}, roughly 4% of DEE of controls, based on a temperature coefficient of 0.10 W°C^{-1} ($= 8.6$ kJ·d^{-1}°C^{-1}) below the critical temperature of about 17°C

Table 2. Variables, other than brood size, explaining variation in parental DEE (kJ·d^{-1}) in a multiple linear regression model. The variables were tested starting from an initial model that also included all 2-way interactions between the variables. Variables that did not contribute significantly are listed separately.

	(increase in) deviance	(increase in) df	P	coefficient	se
null model	125200	24			
final model	86268	21	<.05		
constant		1		980.2	298.7
gender of parent (♂=1, ♀=2)		1	=.02	-447.2	187.1
age of brood (days)		1	=.07	-35.1	18.5
interaction gender·age	26832	1	=.02	29.5	11.5
rejected terms:					
temperature (°C)	11460	1	=.10		
wind speed (m·s^{-1})	4553	1	>.10		
nestling mortality (arcs%)	1463	1	>.10		
parental body mass (g)	13698	1	=.07		

(Dietz *et al.* 1992). In our data, no significant relationship was found between DEE and ambient temperature (Table 2).

We were also unable to show an effect of wind speed on DEE. The average wind speed on DEE measurement days was 3.7 ± 1.1 ms^{-1}. This is in the range where aerodynamic models predict a steep increase in flight costs (2.5-6 W, Masman & Klaassen 1987). Wind speed in June and July is generally 1 ms^{-1} higher in the coastal regions, where our study area is located, than at the site where the meteorological data were obtained (Wieringa & Rijkoort 1983). Thus, the actual wind speed may have been in the range where flight costs are minimal (2-4 W).

Nestling mortality Nestling mortality occurring before the assessment of DEE might have affected parental DEE either because there was one less young to feed, or as a consequence of inadequate feeding rates by the parents. In either case, we may expect a lower DEE for parents of broods in which nestling mortality had occurred. DEE of these parents was within the range

of parental DEE of the experimental group they belonged to (Control group: 437.9 *versus* 426.9 (sd=71.7) kJ·d^{-1}, n=6, Enlarged group: 419.7 *versus* 453.1 (sd=73.8) kJ·d^{-1}, n=8).
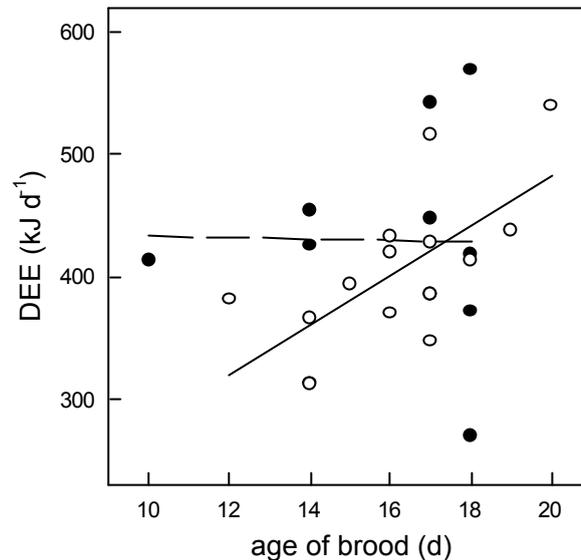

Figure 1. Daily energy expenditure of individual male (filled circles) and female (open circles) parents as a function of age of the brood. The lines indicate linear regressions of DEE o n nestling age: DEE(males) = 403.3 - 3.1 age, r^2=0.01, n=9, ns; DEE(females) = 93.2 + 17.3 age, r^2=0.40, n=16, P<.01.

Division of parental care Dijkstra *et al.* (1990) reported on time budgets of male and female kestrel parents of manipulated broods. They showed that males usually spent more time hunting, which is energetically expensive (Masman & Klaassen 1987). Other behaviours may also differ between male and female parents. Therefore, we accounted for these presumed differences by adding gender as an additional factor in all analyses of parental DEE.

In the Kestrel, the male provisions both the female from courtship until well into the nestling phase and, later on, the brood. In the course of the nestling phase, the female increasingly assumes a greater share of parental care (Masman *et al.* 1988b; Village 1990). This share may depend on demand by nestlings, which may change with nestling age.

We measured DEE over a range of nestling ages (10 to 20 days). The change in behaviour of the female parent during the nestling phase, as observed by Masman *et al.* (1988b) and Village (1990), was reflected in the steep increase (18.7 kJ·d^{-1} per day) in female DEE with nestling age (Figure 1, Table 2). For males, there was no increase in DEE with age of the brood.

Parental body mass Although in female kestrels weight loss during the nestling phase is normal (Masman *et al.* 1989a; Dijkstra *et al.* 1990), in this study we could not show a significant negative relation between female body mass and age of the brood. However, after controlling

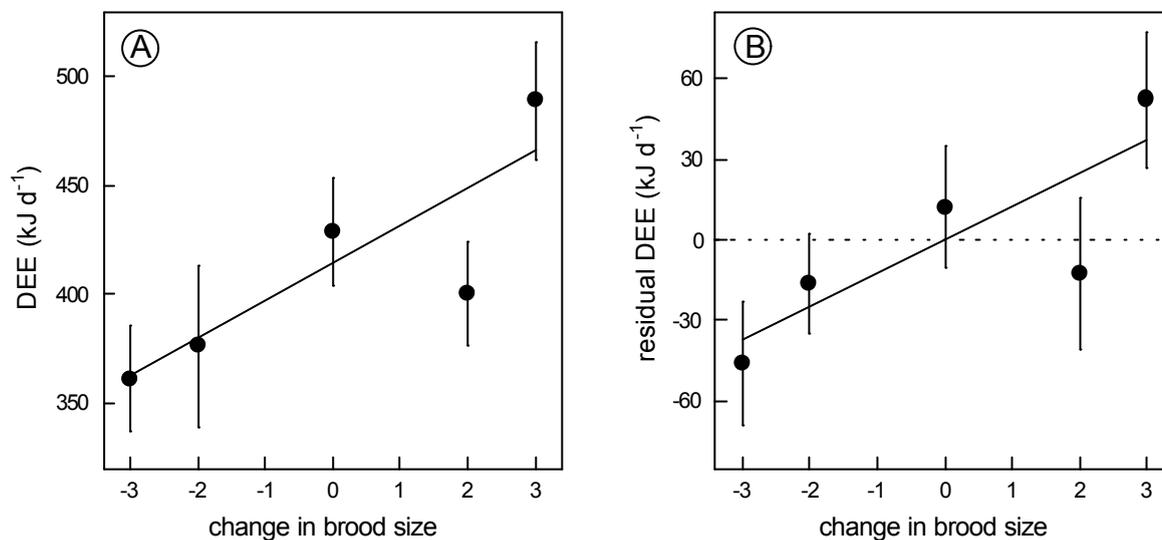for age of the brood, the negative effect of experimental manipulation

Figure 2. Average DEE (kJ·d^{-1}, ± s.e.) of parents of experimental broods as a function of brood size manipulation. A. Observed values of DEE. The line indicates the linear regression o f residual DEE on the number of young manipulated (m): DEE = 414.2 + 17.3 m, r^2=0.29, n=25, P<.01. B. Residuals of DEE, originating from a multiple regression model including sex of the parent and age of the brood (Table 2). Linear regression: residual DEE = 0.0 + 12.3 m, r^2=0.21, n=25, P=.02.

on body mass of females was significant (partial correlation: r^2=0.30, n=16, P<.05). Male body mass did not vary among the experimental groups (Table 1), but male mass decreased with age of the brood (partial correlation r^2=0.49, n=9, P<.05).

Generally, DEE is positively correlated with body mass, although the slope of the regression may differ considerably among species (Bryant & Tatner 1991, Tinbergen & Dietz 1994). We found a non-significant negative association between DEE and body mass (Table 2).

All variables potentially affecting parental DEE, except for manipulation, were tested in a multiple linear regression model. In the final model (r^2=0.31, n=25, P<.05) the variables gender, age of the brood, and the interaction of age with gender contributed significantly to the explained variation in DEE (Table 2). We used the residuals of DEE of this final model to analyze the effects of initial brood size and change in brood size (manipulation) on DEE.

Experimental manipulation of brood size DEE was positively associated with the number of nestlings added to the brood (r^2=0.29, n=25, P<.01; Figure 2A). To account for other factors that were previously shown to affect DEE (Table 2), we analyzed the effects of change in brood size on residual DEE. We tested the hypothesis that DEE is adjusted to the new, experimental brood size against the hypothesis that DEE is only determined by the original brood size. However, variation in original brood size was

Table 3. Multiple linear regression model with (residual) parental DEE (kJ·d^{-1}) as the dependent variable, and brood size, manipulation of brood size, and laying date as explanatory variables (see also Figure 2B). The variables were tested, starting from an initial model including all first order interactions between the variables. Variables that did not contribute significantly are listed separately.

	(increase in) deviance	(increase in) df	P	coefficient	se
null model	86268	24			
final model	67789	23	=.02		
constant		1		0.00	10.9
manipulation (m)	18479	1	=.02	12.31	187.1
rejected terms:					
original brood size (b)	55	1	>.10		
laying date of first egg (ld)	79	1	>.10		

small (brood size 4, n=12; brood size 5, n=12; brood size 6, n=1). Brood size or, more specifically, clutch size is determined by laying date of the first egg (Meijer *et al.* 1990). Therefore, we added laying date to the model. Laying dates of the experimental pairs ranged from day 107 to day 146 (see Table 1).

We started from a complete multiple regression model of residual DEE on original brood size (b, b^2), manipulation of brood size (m, m^2), laying date (day of the year: ld, ld^2), and all first order interactions ($b \cdot m$, $b \cdot ld$, $m \cdot ld$). The model was simplified subsequently, using a stepwise, backward procedure to eliminate non-significant variables. In the final model, only the linear term of manipulation contributed significantly to explain the observed variation in (residual) parental DEE (Table 3, Figure 2B). Hence, in our experiment, parental DEE of kestrels varied with brood size only as a result of experimental manipulation of brood size.

DEE and local survival
Of the breeding population in 1993, 91% of the parents were identified. All birds that were not identified (n=6) were males. Dijkstra *et al.* (1990) reported differences between sexes, and also between experimental categories, in return rate to the breeding area, that is, local survival. Daan *et al.* (Chapter 2) confirmed these findings, and found comparable results for survival estimates based on birds recovered dead, that is, global survival. In our small sample of experimental parents, local survival (% of birds recaptured in 1993) was 67% (6/9) for males, and 31% (5/16) for females (Fisher exact test, one-tailed, P=.02). Local adult survival in the experimental groups was 67%, 43%, and 22% for the Reduced, Control, and Enlarged group, respectively (Logistic regression on manipulation: χ^2=3.74, df 2, ns). Local survival of the Reduced and the Control groups were within the range of global survival estimates given by Daan *et al.* (Chapter 2), which comprised data from six years of experiments. Our estimate for the
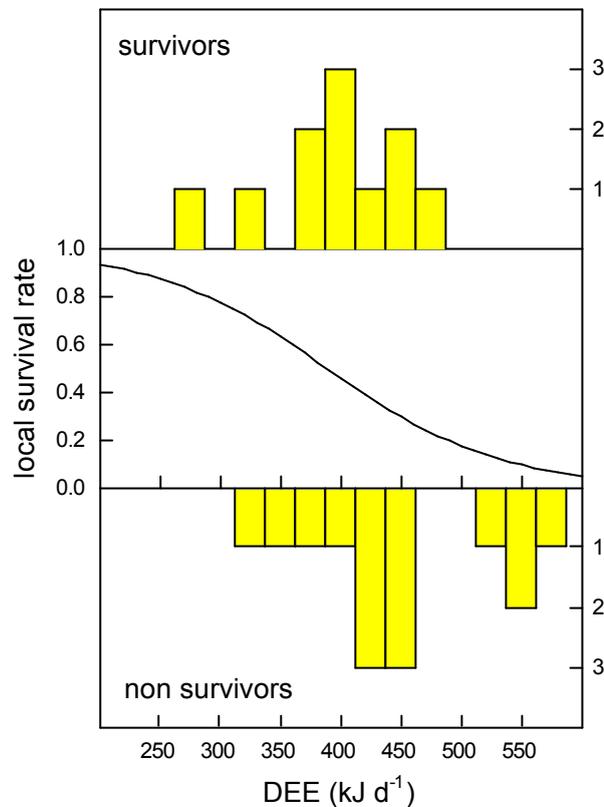
Figure 3. Local survival rate as a function of parental DEE. The upper and lower panels show a frequency distribution of DEE of experimental birds that were recaptured in the study area during the next breeding season (upper panel), and of birds that were not recaptured (lower panel). The middle panel depicts the curve as estimated by the logistic regression of parental local survival rate (S) on DEE $\ln(S/(1-S)) = 5.42 - 0.014$ DEE.

Enlarged group seemed rather low, but this might be a result of either a relatively large proportion of females in the sample, or a small sample size.

We related local survival rates to DEE in a logistic regression model. In the model, we accounted for sex differences in local survival. Addition of DEE to the model improved the fit of the model significantly (χ^2=5.66, df 1, P=.02) when compared to an intermediate model with only sex as an explanatory variable (Figure 3). Thus, DEE affects local parental survival directly.

DISCUSSION

Assessment of parental daily energy expenditure (DEE) has been the topic of many studies since Drent & Daan (1980) suggested DEE as a currency to generalise the problem of optimal parental work rates. In combination with experimental manipulation of brood size, parental

work rates, in particular deviations relative to a control situation, can be used to test DEE as the causal factor that gives rise to the trade-off between current reproduction and parental survival in altricial birds.

Brood size manipulations have been applied widely, and often parents are able to raise a larger brood than their original brood size (review in: Stearns 1992). This suggests that parents generally operate energetically on a submaximal level within one breeding season. We have shown here that parents change their work rate during the nestling phase in response to manipulation of brood size, with an estimated mean increase or decrease of 12.3 kJ·d^{-1} (= 2.9% of mean DEE of parents of control broods) per young. The DEE estimates for male parents based on the time-energy budget (TEB) method (Dijkstra et al. 1990) yielded a change in DEE of 21 kJ·d^{-1} per young (calculated from the difference in average DEE between males of enlarged and reduced broods, divided by the mean difference in experimental brood size). However, the absolute values of DEE for males in our study using the DLW method were within the range of the DEE values obtained with the TEB method by Dijkstra et al. (1990).

The extra young raised constitute the benefit of the increased parental effort. The relation between DEE and experimental change in brood size was approximately linear (Figure 2; Williams 1987; Dijkstra et al. 1990). This does not mean that the relation between DEE and fitness of the current brood is linear. Tinbergen & Boerlijst (1990) documented a diminished fitness return from enlarged broods in Great Tits (*Parus major*) as a result of a decreased survival rate, accompanied by reduced nestling body mass.

The assessment of a fitness cost or investment related to DEE may provide a functional explanation for apparent submaximal parental work rates. In European Kestrels, manipulation of brood size affects parental fitness through a change in survival rate during the following winter (local survival: Dijkstra et al. 1990; local and global survival: Daan et al. Chapter 2). In the present study, in addition to the demonstrated relation between change in brood size and DEE, we have established a direct association of individual work rate and local survival rate.

A causal explanation for apparent submaximal parental work rates requires a quantitative approach to the relation between DEE and a fitness component. The DLW technique is appropriate for estimating DEE as it provides an overall measure, including potential side effects (Masman et al. 1988a). Time-energy budgets are less suitable for estimating DEE because they do not account for potential physiological adjustments to increased rates of activity.

Over the last 10-15 years, there has been frequent use of the doubly labelled water (DLW) technique to estimate DEE in birds (see reviews in: Masman et al. 1989a; Tinbergen & Dietz 1994), but mainly in non-experimental situations. Most of these studies focused on assessing limits to parental DEE, expressed as metabolic level, that is, the ratio of DEE to BMR. Little attention has been given to the observed inter- or intraspecific variation in parental work rates, and to possible costs associated with it. To gain insight into the mechanism of why excess parental energy expenditure entails a cost, we need to understand constraints operating on parental energy expenditure.

Current theories on factors constraining energy expenditure are founded on the observation that metabolic processes are scaled with body mass. These theories involve the concept of a limitation as a result of the animal's physical design. The first is the maximum rate of energy assimilation, DME_{max} (Kirkwood 1983), determined by gut

Table 4. Average DEE of experimental groups, expressed as a fraction of DME_{max} (Kirkwood 1983), or as a multiple of BMR. We used the equation given by Masman *et al.* (1989a) to estimate BMR. DME_{max} and BMR were estimated individually, based on body mass during the DEE-measurements.

	Experimental groups			
	Reduced	Control	Enlarged	
Males:				
DME_{max} ($kJ·d^{-1}$)	526.7	517.8	528.3	
DEE / DME_{max}	0.73	0.81	0.86	(max=1)
Females:				
DME_{max} ($kJ·d^{-1}$)	618.2	620.7	591.6	
DEE / DME_{max}	0.57	0.70	0.76	(max=1)
Males:				
BMR ($kJ·d^{-1}$)	95.5	93.3	95.9	
DEE / BMR	4.0	4.5	4.7	(max=3-7)
Females:				
BMR ($kJ·d^{-1}$)	105.9	106.5	99.6	
DEE / BMR	3.4	4.1	4.5	(max=3-7)

capacity. The second is the maximum sustainable energy expenditure, the metabolic level or metabolic scope, a fixed ratio of DEE to BMR (range 3-7: Drent & Daan 1980; Daan *et al.* 1990b; Peterson *et al.* 1990; Bryant & Tatner 1991; Weiner 1992), while BMR is determined by the size of the metabolic machinery (Daan *et al.* 1989). In Table 4, we present for each experimental category the DEE estimates as a fraction of Kirkwood's DME_{max} and as the ratio DEE over BMR.

DME$_{max}$ has been suggested to represent an absolute limit. If we assume that the birds are balanced energetically, that is, undergo no change in body mass or body composition, and therefore intake of energy equals energy expenditure, then DME_{max} determines the upper limit of the balance. With respect to energy expenditure, maximum metabolic level is strongly affected by the time scale that we apply (Peterson *et al.* 1990). Both ratios (Table 4) suggest that the adults were not limited energetically, because even parents of enlarged broods obviously did not work at their supposed maximum capacity.

Parent birds increase their DEE in response to enlarged brood size, but, in doing so,

reduce their subsequent probability of survival. Reduction of brood size leads to reduction in DEE, which in turn enhances parental survival rates. This series of observations implies that even during normal breeding, which is the phase of the year of maximum DEE (Masman *et al.* 1988a), kestrels face a cost of reproduction. Thus, parental work rates of kestrels are apparently optimized, because they need to balance fitness benefits of high work rates (= number of young raised) against fitness costs associated with these work rates (= reduced chance of survival).

We propose a proximate control mechanism that may define optimal work rate. High work rates may entail physiological weakening ('exhaustion', Cavé 1968), as a result of economizing on other physiological processes according to the 'principle of allocation' (Koehn & Bayne 1986). For example, Apanius *et al.* (1994; Chapter 7) have found evidence for impaired immunocompetence in response to artificial variation in brood size. Resistance in general, cell or tissue repair processes, and/or removal of waste metabolites may suffer as a result of an increased allocation of energy to reproduction (Calow 1979).

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