ECOLOGICAL ENERGETICS OF THE KESTREL: DAILY ENERGY EXPENDITURE THROUGHOUT THE YEAR BASED ON TIME-ENERGY BUDGET, FOOD INTAKE AND DOUBLY LABELED WATER METHODS

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CONTENTS

1. Introduction .................................. 64
2. The annual cycle ............................. 65
3. DEE estimation from time budgets, E_t .......... 67
  3.1. Basal component of energy expenditure .... 68
  3.2. Cost of thermoregulation .................. 68
  3.3. Cost of activity .......................... 70
  3.4. Heat increment of feeding ................. 71
  3.5. Tissue synthesis: body mass, eggs and feathers .... 71
  3.6. Energy allocation in the seasonal cycle ...... 71
4. DEE estimation from food intake, E_m .......... 73
  4.1. Intake adjusted for retained energy ......... 73
  4.2. Energy expenditure through the seasonal cycle ... 74
5. DEE estimated from Doubly Labeled Water turnover, E_d ......... 75
  5.1. Field protocol and calculations ............. 75
  5.2. DLW as a standard for other estimates ....... 76
6. Discussion ................................... 77
  6.1. Three independent methods compared ...... 77
  6.2. Exploring annual cycles in energetics: a first glimpse .... 77
7. Acknowledgements ................................ 79
8. Summary ...................................... 79
9. References .................................... 79
10. Samenvatting: .................................. 80

1. INTRODUCTION

In a seasonal environment the timing of avian reproductive cycles will be adapted to cycles in resource availability. A primary general resource is energy. For evaluating consequences of reproductive timing for reproductive success the exploration of annual variations in energy availability and demand is therefore an important step (Murton & Westwood 1977). The daily balance of energy intake and energy expenditure of individual birds may serve as a link between behavioural decisions and fitness. On the one hand, behavioural actions influence the energy balance, on the other hand a surplus or deficit on this balance will have repercussions for the prospects of survival and hence for fitness.

This view has been the backbone of a long-term year-round study on the European Kestrel Falco tinnunculus (Rijnsdorp et al. 1981, Daan & Aschoff, 1982, Dijkstra et al. 1982, Masman 1986). In this project we have established the annual variation in availability and intake of energy in detail elsewhere (Masman et al. 1986, 1988). In the present paper the annual variation in daily energy expenditure (DEE) is quantified with special emphasis on the comparison of different methods of estimation.

For the estimation of the rate of energy turnover of free-living animals, three methods are currently available: 1) time budget analysis combined with metabolic rates estimated for each component in the behavioural repertoire, (2) measurement of daily food intake rates and assimilation quotient and (3) measurement of CO2 production by the doubly labeled water method (Lifson & McClintock 1966). Methods 1 and 2 involve combinations of field observations with laboratory trials, and the major problem inherent with these methods is the necessity of assuming that quantitative relationships established in the laboratory apply also to field conditions. Methods 2 and 3 yield overall estimates but no insight in the contributions of different behaviours to the total energy expenditure. Time-energy budget (TEB) analysis thereby has merits beyond the determination of daily energy expenditure (DEE). The identification of components in the energy budget would allow us to analyse the energetic consequences of alternative behavioural options open to individuals of a species and to evaluate shifts in energy allocation over the annual cycle.

Time-energy budget analysis has thus become a major instrument in behavioural ecology (reviews by King 1974, Kendeigh et al. 1977, Walsberg 1983). It is in the validation of its basic assumptions, as an overall check on the approach, where the doubly-labeled water (DLW) method renders its primary service (Weathers & Nagy 1980, Ardea 76 (1988): 64-81
Weathers et al. 1984, Williams & Nagy 1984). Another independent check is potentially available in the meticulous recording of energy intake (DME) in the field, which appeared to be possible in some species (Koplin et al. 1980, Sapsford & Mendelshon 1984), although corrections for energetic waste (faeces, urine, pellets) and tissue deposited are necessary.

In our approach to the daily and seasonal organization of behaviour of the Kestrel, we have attempted to estimate the daily energy expenditure combining all three methods. Some of the basic data for the analyses have been reported in previous papers (Masman & Klaassen 1987, Masman et al. 1988). It is the purpose of this paper to integrate these data into estimations of average DEE for each sex and each phase of the annual cycle as well as to present estimations of DEE derived from DME and DLW measurements, as a check on the TEB method.

In constructing the TEB-estimates we cannot rely on simplified general cost factors but must take characteristics of the thermal environment into account (Weathers et al. 1984). In order to do this we used meteorological recordings of wind, temperature and radiation, and established correction factors for sheltered and open sitting positions. We further made use of empirically established relationships between these environmental factors and the power consumption of a heated taxidermic mount (Bakken et al. 1981). The relationship between power consumption of this mount and thermostatic energy requirements of real Kestrels was assessed by indirect calorimetry in a windtunnel at 1 m/sec wind velocity. This approach entails some rough approximations, but is an obvious improvement on the use of ambient temperature only.

For the comparison of methods, we pooled data from different years and different individuals. The data from two independent methods turn out to be in reasonable agreement with our TEB estimates.

We used our TEB data set to make a reliable description of the annual pattern of daily energy expenditure in the Kestrel, and its partitioning in different components, for male and female separately. The quantification of this annual pattern makes it possible to illuminate some aspects of the evolution of the life history of the Kestrel as it shows a strong task differentiation between the dimorphic sexes.

2. THE ANNUAL CYCLE

The abiotic and biotic environmental variables in the Lauwersmeer study area in the Netherlands (53° 21' N, 6° 12' E) reveal characteristic seasonal fluctuations. Summers with long, warm days and high food availability alternate with winters with short, cold days where food is hard to come by (Fig. 1). Daylength, windspeed, rain, radiation, ambient temperature and prey density all have repercussions for the daily energy expenditure of

![Fig. 1. Seasonal variation in environmental variables. A. Daylength measured from dawn to dusk civil twilights (sun 6° below horizon; 53° 20' N). B. Windspeed at 10 m above ground. Average for observation days pooled in 10-day intervals. C. Rain: Average proportion of observations hours with > 2 mm precipitation. D. Daily solar radiation at the weather station of Eelde. E. Temperature: Average daily minima and maxima on Kestrel observation days. F. Mammal index: Mean numbers of voles and shrews caught in 1500 trap-nights in bi-monthly intervals over 1981-1984.]
Kestrels. Prey density is reflected in the *Microtus arvalis* trapping index obtained every two months - with voles increasing throughout the summer (May-September) and decreasing from September till May. However, prey availability to the Kestrel is more properly measured as the hunting yield, i.e. the number of prey obtained per hour of flight-hunting (Masman *et al.* 1988).

During winter the Kestrels in our study area live in territories either singly or as a pair. In spring there is a new influx of migrant Kestrels. Around April definitive pair formation and territorial settling occurs, as illustrated by increased interactions (Fig. 2A). Territorial conflicts arise again in autumn when winter territories are established.

The reproductive period lies in between March and August. Copulations are observed mainly in March and April (Fig. 2B). They become gradu-
ally associated with a prey delivery from male to female (Fig. 2C). From about two weeks before clutch initiation until the nestlings are 10 days of age the food provisioning of the female depends completely on the male. Clutches in our study population are initiated over a period of more than two months and decline in size from 6 eggs for clutches initiated in the beginning of April to 4 for those initiated in the end of May (Cave 1968, Dijkstra et al. 1982). The incubation period lasts 29 days and all eggs in a clutch hatch normally within two days. Young fledge at about 30 days of age and are provisioned with food for an additional period of 5 to 30 days after fledging. Females generally start moulting slightly ahead of males. Some females replace a few flight feathers during incubation. Most of the moult occurs after breeding in both sexes (Fig. 2G).

From behavioural observations we know that the diet of the Kestrels in the Lauwersmeer consists for 97.7% of small mammals (Masman et al. 1988). During winter (September-March) 98.0% of small mammals caught are common voles *Microtus arvalis*, the rest is common shrew *Sorex araneus*. Only few songbirds, mainly *Sturnus vulgaris*, appear on the menu (Fig. 3). In summer common shrews increase in the Kestrels menu and more avian prey, juvenile waders in addition to some songbirds, is caught (Masman et al. 1986).

3. DEE ESTIMATION FROM TIME BUDGETS, $E_t$

We shall use $E$ as a symbol for daily energy expenditure, with subscripts $t$, $m$, $d$ indicating the basis of estimation: Time budget ($t$), Metabolizable energy intake ($m$) or Doubly Labeled Water ($d$).

The reconstruction of $E_t$ was based on averages per month, phase and sex of each of five components:

$$E_t = B + T + A + H + S \text{kJ.day}^{-1}$$  \hspace{1cm} (1)

where $B =$ basal component, a value for energy expenditure under fasting, thermoneutral conditions; $T =$ energy expenditure for thermoregulation; $A =$ energy expenditure for activity; $H =$ heat increment of feeding; $S =$ energy costs of tissue synthesis, including moult, but excluding the energy content $D$ of tissues (fat, eggs, feathers) deposited.

Our reconstruction of $B$, $T$ and $A$ is based on 366 time budgets obtained in focal birds observed essentially from dawn to dusk. These behavioural protocols are the same as those analysed by Masman et al. (1988). They were selected from a larger material of 653 protocols on the basis of two criteria: (1) budget time (from beginning to end of observation) exceeded 75% of the birds ‘active day’ (i.e. time from dawn civil twilight to dusk civil twilight = 0.71 hrs); (2) birds were in sight more than 75% of the budget time. Of these 366 behavioural protocols 278 were used for the estimation of daily energy intake by Masman et al. (1986), again on the basis of reliability criteria. For the estimation of $H$, we have to take food intake and its temporal distribution over the day into account. This analyse is based on the same 278 daily protocols, in which food intake was recorded with sufficient reliability. Finally, S was derived from moult and body mass scores obtained from free living Kestrels across the seasonal cycle.
Table 1. Average body mass and body mass change applied in the calculations of B, T, A, S and D when individual values of observed birds were unavailable.

<table>
<thead>
<tr>
<th>Phase</th>
<th>Month</th>
<th>Body mass W (g)</th>
<th>Body mass change ΔW (g.day⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1, 2</td>
<td></td>
<td>Male</td>
<td>Female</td>
</tr>
<tr>
<td></td>
<td>Nov.</td>
<td>205.4</td>
<td>239.6</td>
</tr>
<tr>
<td></td>
<td>Dec.</td>
<td>210.6</td>
<td>236.3</td>
</tr>
<tr>
<td></td>
<td>Jan.</td>
<td>202.8</td>
<td>244.8</td>
</tr>
<tr>
<td></td>
<td>Feb.</td>
<td>203.8</td>
<td>233.9</td>
</tr>
<tr>
<td></td>
<td>other</td>
<td>193.9</td>
<td>237.1</td>
</tr>
<tr>
<td>3</td>
<td>courtship</td>
<td>206.2</td>
<td>263.0</td>
</tr>
<tr>
<td>4</td>
<td>laying</td>
<td>212.6</td>
<td>305.1</td>
</tr>
<tr>
<td>5</td>
<td>incubation</td>
<td>203.9</td>
<td>275.2</td>
</tr>
<tr>
<td>6</td>
<td>nestlings ≤ 10 d</td>
<td>188.4</td>
<td>266.9</td>
</tr>
<tr>
<td>7</td>
<td>nestlings &gt; 10 d</td>
<td>196.2</td>
<td>235.4</td>
</tr>
<tr>
<td>8</td>
<td>fledglings</td>
<td>186.2</td>
<td>196.7</td>
</tr>
<tr>
<td>9</td>
<td>moult</td>
<td>203.5</td>
<td>228.5</td>
</tr>
</tbody>
</table>

3.1. BASAL COMPONENT OF ENERGY EXPENDITURE

B is the level of energy expenditure of a fasting, postabsorptive non-moulting bird under thermoneutral conditions. We established (Masman 1986) that this level is proportional to body mass W (kg) and different for the two sexes and for their rest and activity phases of the circadian cycle but independent of time of year. Thus:

\[
B = (a \cdot b_a + p \cdot b_p) \cdot 3.6 \text{ kJ.day}^{-1}
\]  

where \( a = \) activity time in hours (= civil daylength - 0.71); \( p = 24 - a \) hours; \( b_a = \) day-time fasting metabolic rate in Watt, and \( b_p = \) night-time fasting metabolic rate in Watt. The metabolic rates \( b_a \) and \( b_p \) are average levels and exceed the minimum level customarily measured as basal metabolic rate (BMR). From indirect calorimetry (Masman 1986), we know that

\[
b_a = 6.050 \text{ W Watt}; \quad b_p = 4.588 \text{ W Watt}
\]  

Body mass (W,kg) was occasionally measured in focal birds observed, within 15 days of the observation day. In all other cases we took the average daytime body mass for the particular sex, month of the year and phase of the annual cycle (Table 1) as a best estimate.

3.2. COSTS OF THERMOREGULATION

T is the extra expenditure above basal levels incurred by fasting birds to overcome heat loss under thermal conditions below the thermoneutral zone. T was derived by summing separate estimates for different behaviour conditions in daytime (\( T_o \)) and at night (\( T_p \)):

\[
T = T_o + T_p = 3.6 \sum_{i=1}^{7} f_i t_i + 3.6 p t_8 \text{ kJ.day}^{-1}
\]  

where \( f_i = \) hours per day in the condition \( i \), derived from the time budget, and \( t_i = \) thermoregulatory expenditure in condition \( i \) in Watts. For conditions \( i = 1 \) (flight hunt) and \( i = 2 \) (flight) \( t_i \) was assumed to be zero, since excess heat production during flight must easily cover heat loss. For the other conditions (\( i = 3 \) soar, \( i = 4 \) perch, \( i = 5 \) ground, \( i = 6 \) shelter, \( i = 7 \) box, \( i = 8 \) night) we estimated \( t_i \) in a three-step approach:

(1) Energy expenditure was measured by indirect calorimetry in two trained Kestrels during postabsorptive rest in a closed windtunnel, exposed to a windspeed of 1 m.sec⁻¹ and at air temperatures ranging from -12 to 32 °C (see Bakken et al. 1981 for the reasons to choose 1 m.sec⁻¹). To the excess energy consumption above the thermoneutral level the equation

\[
t_i = 3.92 - 0.26 t_a \text{ Watt.kg}^{-1}
\]  

(6) \((t_a \text{ in °C}; n = 14, r = 0.88, p < 0.001)\) was fitted by linear regression. In the same windtunnel we placed a heated taxidermic mount of a Kestrel (constructed following instructions by Bakken et al. 1981) and recorded the power (\( t_{mod} \text{ Watt} \)) required to keep the core temperature of this mount at 40°C. The resulting equation was

\[
t_{mod} = 2.56 - 0.062 t_a \text{ Watt}
\]  

(7)

Combining equations (6) and (7), we estimate Kestrel thermoregulatory costs as:

\[
t_i = -6.82 + 4.19 t_{mod} \text{ Watt.kg}^{-1}
\]  

(8) or \( t_i = 0 \) whenever equation (8) yields negative \( t_i \).
The same heated taxidermic mount was placed on a pole on the roof of the field station, and $t_{\text{mod}}$ was continuously recorded for 30 days in summer and autumn of 1985, with simultaneous recording of wind speed ($u$; m.sec$^{-1}$), radiation ($q$; Watt.m$^{-2}$; 305-2800 nm) and air temperature ($t_a$; °C). A wind vane kept the rotating bird model with its head in the wind. The model was removed during rain. Average 10 min values ($n = 1415$) of all four variables were stored on file, and the dependence of model power ($t_{\text{mod}}$) on the three variables was approximated as follows. Since convective cooling rate is theoretically proportional to the square root of wind velocity we subdivided all observations into six classes with width 0.5 $u_0$ s. In each class a function of the form

$$t_{\text{mod}} = k_1 (40 - t_a) + k_2 q \text{ Watt}$$

(9) was fitted by least squares approximation to the observed values of $t_{\text{mod}}$, $t_a$ and $q$. The form of equation (9) was chosen to obtain linear dependence of $t_{\text{mod}}$ on $t_a$ and $q$, and zero power at $t_a = 40$ and $q = 0$. The six wind speed classes and fitted $k_1$ and $k_2$ values are presented in Table 2. For known $u$, $t_a$ and $q$, $t_i$ can be estimated from equations (8) and (9) using the appropriate $k_1$, $k_2$ values from Table 2.

Air temperature $t_{ai}$ (°C), wind velocity $u_i$ (m.sec$^{-1}$) and radiation flux density $q_i$ (Watt.m$^{-2}$) were estimated for the six behavioural conditions ($i = 3$ ...... 8) in the field from meteorological recordings made in a weather station in the study area, simultaneous with the time budget observations. These recordings were reduced to $t_{ad}$ (average daytime air temperature, °C), $t_{an}$ (average night air temperature, °C), $u_i$ (recorded mean wind speed, m.sec$^{-1}$), $q_i$ (average daytime radiation flux density, Watt.m$^{-2}$). We assumed the following relationships between $t_{ai}$, $u_i$, $q_i$ and $t_{ad}$, $t_{an}$, $u_i$, $q_i$ to apply:

$$t_i = t_{ad} \text{ °C for } i = 3 \text{ (soar)}, 4 \text{ (perch)}, 6 \text{ (shelter)},$$

7 (nestbox)

$$t_8 = t_{an} \text{ °C (night)}$$

$$t_s = t_{ad} - 0.4 + 0.0077 \times q_s \text{ °C (on ground)}.$$  

Thus, air temperatures recorded were assumed to be representative of those experienced by Kestrels except when sitting on the ground ($i = 5$), where air temperatures were increased due to radiation as measured by us.

During moult the insulative properties of Kestrel plumage are altered. We therefore have to add a component $T^*$ (kJ.day$^{-1}$), being the extra energy for thermoregulation during moult. This was derived from indirect calorimetry of two birds during and after moult in a windtunnel at 1 m.sec$^{-1}$, at night, postabsorptive, at temperatures ranging from -12 to 32 °C. Thermoregulatory costs were derived by linear regression for the non-moulting condition ($T = 5.66 - 0.26 t_a$ Watt.kg$^{-1}$) and the mouling conditions ($T_r = 8.66 - 0.41 t_a$ Watt.kg$^{-1}$). The difference $T^* = T_r - T$ can be expressed as a

Table 2. Coefficients of air temperature (40 - $t_i$; °C) and radiation flux density ($q_i$; Watt.m$^{-2}$) predicting power of a heated ($t_b = 40$ °C) taxidermic Kestrel mount at six classes of wind-speed. ($t_{\text{mod}} = k_1 (40 - t_a) + k_2 q \text{ Watt}$).

<table>
<thead>
<tr>
<th>Windspeed $u$ (m.sec$^{-1}$)</th>
<th>$k_1$ (W. °C$^{-1}$)</th>
<th>$k_2$ (m$^2$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>&lt; 0.25</td>
<td>0.057</td>
<td>0.00115</td>
</tr>
<tr>
<td>0.25 - 1.00</td>
<td>0.066</td>
<td>0.00145</td>
</tr>
<tr>
<td>1.00 - 2.25</td>
<td>0.087</td>
<td>0.00070</td>
</tr>
<tr>
<td>2.25 - 4.00</td>
<td>0.097</td>
<td>0.00025</td>
</tr>
<tr>
<td>4.00 - 6.25</td>
<td>0.129</td>
<td>0.00022</td>
</tr>
<tr>
<td>&gt; 6.25</td>
<td>0.151</td>
<td>-0.00031</td>
</tr>
</tbody>
</table>
function of $T$:

$$T^* = -0.265 + 0.577 \, T \, \text{Watt.kg}^{-1} \quad (11)$$

Since the intercept is negligible, and theoretically meaningless, we approximated the extra thermoregulatory costs of moult for field conditions by

$$T^* = 0.58 \, T \, \text{Watt.kg}^{-1} \quad (12)$$

### 3.3. COSTS OF ACTIVITY

Total costs of activity are again derived by summing separate estimates:

$$A = 3.6 \sum_{i=1}^{8} a_i \, \text{kJ.day}^{-1} \quad (13)$$

where $a_i =$ activity cost (increment in metabolic rate above the basal component) in behavioural condition i in Watt.

During sitting, Kestrels perform no notable activities which they would not perform during sitting on a perch in the gas analysis chamber. One exception is incubation and brooding behaviour of females sitting on the nest in phases 5 (incubation) and 6 (nestling ≤ 10 days old). Incubation costs have rarely been measured in birds, and empirical measurements differ widely from each other (King 1974, Biebach 1977, 1979, 1981, Gessaman & Findel 1979, Vleck 1981) and from theoretical predictions (Ricklefs 1974, Kendeigh et al. 1977). We therefore preferred to use our own, admittedly scanty, data based on two $D_2^{18}$O turnover measurements in incubating females in an outdoor captive breeding colony. These females were incubating essentially 100% of the time and their $D_2^{18}$O turnover rates pointed to energy expenditures of 13.52 and 13.76 Watt.kg$^{-1}$ respectively (mean 13.64 Watt.kg$^{-1}$). We subtracted from the mean rate the calculated values for $B$ (4.953 Watt.kg$^{-1}$), $H$ (1.92 Watt.kg$^{-1}$, based on 0.17 times (equation 17) the metabolic energy intake of 12.01 Watt.kg$^{-1}$, derived from deuterium dilution), and $T$ (4.09 Watt.kg$^{-1}$ at the average ambient temperature of 16.6 °C). We thus arrived at a tentative value for females in phase 5, 6 of $a_{2,8} = 2.68$ Watt.kg$^{-1}$ (14) which corresponds to an excess above non-incubation expenditure of 23%, in the same order as careful measurements in Starlings (Biebach 1977, 1979, 1981), in Great Tits (Mertens 1977), in Zebrafinches (Vleck 1981) and Canaries (Weathers 1985) have shown.

During perching, energy expenditure may be increased due to the work in keeping balance on tree branches, especially in strong winds. We have no data to quantify these effects, and currently we regretfully neglect such possible energy expenditure. Energy expenditure during flight and flight-hunting was estimated on the basis of $D_2^{18}$O trials combined with continuous observation of injected birds in the field (Masman & Klaassen 1987): 68.50 Watt.kg$^{-1}$. Since we found essentially the same value by a combination of food balance trials and

<table>
<thead>
<tr>
<th>Time budget</th>
<th>Food intake</th>
</tr>
</thead>
<tbody>
<tr>
<td>M – D = $E_m$ diff.</td>
<td>M – D = $E_m$ diff.</td>
</tr>
<tr>
<td>Monthly mean</td>
<td>Monthly mean</td>
</tr>
</tbody>
</table>

### Table 3. Monthly estimates of daily energy expenditure from time budgets ($E_i$) and from food intake (culminating in $E_m$ after correction for D in kJ.day$^{-1}$). (Means ± SE followed by sample size). The column 'diff.' shows the difference ($E_i - E_a$ in kJ.day$^{-1}$) between the estimates. Significant differences (Student-t test; $p < 0.05$) are indicated by an asterisk.
indirect calorimetry in trained birds flying in captivity, we deduced that the costs of directional flight and flight-hunting are similar. Extra costs of flight above the basal component (for $\phi$ in day-time, equation 3) are thus estimated by:

$$a_{1,2} = 68.50 - 6.05 = 62.45 \text{ Watt.kg}^{-1} \quad (15)$$

During moult, both the surface area of the wing and wingspan are reduced and one might expect these changes to have repercussions for the energy expenditure in flight. Unfortunately we were unable to provide an empirical value for flight energy expenditure during moult, since flight behaviour is sharply reduced in this phase of the cycle. Theoretically the effect can be approximated by an equation for power output at the flight speed of minimum power ($P_{\text{min}}$) presented by Greenewalt (1975):

$$P_{\text{min}} = 0.1261 \cdot W^{1.394} \cdot S_w^{0.189} \cdot b_w^{-1.378} \text{ Watt} \quad (16)$$

where $W =$ body mass (gram), $S_w =$ wing surface area (cm$^2$), $b_w =$ wingspan (cm). From morphometric data on wild caught Kestrels, we know that during moult $S_w$ is reduced by approximately 10% and $b_w$ by 2%. If in moult $S_w^* = 0.9 S_w$ and $b_w^* = 0.98 b_w$, then the predicted minimum power output during moult would equal $P_{\text{min}}^* = 1.007 P_{\text{min}}$. This theoretical increase of less than 1% in power output, gives some justification to our present approach to apply the same flight cost figure $a_1 = a_2 = 62.45 \text{ Watt.kg}^{-1}$ to both the moult and non-moult conditions.

For soaring, again no empirical data are presently available. Theoretical analysis suggests that soaring involves little extra energy expenditure above sitting (Pennycuick 1972). Support for this notion comes from both windtunnel measurements of $O_2$-consumption (Baudinette & Schmidt-Nielsen 1974) and heart rate monitoring in Larus argentatus (Kanwisher et al. 1978). We therefore decided to disregard extra activity costs due to soaring. The small share of soaring in the time budget makes the analysis relatively insensitive to this factor. A in equation (13) is thus primarily determined by the hours of flight-hunting ($f_1$) and flying ($f_2$).

### 3.4. Heat Increment of Feeding

The heat increment of feeding $H$ is a significant although rarely measured component of the energy expenditure. It represents the increment of metabolic rate above the fasting rate as a consequence of food intake and digestion. $H$ depends on the amount of food digested, on the time elapsed since the meal and on the thermoregulatory heat loss which can to some extent be compensated by digestive heat production. These relationships were established for the Kestrel by Masman (1986). We apply these to field estimates based on 278 full day observations of focal birds for which food intake was reliably established (Masman et al. 1986) as follows.

For each meal, taken at time $i$ and of metabolizable energy content $m_i$ (kJ), we calculated $h_i$ (total heat increment of feeding above basal) from:

$$h_i = 0.17 m_i \text{ kJ.meal}^{-1} \quad (17)$$

The heat increment of feeding declines linear over 20 h following a meal. The parts of $h_i$ representing heat loss during the day ($h_d$) and night ($h_n$) can be calculated by integration over the episodes of $h_i$ occurring during active day and night respectively. Summation of nocturnal and diurnal heat increments over all meals of a day gives:

$$H_d = \Sigma h_d \text{ and } H_n = \Sigma h_n \text{ kJ.day}^{-1} \quad (18)$$

From these values the parts $H_d^*$ and $H_n^*$ which could compensate for thermoregulatory heat loss should be subtracted. Although this is imprecisely known, we have based the following procedure on the data presented by Masman (1986):

$$H_d^* = 0.5 \tau_d H_d \text{ and } H_n^* = 0.5 \tau_n H_n \text{ kJ.day}^{-1} \quad (19)$$

where $\tau_d =$ minimum of $[1, T_d/t_9]$ and $\tau_n =$ minimum of $[1, T_n/t_9]$, where $t_9$ is thermoregulation costs (kJ.h$^{-1}$) at 9°C, derived from the costs of 6.66 kJ.h$^{-1}$.kg$^{-1}$, measured in indirect calorimetry. $T_d$ is total thermoregulation in day-time, and $T_n$ is total thermoregulation at night. This insures that $H_d^*$ and $H_n^*$ are 0 when thermoregulatory expenditure rises above the value corresponding with $t_9$, i.e. the extra metabolism at 9°C in indirect calorimetry.

We arrive then at an estimate of the total heat lost due to feeding and digestion in daytime and at night by:

$$H = H_d - H_d^* + H_n - H_n^* \text{ kJ.day}^{-1} \quad (20)$$

$H$ was again averaged per season, month and sex.

### 3.5. Tissue Synthesis: Body Mass, Eggs and Feathers

For the estimation of the energy expenditure involved in the synthesis of body tissues, we have
to rely in part on generalizations from the literature, augmented with our own Kestrel data on the energetic equivalents of mass change ($\Delta W$) and moult. We separated tissue synthesis (exclusive of the energy retained in the tissue ($D$), see section 4.1) in three categories: general mass change ($S_w$), egg development ($S_e$) and feather synthesis during moult ($S_r$):

$$S = S_w + S_e + S_r \text{ kJ.day}^{-1} \quad (21)$$

General mass change of individuals ($\Delta W \text{ g.day}^{-1}$) was based on the monthly changes in average body mass of male and female wild caught Kestrels during the winter (October-March) and on phase-specific changes in average body mass during summer. Body mass change was calculated exclusive of the eggs formed during the last two weeks of courtship (phase 3) and during laying (phase 4). The $\Delta W$-data used are presented in table 1. We assumed that the energetic equivalence of mass change equals the equivalence measured in the laboratory, i.e. $19.2 \text{ kJ.g}^{-1}$ (Masman 1986). We have not measured the efficiency of tissue production but assumed a value of 70% (see Ricklefs 1974, Walsberg 1983). Therefore $S_w$ was estimated by:

$$S_w = 0.3 \cdot 19.2 \Delta W \text{ kJ.day}^{-1} \text{ when } \Delta W \geq 0 \text{ and } S_w = 0 \text{ kJ.day}^{-1} \text{ when } \Delta W < 0 \quad (22)$$

Energy expenditure for egg synthesis $S_e$ by females in the last 14 days of phase 3 (courtship) and in phase 4 (laying) was calculated on the basis of literature data. Kestrel eggs weigh on average 21.0 g, and an energy content of 5.04 kJ.g$^{-1}$ or 105.84 kJ.egg$^{-1}$ was based on Ricklefs' (1974) review. Assuming again an energetic efficiency of 70% (Ricklefs 1974, King 1974) total costs of synthesis of a clutch of $n$ eggs would be

$$S_e = 45.36 n/(12 + 2n) \text{ kJ.day}^{-1} \quad (23)$$

Finally, the costs of feather replacement $S_r$ were based on laboratory measurements in the Kestrel.

---

**Fig. 4.** Monthly average daily energy expenditure ($E_i$) estimated from TEB, for males (A) and females (B). Partitioning of total $E_i$, in a basal component $B$, the extra energy required for tissue synthesis, $S$, the extra energy requirements for thermoregulation $T$ and $Tr$ (increment due to moult), the extra energy expenditure for activity, incubation and brooding, $Ab$, flight, $Af$, flight-hunt, $Ah$ and the heat increment of feeding, $H$, which does not substitute for $T$, is indicated. Numbers in top indicate sample size (number of observation days).
This variation is primarily due to the increased activity costs (A) from March to July (phases 3 to 8). The basal component of energy expenditure (B) is virtually constant around 100 kJ.day⁻¹, the increased daylength and thereby increased ρ : ρ ratio in summer being offset by the reduced body mass. Costs for thermoregulation (T) are of course highest in winter, but cause only a slight elevation of Eₜ above August levels when costs of feather synthesis (S) and enhanced conductance keep Eₜ at around 250 kJ.day⁻¹.

Variations in Eₜ calculated for females were less extreme and nearly opposite in direction from those in males. Energy expenditure by females was maximal in June and during the winter months, and considerably less during the first part of the reproductive season (Fig. 4). This is clearly a consequence of task differentiation, and reduction of female activity from laying through young nestling care. The female cooperates with the male in provisioning food for the older nestlings (phase 7), which underlies the high Eₜ value for sure (Fig. 5). Female energy expenditure exceeded male Eₜ in winter, primarily caused by the higher female body mass and remained well below male Eₜ during reproduction.

4. DEE ESTIMATION FROM FOOD INTAKE, Eₘ

4.1. INTAKE ADJUSTED FOR RETAINED ENERGY

Daily energy expenditure equals metabolizable energy intake per day (M) minus the energy retained (D):

$$E_m = M - D \text{ kJ.day}^{-1}$$

(24)

Since M varies dramatically from day to day (Masman et al. 1986), information on retained energy D should also be available on a daily basis in order to calculate Eₘ for individual days. This is rarely possible. Only in D₂¹⁸O-trials birds were captured and recaptured and their mass change recorded. We have therefore constructed monthly average estimates of M, D and hence Eₘ.

Metabolizable energy intake was integrated per observation day over all meals observed:

$$M = \alpha / \rho \sum \left( k_i, l_i, q_i \right) \text{ kJ.day}^{-1}$$

(25)

where α = length of the activity time (time from dawn civil twilight to dusk civil twilight -0.71 h), f = observation hours, n = number of meals, kᵢ =
mass estimation of prey (g), \( l_i \) = energy content of prey (kJ.g\(^{-1}\)), \( q_i \) = assimilation quotient of prey type. Mass estimation was based on prey species, handling time, and prey size selection, energy content and assimilation on laboratory trials. The full analysis of \( M \) has been presented elsewhere (Masman et al. 1986). The analysis could be made for Kestrel observation days obeying a number of reliability criteria. These data were summarized per month (♂♀) or two months (♂♂), as well as per phase of the reproductive cycle.

Energy retained in tissues (\( D \)) was estimated separately for general body mass change (\( D_w \)), egg formation (\( D_e \)) and feather formation (\( D_r \)):

\[
D = D_w + D_e + D_r \text{ kJ.day}^{-1}
\]

(26)

Energy retained in generalized body mass change (Table 1) was estimated from the energy equivalence of mass change measured in the laboratory, \( i.e. 19.2 \text{ kJ.g}^{-1} \) (Masman et al. 1987b), under the assumption of a 70% efficiency of tissue production (see 3.5):

\[
D_w = 0.7 \times 19.2 \times \Delta W \text{ kJ.day}^{-1}
\]

(27)

Note that \( D_w \) is negative for body mass decrease. The energy retained in eggs (\( n.105.84 \text{ kJ.clutch}^{-1} \), see 3.5) was attributed to females in the laying phase as well as 14 days before laying:

\[
D_e = 105.84 n/(12 + 2n) \text{ kJ.day}^{-1}
\]

(28)

Energy retained in feathers during moult was estimated as plumage dry weight (♂♂ 17.2 g; ♀♀ 23.0 g) \( \times \) plumage energy content (23.4 kJ.g\(^{-1}\)dry), divided by moult duration (160 days), or

\[
D_r = 2.5 \text{ kJ.day}^{-1} (♂♂ \text{ in phase } 8, 9)
\]

\[
D_r = 3.4 \text{ kJ.day}^{-1} (♀♀ \text{ in phase } 7, 8, 9)
\]

(29)

4.2. ENERGY EXPENDITURE THROUGH THE SEASONAL CYCLE

The results on seasonal variation in metabolizable energy intake (\( M \)) have been published elsewhere (Masman et al. 1986). \( M \) has only a minor contribution to make for most phases, but reached a maximal value (32 kJ.day\(^{-1}\)) for females during courtship (March-April) when appreciable mass increase occurs and a minimum value (\( \approx 43 \text{ kJ.day}^{-1} \)) for females during nestling care (June), when female body mass decreases rapidly (Table 1).

Monthly values of \( E_m \) in males range from 145 kJ.day\(^{-1}\) in September to 417 kJ.day\(^{-1}\) in June (Table 3). These extremes coincide with the minimum and maximum \( E_r \). There is a significant positive correlation between \( E_m \) and \( E_r \) (\( r = 0.769, p < 0.005, n = 18 \)). However, \( E_r \) estimates on average exceed \( E_m \) by 37 kJ.day\(^{-1} \) (11.9%) in males and by 30 kJ.day\(^{-1} \) (10.1%) in females (both discrepancies significant different from zero). In some months the discrepancies are statistically significant (males: April, September; females: January, February).

Food intake is likely to be biased downwards since the observer occasionally misses a prey capture. This bias may be phase-dependent. Underestimation is possibly the case when a few insects are taken in late summer, or when male Kestrels provisioning their females during courtship, egg laying and incubation tend to hide out of sight from both their partner and observers, when eating a prey themselves. The underestimation of \( E_m \) for females in January and February may possibly be due to the conservative adjustment of \( M \) for energy mobilized from body reserves in some individuals. During the severe winter of 1979-1980 two females were observed for 6 days, on which the average daily metabolizable energy intake was estimated as 175 kJ.day\(^{-1}\) while ambient temperature was far below freezing and a thick snow cover precluded high prey capture rates. Under these circumstances body reserves must have been mobilized, but exact quantification is impossible since the birds were not caught. From laboratory starvation trials, we know that body mass loss of up to 12 g per day is a regular feature (yielding approximately 230 kJ). The birds during the snow-bound winter conditions could therefore have attained a daily energy expenditure of more than 400 kJ. This example illustrates the potential error introduced by the food intake method unless daily mass changes of the birds observed can be followed. Excluding these six exceptional days, the remaining data for January and February from the \( E_m \) set (\( n = 9 \)) average 313 kJ daily intake, in close agreement with the prediction from the time budget approach (322 kJ).

Accepting the shortcomings of the \( E_m \) method under the specific situations mentioned (periods of extensive snow cover, the male during the provisioning phase, and possibly the period when insects are taken) we can evaluate the potential of the food intake approach by considering all other pe-
Fig. 6. Field protocol for behavioural observation and application of DLW-method. In our behaviour protocol we distinguished sitting in different positions. Perched (P), sheltered on the ground and in the nestbox; Flight (F), sometimes with prey (Fpr); Wind-Hovering (WH) sometimes interrupted to the lower position or to make a Strike (S) an attempt to catch a small mammal; prey-capture is followed by Eating (E), cashing or a prey delivery. Total carbon dioxide production was measured by the DLW method, sometimes combined with a behaviour protocol.

5. DEE ESTIMATED FROM DOUBLY LABELED WATER TURNOVER, $E_d$

5.1. FIELD PROTOCOL AND CALCULATIONS

Rates of carbon dioxide output were determined on 28 free-living Kestrels by means of turnover rates of $^{18}O$ and H isotopes (Fig. 6). Of these, 15 determinations concern Kestrels in which a continuous behavioural protocol was obtained. In the other 13 we either made no attempts to observe the birds or failed to observe them for more than 75% of daylight. A further 10 birds were captured and injected with $D_2^{18}O$ but not recaptured. Upon initial capture a 25 μl blood sample was taken from the posterior tibial vein to determine background isotopic enrichments. The bird then received a subcutaneous abdominal injection (ca. 0.2 ml) of enriched water ($H_2^{18}O$, 95.3 atom % and $D_2O$, 99.8 atom %, mixed in a mass ratio of 2:1). The bird was then left for about 3 h in a dark box for the isotopes to equilibrate in the body water. Before release a second blood sample was taken, and after recapture ($X$ h later), a third one. Body mass at release and recapture were recorded (Fig. 6). Concentrations of $^{18}O$ and Deuterium in blood samples 1-3 were determined by mass spectrometry as described by Masman & Klaassen (1987). Total production of $CO_2$ over the time interval between the second and third blood sample was calculated using equation (35) of Lifson & McClintock (1966). Body water volume was determined from isotope dilution during equilibration, i.e. from the difference in isotope concentrations between the first and second sample (Schoeller et al. 1980). Total body water was on average 65.9% (s.d. 5.9; n = 13) of body mass in males and 67.7% (s.d. 5.1; n = 18) in females. These mean values were taken whenever the amount of isotopes injected was inaccurately known. The calculation of total energy expenditure $EE$ over the time interval between the second and third blood sample was achieved by application of an equivalent of 528 kJ/(Mol $CO_2$)$^{-1}$ based on an RQ of 0.83 and an energy equivalent of 19.5 kJ/(L $O_2$)$^{-1}$ (see Masman & Klaassen 1987). Since day and night are not always equally represented in the interval $X$ between second and third sample, $E_d = EE/X$ may occasionally give a biased estimate of the daily energy expenditure. For a methodological comparison we have chosen to analyse in 15 birds total energy expended (EE) over interval $X$ as assayed with TEB and DLW methods before reducing these estimates to $E_d$. 

Periods. For females we are left with 5 data sets, for the males 10. In both cases the $E_d$ data lie above the $E_m$ values, but the mean discrepancy is only 6.5%.
5.2. DLW AS A STANDARD FOR TEB ESTIMATES

Total energy expenditure, estimated by $D_2^{18O}$ and time budget analysis show satisfactory correlation ($r = 0.945, p < 0.001$; Fig. 7A). This is partly due to the differences in duration of the experiments. We therefore reduced these data to average metabolic rates, $E_d$ (from $D_2^{18O}$) and $E_t$ (from time budgets). These again were significantly correlated ($r = 0.832, p < 0.001$; Fig. 7B). However, there was a significant average excess ($E_t - E_d$) of 0.276 Watt (s.d. 0.708), or 7.0% of the mean rate ($E_d$) of 3.97 Watt in the 15 points.

The significant correlation in Fig. 7B is not a trivial consequence of the fact that we estimated flight energy expenditure from some of the same data (Masman & Klaassen 1987). The flight cost analysis made no assumption on the rest of the energy budget. Furthermore the relation of $E_t$ and $E_d$ based on data not included in the flight cost analysis (squares in Fig. 7) shows an average excess ($E_t - E_d$) of 10.5%, and covers budgets in which flight accounts for a range of 0.1 to 46.5% of total energy expenditure.

Altogether 27 DLW data points are available for adult Kestrels in the normal sequence of the reproductive cycle. The 15 for which reliable TEB data are available have already been considered in Fig. 7. For the remainder (12) a more global comparison of the $E_d$ values with the average estimated $E_t$ values for the appropriate sex and phase of the annual cycle is provided in Table 4. These data show the same general trend of a slight overestimation by $E_t$ (on average 1.3% for the 8 male and 4 female data points together). We therefore interpret the data in Fig. 7 and Table 4 as indicating that our calculation of $E_t$ generally overestimates daily energy expenditure. For delimiting the dis-

Table 4. DLW estimates of daily energy expenditure ($E_d$ in kJ.day$^{-1}$) for 8 males and 4 females, for which no accurate time budget is available, compared with the mean energy expenditure derived from TEB data ($E_t$ in kJ.day$^{-1}$) for the corresponding phase of the annual cycle. The discrepancy between DLW and TEB prediction for all 12 birds averages 1.3% (TEB overestimating).

<table>
<thead>
<tr>
<th>Phase</th>
<th>Male</th>
<th>Female</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$E_d$</td>
<td>$E_t$</td>
</tr>
<tr>
<td>1</td>
<td>296</td>
<td>292;283</td>
</tr>
<tr>
<td>5</td>
<td>411</td>
<td>283</td>
</tr>
<tr>
<td>6</td>
<td>606</td>
<td>394</td>
</tr>
<tr>
<td>7</td>
<td>374;330;290</td>
<td>389</td>
</tr>
<tr>
<td>Mean</td>
<td>366</td>
<td>378</td>
</tr>
<tr>
<td>Discrepancy</td>
<td>$+3.3%$</td>
<td>$-3.2%$</td>
</tr>
<tr>
<td>$(E_t - E_d)/E_d$</td>
<td>100</td>
<td></td>
</tr>
</tbody>
</table>

Fig. 7. Comparison of energy expenditure estimated by TEB and DLW in individual birds, expressed as total energy expenditure during one experiment (kJ.exp.$^{-1}$; left) and the same data reduced to the average metabolic rate (Watt; right). Each point indicates one experiment (dots: experiments included in flight-cost estimation by Masman & Klaassen 1987; squares: not included in this flight-study).
crepancy we consider the data with complete time budget data as the most reliable, and hence conclude that our time budget model exceeds real energy expenditure by about 7%.

6. DISCUSSION

6.1. THREE INDEPENDENT METHODS COMPARED

The comparison of daily energy expenditure estimates of free-living adult Kestrels derived by three different methods reveal the difficulties inherent to each of these methods. Estimation by doubly labeled water turnover is certainly the most precise method, but could only be applied to a limited number of animals. In view of the large variability in for instance conditions of weather, food availability and reproductive phase, a much greater sample size would have been necessary to cover the annual cycle for both sexes.

Time budget analysis provided the most complete picture of daily energy expenditure in both sexes throughout the year. When applied to individuals simultaneously assayed by D$_2^{18}$O turnover, there was a good correlation between E$_d$ and E$_t$, giving some confidence in the basic tenets of E$_t$, estimation. However, there was a consistent over-estimation of E$_d$ by E$_t$ (7%). We are therefore tempted to speculate that some extra energy savings were incurred by the birds in the field unanticipated on the basis of the laboratory trials. There is a multitude of possibilities, both behavioural and physiological, which would account for the discrepancy, but no evidence in special favour of any.

E$_m$-estimates on individuals are not precise enough, due to uncertainties in prey size estimation (M) and in body tissue deposition (D) to make comparison of individual E$_m$ with E$_d$ values productive. We therefore turn to a more global comparison of average E$_t$, E$_m$ and E$_d$ values.

E$_t$ exceeds E$_m$ on average by 11% (Table 3), although this excess was only 6.5% when some exceptional conditions were excluded. By inference the DLW standard (E$_d$) and the food intake estimate (E$_m$) should be in substantial agreement for large parts of the annual cycle.

Since the pioneering studies of Utter & LeFebvre (1973), a growing body of evidence has accumulated tending to confirm the potential of the time budget method in obtaining accurate assessments of daily energy expenditure in birds. Two questions are paramount: does the TEB estimate indeed approximate the true value as obtained by the DLW technique, and secondly, is the TEB sufficiently sensitive to generate individual values that can meaningfully be compared with individual DLW values. Table 5 collates the studies now available and shows that with one exception (Weathers & Nagy's study on the Phainopepla presumably suffering from heat stress in an outdoor aviary) the first condition is met. The second question can be answered in four studies. In three cases significant correlation coefficients for the association between TEB and DLW values for individuals were found. This Kestrel study, however, provides the first TEB model validated for free-living individual birds.

6.2. EXPLORING ANNUAL CYCLES IN ENERGETICS: A FIRST GLIMPSE

The general trend supported by all three estimates of DEE is that males sharply increase their energy expenditure during reproduction to a fairly

<table>
<thead>
<tr>
<th>Species</th>
<th>Condition</th>
<th>Mean body mass (g)</th>
<th>Sample size</th>
<th>A Mean (range)</th>
<th>B r</th>
<th>p Value</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mimus polyglottos</td>
<td>FL</td>
<td>55</td>
<td>6</td>
<td>+ 5.2 (-31 to +45)</td>
<td>—</td>
<td>—</td>
<td>Utter, 1971 in: Weathers et al. 1984</td>
</tr>
<tr>
<td>Phainopepla nitens</td>
<td>AH</td>
<td>23</td>
<td>6</td>
<td>-39.2 (-44 to -29)</td>
<td>0.711</td>
<td>&gt; 0.05</td>
<td>Weathers &amp; Nagy 1980</td>
</tr>
<tr>
<td>Passerculus sandwichensis</td>
<td>FL</td>
<td>19</td>
<td>6</td>
<td>+ 2.7 (-20 to +18)</td>
<td>—</td>
<td>—</td>
<td>Williams &amp; Nagy 1984</td>
</tr>
<tr>
<td>Lanius ridovicianus</td>
<td>AH</td>
<td>46</td>
<td>8</td>
<td>-0.1 (-8 to +8)</td>
<td>0.791</td>
<td>&lt; 0.02</td>
<td>Weathers et al. 1984</td>
</tr>
<tr>
<td>Melopsittacus undulatus</td>
<td>AH</td>
<td>36</td>
<td>12</td>
<td>+ 0.3 (-13 to +12)</td>
<td>0.853</td>
<td>&lt; 0.001</td>
<td>Buttemer et al. 1986</td>
</tr>
<tr>
<td>Falco tinnunculus</td>
<td>FL</td>
<td>220</td>
<td>15</td>
<td>+ 7.0 (-63 to +18)</td>
<td>0.832</td>
<td>&lt; 0.001</td>
<td>this study</td>
</tr>
</tbody>
</table>
Table 6. Total annual energy expenditure, estimated from $E_t$ and $E_m$ in kJ.year$^{-1}$ for adult male and female Kestrels (mean body mass 203 and 242 g respectively) in the Lauwersmeer area.

<table>
<thead>
<tr>
<th></th>
<th>Males</th>
<th>Females</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>kJ.year$^{-1}$</td>
<td>%</td>
</tr>
<tr>
<td>B. Basal component</td>
<td>34,608</td>
<td>30.5</td>
</tr>
<tr>
<td>S. Tissue synthesis</td>
<td>1,481</td>
<td>1.3</td>
</tr>
<tr>
<td>T. Thermoregulation</td>
<td>25,811</td>
<td>22.8</td>
</tr>
<tr>
<td>A. Activity</td>
<td>38,553</td>
<td>34.0</td>
</tr>
<tr>
<td>H. Heat increment of feeding</td>
<td>12,942</td>
<td>11.4</td>
</tr>
<tr>
<td>$E_t = B + S + T + A + H$</td>
<td>113,395</td>
<td>100.0</td>
</tr>
<tr>
<td>M. Metabolizable energy intake</td>
<td>100,375</td>
<td></td>
</tr>
<tr>
<td>D. Tissue deposited (incl. eggs, feathers)</td>
<td>365</td>
<td></td>
</tr>
<tr>
<td>$E_m = M - D$</td>
<td>100,010</td>
<td></td>
</tr>
<tr>
<td>Difference $E_t - E_m$</td>
<td>13,385</td>
<td>11.8%</td>
</tr>
</tbody>
</table>

Constant level about 30% above their winter energy expenditure, while the reverse is observed in females (Fig. 4). By this reduction, the females have a slightly smaller average energy expenditure than the males, in spite of their larger size. The average contributions of the components of the annual energy budget according to the $E_t$ and $E_m$ estimations, are presented in Table 6.

The finding that in the course of the year the total energy expenditure of both male and female is of the same order, despite the considerable difference in body size, is a totally unexpected result. Both sexes arrive at the same total expenditure by different pathways. The female economizes on activity by suppressing flight during the breeding period. In contrast, the male has a lower basal component of energy expenditure, related to its smaller size.

It is gratifying to note that both modes of estimation lead to congruence between the sexes in absolute annual amount of energy expended, with a slight preponderance on the part of the male (note that if we apply the correction of 7% overestimation to the $E_t$ data the values for male and female are $105 \times 10^3$ kJ and $100 \times 10^3$ kJ respectively, within a few per cent of the $E_m$ values).

In spite of the larger body mass of female than of male Kestrels, females do not appear to use more energy per year. If we express the energy turnover on a mass specific basis males have thereby much higher rates ($105.10^3$ kJ.yr$^{-1}$; 203 g = 0.0164 Watt.g$^{-1}$) than females ($100.10$ kJ.yr$^{-1}$; 242 g = 0.0131 Watt.g$^{-1}$). The difference is 20%, while only 6% would be expected on the basis of predicted BMR in Falconiformes (Wasser 1986), and also only 6% on the basis of known sex differences in BMR in the Kestrel (Masman 1986). With such a large difference in relative metabolic rates it would be interesting to discuss possible consequences for expected lifespan.

At least one theory presumes a size independent lifetime mass-specific energy expenditure (Sacher 1959, 1977, Lindstedt & Calder 1981, Daan & Aschoff 1982). This theory is based on similar exponents of allometric relations of mass-specific basal metabolism and life span with body mass. If this concept is valid for natural energy turnover rates, high energy expenditure would predict a 20% shorter life span in Kestrel males than in females. However, males tend to refrain from breeding as yearlings more often than females (Dijkstra et al. 1988). Since much of the male excess energy expenditure is allocated to reproduction, the average male mass-specific energy expenditure including non-reproductive years may well be much closer to that of females. In that case similar life spans might be predicted. Future analysis of sex differentials in survival and frequency of breeding should help us solve questions concerning sex differences in trade offs between energy turnover, reproduction and survival.

Comparing avian studies in annual variation in energy expenditure reveals that the overall pattern shown by the Kestrel conforms to that for the Long-eared Owl Asio otus, reconstructed from the $E_m$ method by Wijnands (1984): the male experiences his annual peak expenditure during the provisioning phase. This result of a division of labour between the sexes is also apparent in the reconstruction of the annual course of energy expendi-
ture in the Black-billed Magpie *Pica pica*, studied by Mugaas & King (1981) using the TEB approach. In all three studies seasonal variations in time devoted to flight activity account for the major part of the seasonal fluctuation in energy expenditure. We agree with Mugaas & King's (1981) recommendation that in TEB studies particular care be devoted to establishing the time in flight. Of course determining the cost factor for this activity is the crux of the issue. In view of the close match between DLW and TEB as achieved by the model as used here, it would appear that an exploration of energetic profiles of individual animals provides perspectives. This can only be pursued profitably if the fitness component can also be evaluated and this is the direction our study is taking now.

7. ACKNOWLEDGEMENTS

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8. SUMMARY

1. Three methods were employed to determine the daily energy expenditure (DEE) of free-living Kestrels, throughout the year in a study area in the northern Netherlands.
   - TEB (time budget analysis)
   - Food intake (observational method)
   - DLW (doubly labeled water method)

2. The TEB model used here relies on empirically determined cost factors for the behaviour categories distinguished. To obtain average daily energy expenditure the average fasting metabolic rate for birds under thermoneutral conditions as determined in the laboratory is adjusted for thermoregulatory cost under field conditions. The environmental factors impinging on the animal were evaluated by exposing a heated taxidermic mount to ambient conditions. To this value were added the cost factors for activity as well as for tissue synthesis and empirically determined values for the heat increment of feeding. Where appropriate, the increased energetic expenditure associated with moult has also been added.

3. In all, comparison of TEB predictions and DLW measurements is possible for 15 sessions lasting from one to three days (Fig. 7). Agreement was good, the time budget model tending to overestimate actual energy expenditure by about 7%. A further 12 DLW determinations, lacking complete time budget data, when compared to the mean, expected by TEB prediction for the period of the year concerned, confirm this (discrepancy about 1%, TEB again overestimating, Table 4).

4. The estimation of daily expenditure from the observations of prey capture (Masman et al. 1986) when corrected for body mass changes (D) yields figures lower than the TEB prediction by about 11%. After excluding episodes of extreme discrepancies, which are probably due to shortcomings of the food intake method under special circumstances, food intake estimated DEE about 6.5% lower than TEB predictions. We conclude that this method is for a large part of the annual cycle essentially in agreement with the DLW value.

5. The seasonal pattern of energy expenditure in the Kestrel as estimated by the TEB approach is given in Fig. 4 (monthly means) and Fig. 5 (means for phases of the annual cycle). Males experience an extended annual peak during reproduction when they provision both their mate and progeny, whereas females peak during the late nesting phase when they actively participate in feeding.

6. On account of the energy subsidy provided by the male and lower mass-specific basal metabolic rate, the total annual energy consumption of the heavier female Kestrel is slightly less than that of her mate (Table 5). Consequently the mass-specific metabolic rate in males is 20% higher than in females, which might have, still unknown, different consequences for the expected longevity of the sexes.

9. REFERENCES


10. SAMENVATTING
1. Op drie manieren bepaalden we de dagelijksche energie uit­
gave (DEE) van vrijlevende Torenvalken, zoals die door het jaar heen varieert in het Lauwersmeergebied.
   - TEB (tijdsbestedings analyse)
   - Voedselopname (door waarneming in het veld)
   - DLW (dubbel gelabeld water methode)
2. Het TEB-model dat we toegepast hebben berust op gedetail­
leerde gedragswaarnemingen in het veld en empirisch vastge­
stelde energetische kosten verbonden aan de verschillende ge­
dragshandelingen. Het gemiddelde dagelijkse energieverbruik
werd opgebouwd vanuit de gemiddelde energie-uitgave van
vastende vogels onder thermo-neutrale omstandigheden in het
laboratorium, verhoogd met de kosten voor thermoregulatie
zoals die in het veld wilen optreden. Deze weersinvloeden
werden bepaald door het stroomverbruik van een constant op
40 °C gehouden torenvalk-model, blootgesteld aan weer en
wind, te meten. Deze basisuitgave werd verhoogd met kosten
voor activiteit, zoals vliegen, en voor de synthese van weefsel,
een empirisch vastgestelde waarde voor het extra energie­
verbruik nodig om het voedsel te verteren. Voor de periode van
het jaar waar rui optreedt verhoogden we de uitgaveschatting
met de kosten voor veersynthese en extra thermoregulatie­
kosten als gevolg van de rui.
3. In totaal beschikken we over 15 waarnemingsperioden, va-
riërend tussen de één en drie dagen, waarvoor we de energie-uitgave van individuele Torenvalken, geschat op basis van ons TEB-model, kunnen vergelijken met de energie-uitgave gemeten via de dubbel gelabeld water methode (Fig. 7). De overeenkomst is goed, het TEB-model overschat de uitgaven gemiddeld met 7%. Verder beschikken we nog over 12 DLW meetperioden, waarbij we geen goede tijdsbestedingswaarnemingen hebben verzameld. Wanneer we deze 12 waarden vergelijken met wat we verwachten vanuit de gemiddelde TEB-waarde voor die bepaalde perioden van het jaar, wordt de goede overeenkomst tussen TEB- en DLW-methode bevestigd (TEB overschat met 1%, Tabel 4).

4. De dagelijkse energie-uitgave geschat op basis van de dagelijkse voedselopname (Masman et al. 1986), door correctie voor veranderingen in lichaamsgewicht, levert schattingen op die gemiddeld 11% lager liggen dan de schattingen via het TEB-model. Deze verschillen worden vooral veroorzaakt door extreme periodes waarin de voedselopname schattingsmethode minder accuraat is. Wanneer we deze extremen buiten beschouwing laten zijn de schattingen gebaseerd op de voedselopname 6.5% lager dan die op basis van het TEB-model. Dit betekent dat de voedselopnamemethode voor grote delen van de jaarlijkse cyclus sterk overeenkomt met de DLW-metingen.

5. Uiteindelijk hebben we het seizoenspatroon in dagelijkse energie-uitgave kunnen reconstrueren op basis van het TEB-model voor de verschillende maanden van het jaar (Fig. 4) en voor de verschillende fasen van de voortplantingscyclus (Fig. 5). De mannetjes vertonen een lange periode tijdens de voortplanting gedurende welke de energie-uitgave de hoogste waarde bereikt. In die periode zorgt het mannetje voor het voedsel voor zijn vrouwje en de nakomelingen. De vrouwjes vertonen de hoogste energie-uitgave gedurende de veel kortere periode dat ze het mannetje helpen met het voeren van de jongen.

6. Als gevolg van de voedselaanvoer tijdens de voortplanting door het mannetje aan het vrouwje, en haar lagere basaal metabolisme per gewichtseenheid, is de totale jaarlijkse energie-uitgave van het zwaardere vrouwje (gemiddeld 242 g) zelfs iets lager dan van het mannetje (gemiddeld 203 g; Tabel 5). Dit verschil leidt tot een 20% hogere energie-uitgave op jaarbasis per gewichtseenheid door het mannetje vergeleken met die door het vrouwje, hetgeen wel eens consequenties zou kunnen hebben voor de gemiddelde levensverwachting van de verschillende sexen.