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## **The Energy Budget of the House Martin (*Delichon urbica*)**

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# THE ENERGY BUDGET OF THE HOUSE MARTIN (*DELICHON URBICA*)

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## 1. INTRODUCTION

Development of the doubly-labelled water ( $D_2O^{18}$ ) technique for measuring rates of energy expenditure (Lifson *et al.* 1955, Lefebvre 1964) has allowed the difficult problem of energy budgets in free-living birds to be investigated (Utter & Lefebvre 1970, 1973, Hails 1977, 1979, Hails & Bryant 1979). Availability of data of this type for a range of species will clearly allow more precise evaluation of energy flow in populations and communities than has been possible previously. Attention in this study however was focussed on the individual House Martin *Delichon urbica* L. and on gaining an understanding of population processes by investigating energy balance at the individual level using the  $D_2O^{18}$  technique. Measuring rates of energy gain from foraging and energy expenditure under a variety of conditions, allowed energy constraints on successful breeding at different stages of the reproductive cycle to be examined.

## 2. MATERIALS AND METHODS

The study was carried out during 1977 and 1978 at a colony of about 20 pairs of House Martins in S.E. Perthshire, Central Scotland. All pairs nested in boxes and could be caught repeatedly by closing a trap door at the nest en-

trance. An ability to recapture birds is an important prerequisite for the successful operation of the stable isotope technique. The most satisfactory field procedure involved capturing birds as they returned to their nestboxes at night. After processing, the birds were returned to their nest boxes and normal free-living activity ensued on the following day. In the first year of study (1977) however the majority of measurements using the  $D_2O^{18}$  technique (referred to below as "experiments") were made with captures and recaptures at dawn rather than dusk. The field protocol is summarised in Fig. 1; further details can be found in Hails (1977) and Hails & Bryant (1979). Simultaneously with the introduction of stable isotopes by intraperitoneal injection on first capture, and removal of blood on both initial and final capture, individual birds were examined in detail. Weights ( $\pm 0.01$  g), winglengths ( $\pm 1$  mm) keel lengths ( $\pm 0.1$  mm) and fat scores were recorded. The fat reserves in the interclavicular pit and behind the sternum were scored on a five point scale, where 1 corresponded to a full store and 5 to no fat. The combined value for the two scores was highly correlated with the fat content as determined by carcass analysis ( $r = -0.88$ ,  $P < 0.001$ ) (Bryant & Westerterp in prep.). The sex and age of all birds was known (Bryant 1979). Experimental birds were matched with controls (handled, weighed and measured only) at a similar stage in the breeding cycle. In a few cases a disturbing effect of the  $D_2O^{18}$  technique on experimental birds was evident but their activity was always within the range displayed by the population as a whole. Adverse effects on breeding success were observed only during the laying stage, where all females interrupted laying for two or more days. Experiments were conducted on both members of pairs simultaneously in nearly all cases. Comparisons are made in this paper between daily levels of energy expenditure and the basal metabolic rate (BMR) of the House Martin. For this purpose a BMR of  $2.27 \text{ cm}^3$

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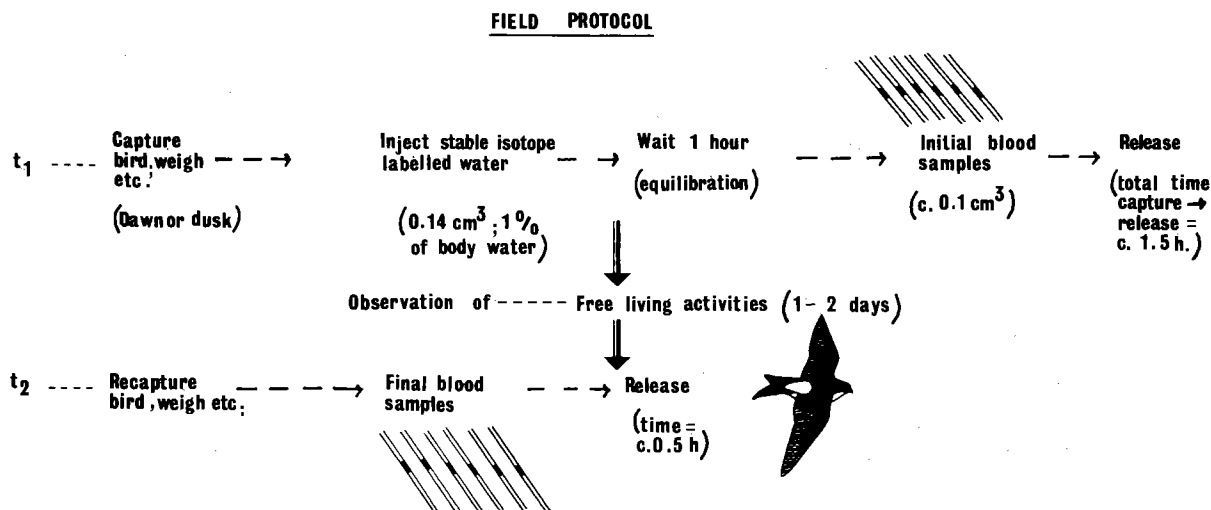


Fig. 1. Protocol for  $D_2O^{18}$  technique under field conditions. Stable isotopes were introduced by intraperitoneal injection (c. 0.14  $cm^3 = 1$  per cent of body water). The initial blood samples were taken 1 hour after injection and consisted of six capillaries, together containing c. 0.1  $cm^3$  blood. A similar volume of blood was collected after one or two days of free living activity. Further details of methods are given by Hails (1977) and by Hails & Bryant (1979).

$CO_2g^{-1}h^{-1}$  has been used (Westerterp in prep.): a figure very similar to the value predicted from the equation of Aschoff and Pohl (1970) (*i.e.* 2.25  $cm^3 CO_2g^{-1}h^{-1}$  for an 18.77 g bird, Table I).

During experiments a full time watch was kept at the nest and the activities of experimental and control birds recorded to the nearest minute. Away from the nest the main feeding site for the colony birds (which were individually colour-dyed) was identified on each day. The aerial feeding station was recorded on a three point scale according to whether low down (1), intermediate (2), or high over trees or open country

(3) (see Waugh 1979). The proportion of the flight period spent in flapping flight (as opposed to gliding) was sampled by observing 20 to 50 bird sightings, each for 15–60 sec, mainly at the principal feeding site around midday. The percentage of the experimental period spent flying is referred to below as %FLY and the percentage flight time spent flapping as %FLAP.

Food supply was monitored with a 40 foot (12.3 m) suction trap (Taylor & Palmer 1972) and weather records were from the meteorological station at the University of Stirling.

Table 1. Statistics for House Martin attributes and activities during each breeding stage ( $\pm$  s.d.). Between stage differences shown by analysis of variance (ANOVA) where  $P < 0.01$ , \*\* and  $P < 0.001$ , \*\*\*

	Non-breeding	Laying period (1)	Incubation period	Nesting rearing	Overall	Anova
Mean weight (g)	20.11 $\pm$ 1.12	20.28 $\pm$ 2.15	18.88 $\pm$ 0.92	18.24 $\pm$ 0.98	18.77 $\pm$ 1.43	**
$\Delta$ weight (g)	-0.77 $\pm$ 0.78	-1.30 $\pm$ 1.10	0.00 $\pm$ 0.28	-0.67 $\pm$ 0.53	-0.70 $\pm$ 0.70	***
Food supply (2)	0.82 $\pm$ 0.47	0.76 $\pm$ 0.42	1.10 $\pm$ 0.16	1.01 $\pm$ 0.24	0.96 $\pm$ 0.31	**
% of period in flight (%FLY)	47.1 $\pm$ 11.5	39.6 $\pm$ 7.0	26.4 $\pm$ 7.4	58.9 $\pm$ 14.7	52.7 $\pm$ 16.9	***
% of flight time spent flapping (%FLAP)	33.2 $\pm$ 5.9	20.0 $\pm$ 10.7	45.8 $\pm$ 3.0	40.4 $\pm$ 10.1	37.7 $\pm$ 11.6	***
n	10	8	7	53	78	

(1) Significant differences between the sexes only occurred for mean weights during the laying period, where  $\sigma = 18.88 \pm 1.30$  (5) and  $\phi = 21.68 \pm 1.95$  (5);  $t = 4.8$ ,  $P < 0.01$ .

(2) Units:  $\log_{10}(\text{volume insects in catch (cm}^3) + 1)$ .

## 3. RESULTS

## 3.1. FOOD SUPPLY

Suction trap catches (recorded as daily insect volumes  $V$   $\text{cm}^3$  and transformed for analytical purposes  $\text{Log } V + 1$ ) during 1977 and 1978 showed a marked rise in May (Fig. 2). They stayed at their highest levels during July and August. The decline in catch size associated with the end of the breeding season began about mid-September but by this time the majority of

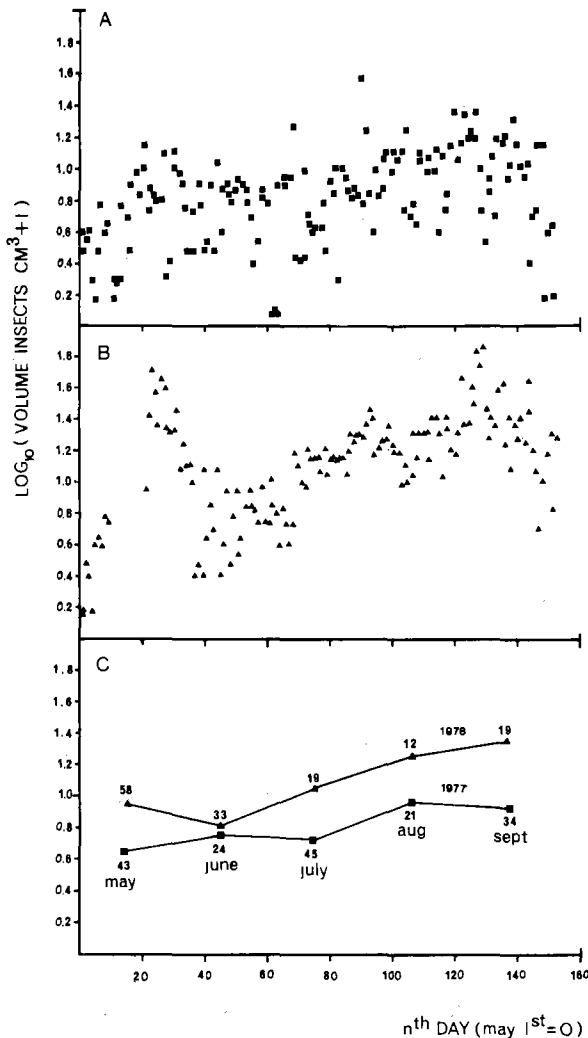


Fig. 2. Aerial food abundance (*i.e.* daily suction trap catches) during the 1977 (A) and 1978 (B) breeding seasons. Points refer to daily catch volumes. The mean catches in each month (and coefficient of variation) are given in C.

broods had fledged and the experimental programme was completed. The average catch volume was much lower in 1977 (0.81) than in 1978 (1.10) ( $P < 0.001$ ).

## 3.2. ENERGY EXPENDITURE BY BREEDING HOUSE MARTINS

The highest daily rates of energy expenditure (hereafter called the average daily metabolic rate A.D.M.R.) were recorded during the nestling rearing period (Fig. 3). Earlier in the breeding cycle ADMR was generally lower with no significant differences between stages.

Predictably, non-breeding birds, both before laying and after their young had fledged, gave low values for ADMR. During the laying period when males were defending their nest and mates, ADMR of territorial males was marginally lower than among non-breeding birds probably because sitting in the nest or defending it is less energy demanding than an equivalent period spent in flight. In accordance with this difference in ADMR, territorial males spent 39.0 per cent of the 24 hours day in flight ( $n = 4$ ) whereas non-breeding males spent 51.2 per cent ( $n = 4$ ). The data for laying females ( $n = 3$ ) were amongst the most variable of all the stages, although the average level was similar to that of their mates. Unfortunately, in none of the three cases did laying proceed normally. Presumably the trauma of initial handling disturbed the ovulation cycle, leading to an interruption in laying. It seems certain that in no case did the birds continue to collect food for yolk synthesis, although in one bird albumen and shell must have been laid down and formed entirely during the experiments. Interestingly this bird had the highest ADMR among the laying females. The problem of some of the doubly labelled water being incorporated into the eggs (hence violating one of the assumptions of the methodology) has not yet been investigated but could have affected the accuracy of the result for laying females.

Overall the ADMR for incubating birds was  $6.40 \pm 0.69 \text{ cm}^3 \text{ CO}_2 \text{ g}^{-1} \text{ h}^{-1}$ , but the mean value for females ( $6.20 \pm 0.66$ ,  $n = 4$ ) was lower than for males ( $6.67 \pm 0.76$ ,  $n = 3$ ) (Fig. 3) again in accordance with the small difference in %FLY for the sexes ( $\text{♀♀ } 25.3 \pm 9.2$ ,  $n = 4$ ;  $\text{♂♂ } 28.0 \pm 5.6$ ,  $n = 3$ ). Female House Martins have a fully

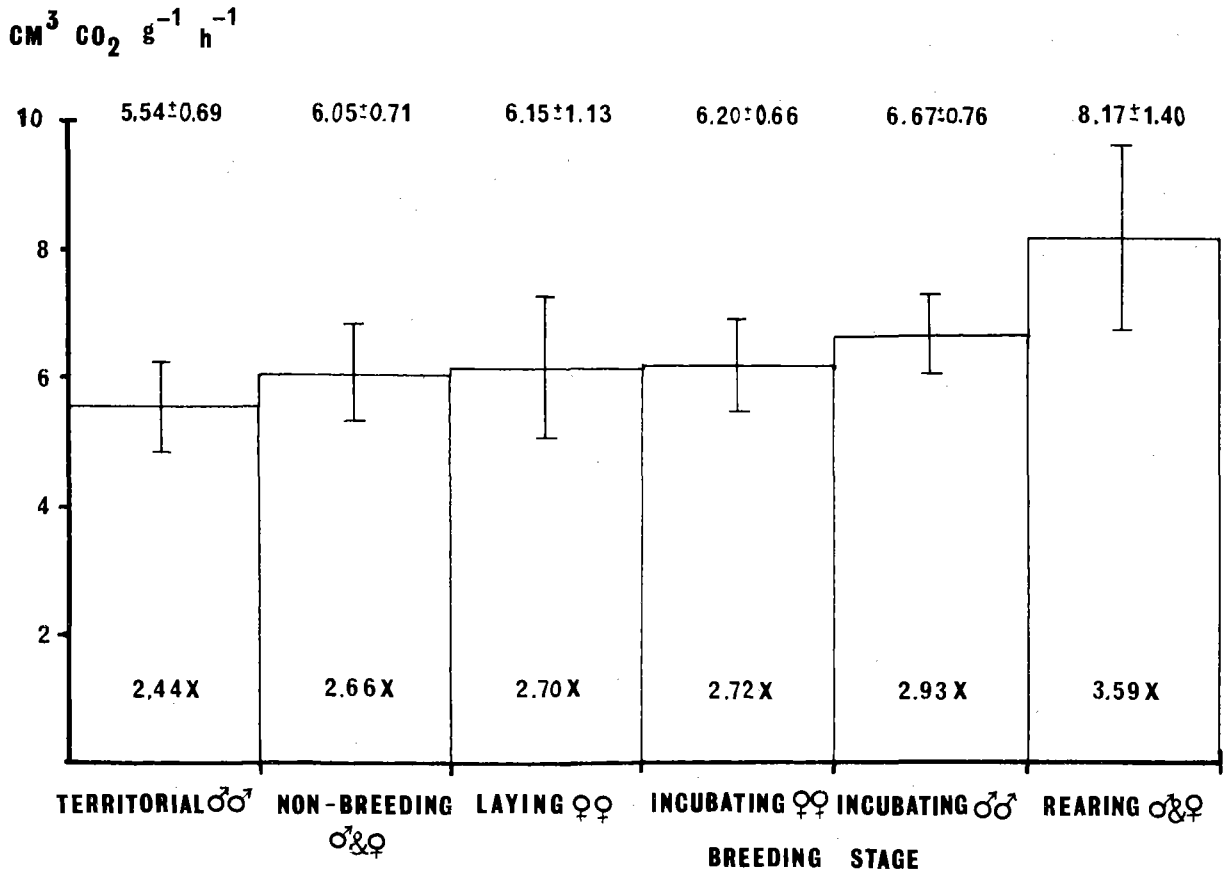


Fig. 3. Mean carbon dioxide output for each breeding stage. Mean values are given at top of diagram and same values as multiples of BMR at bottom of diagram.

developed brood patch, whereas vascularization is less marked in males (Bryant 1975b). Presumably heat transfer to the clutch can proceed at a greater rate in females and yet this had no marked effect on ADMR.

Virtually all experimental pairs (and their controls) had four young during the rearing stage. This was achieved when necessary by artificial adjustment of brood size, especially during the second broods when an additional youngster was often required. The purpose of this adjustment was to eliminate the effect of brood size (or brood mass) on feeding rates and hence activity budgets, as has already been demonstrated by Hails (1977) and Hails & Bryant (1979). By keeping brood age relatively constant as well (at about 15 days) the effects of adult attributes and the environment on ADMR (acting directly or

via the time-activity budget) could also be more easily identified. ADMR was at its most variable during the nestling stage (Fig. 3) although this can be attributed in part to the wide seasonal scatter of these experiments. Hence in spite of the standardized demands we placed on the parents during the nestling period, and of the fact that laboratory trials have shown the method to be accurate to within 7 percent (Hails & Bryant, 1979) the highest values of ADMR were about 100 per cent greater than the lowest.

### 3.3. FACTORS AFFECTING ENERGY EXPENDITURE IN BREEDING BIRDS

Although governed partly by the distribution of experiments between stages, the general pattern of energy expenditure by adults during breeding can be observed by plotting the indi-

vidual results against date (Fig. 4). Initially ADMR was at a low level among pre-breeding, laying and incubating pairs and rose when young were being fed; the highest level of energy expenditure coincided with the period of greatest food abundance (as indicated by the volume of the suction trap catch). A decline in ADMR occurred in August until the time the final samples were gathered in early September. The reality of this decline as a general phenomenon may be questionable however as the August-September data for 1977 alone, and the earlier data of Hails (1977) showed no comparable drop. The positive association between food level and ADMR is reinforced when the two years are contrasted. The season of poor food supply and breeding success (1977) shows generally lower values for ADMR during the nestling stage than in the good year (1978).

Amongst the adult attributes, adult weight was the only factor significantly correlated with ADMR: heavier birds having lower ADMRs (Table 1, 2). The correlation was only slightly lower when ADMR was expressed as a multiple of BMR (dropping from  $r = -0.39$  to  $r = -0.35$ ,  $P < 0.001$ , see Table 2) confirming that the effect was not simply due to the greater metabolic economies normally linked to higher body weights (Brody 1945).

The effects of environmental factors on ADMR were in broad agreement at the level of correlation analysis. Date, temperature and food abundance were positively correlated with ADMR while wind (high winds lead to low suction trap catches) was negatively correlated (Table 2). Hence in general poor conditions were associated with low levels of ADMR. Clearly this association follows in part from the type of ac-

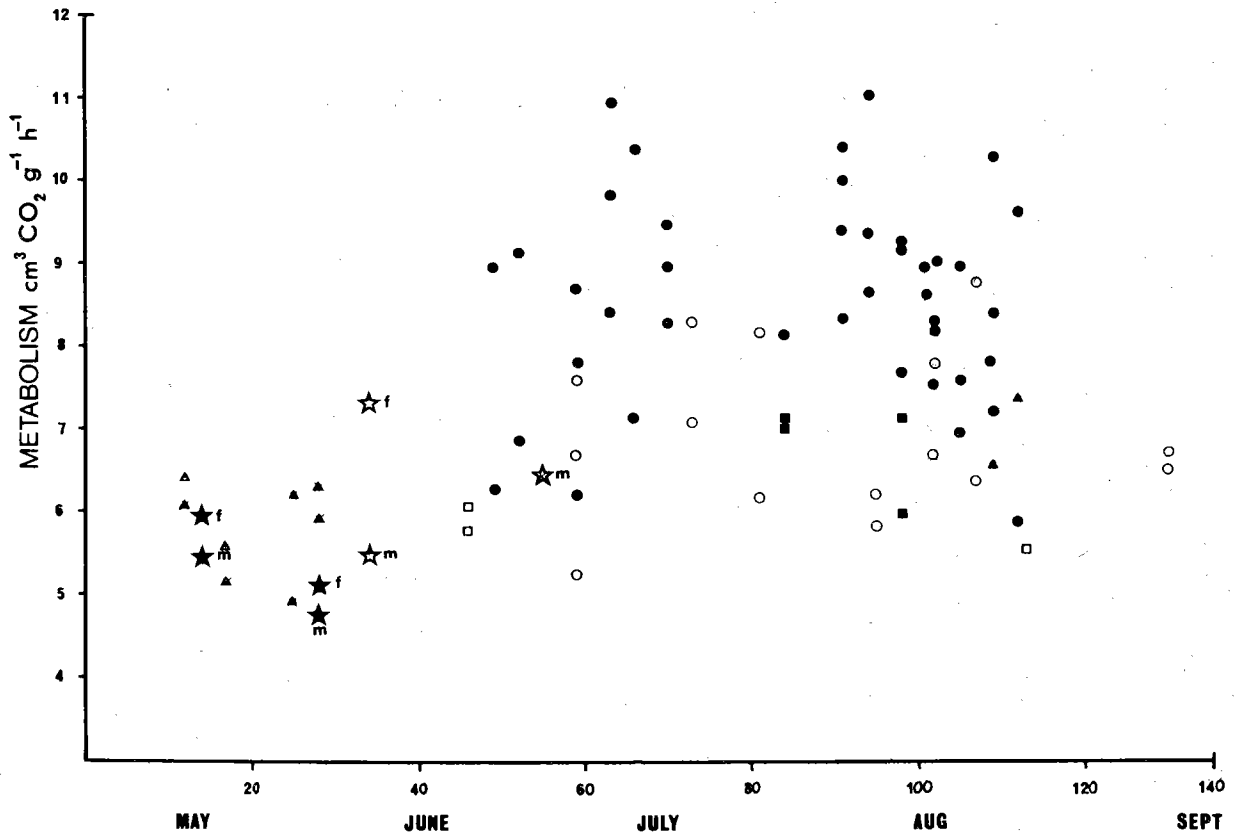


Fig. 4. Individual measurements of ADMR throughout the breeding season. Four breeding stages are distinguished: non breeding  $\triangle$ , laying  $\star$  (males, m; females, f), incubation  $\blacksquare$  and rearing  $\bullet$ . Open symbols 1977 data, closed symbols 1978 data. Metabolism plotted on data, where May 1 = 0.

Table 2. Correlations for average daily metabolic rate (ADMR,  $\text{cm}^3 \text{CO}_2 \text{g}^{-1} \text{h}^{-1}$ ) of nesting House Martins. Significance is indicated by asterisks;  $P < 0.05^*$ ,  $P < 0.01^{**}$ ,  $P < 0.001^{***}$ . Correlations for ADMR and circumstances associated with the nest (such as feeding rates) have been omitted (Bryant & Westerterp, in prep.). A dot indicates inclusion in a multiple regression analysis of factors affecting ADMR

Adult attributes		Weather and food supply		Time-activity budgets	
(1) Initial weight (g)	-0.391 (79)***	Date (May 1 = 0 days)	0.418 (79)***	% of period in flight (%FLY)●	0.485 (74)***
(1) Final weight (g)	-0.280 (79)**	Daylength (h) ●	-0.035 (79)N.S.	Period feeding station (1 = low, 3 high) ●	0.389 (68)**
Mean weight (g) ●	-0.347 (79)***	Maximum temp. (°C) (4)	0.069 (79) N.S.	% of flight time spent flap- ping (%FLAP) ●	0.314 (68)***
(2) $\Delta$ weight (g) ●	0.210 (79)*	Minimum temp. (°C) (4)	0.366 (79)***	Foraging distance (km)	-0.516 (71)***
(1) Initial fat score ●	-0.035 (59) N.S.	Mean temp. (°C) (4) ●	0.264 (79)***	ADMR of mate ( $\text{cm}^3 \text{CO}_2 \text{g}^{-1} \text{h}^{-1}$ )	0.481 (67)***
(1) Final fat score	-0.096 (55) N.S.	Rainfall (mm) (4) ●	0.237 (79)*		
(2) $\Delta$ fat score ●	0.046 (54) N.S.	Windspeed (4) ●	-0.209 (79)*		
Sex ( $\varphi = 1$ ; $\sigma = 2$ ) ●	0.062 (79) N.S.	Food supply $\text{Log}_{10}$ (Volume of insect catch + 1) ●	0.306 (79)***		
Winglength (mm) ●	0.092 (79) N.S.				
(3) Keel length (mm) ●	-0.165 (79) N.S.				
Age (years) ●	-0.033 (79) N.S.				

(1) Initial weights and fat scores measured at first capture. Final weights and fat scores measured on recapture.

(2) Weight and fat score changes are differences between initial and final values.

(3) Based on measurements taken throughout the breeding season.

(4) Based on 24 h daily weather records.

tivity early in the season when food levels are at their lowest. However it persisted even when the nestling rearers were analysed separately (Bryant & Westerterp in prep.). Exceptionally, ADMR was high on rainy days, although in this case the correlation was lost when nestling rearers alone were analysed whereas all other weather and food correlations with ADMR remained. Presumably the effects of rainfall on ADMR are small.

Amongst the time-activity budget factors, %FLY had a clear and predictable effect on ADMR (Tables 2 & 3); the more time spent in energy demanding flight the greater the ADMR (Fig. 5). The intensity of flight metabolism in aerial feeding birds probably depends mainly on

the proportion of time spent in flapping as opposed to gliding flight, because flapping flight is usually taken to require more than 2.5 the power for gliding flight, which may thus often approximate more closely to resting metabolism than to powered flight (Pennycuik 1972, Baudinette & Schmidt-Nielsen 1974).

In House Martins %FLAP ranged from 10 per cent to 62 per cent on an average daily basis although individual records included both nil and 100 per cent FLAP. The percentage FLAP was positively correlated with ADMR (Table 2). Also when foraging was relatively high up, over trees or in open country or was close to the colony, ADMR was high (Table 2). The percentage FLAP, foraging height and foraging distance are

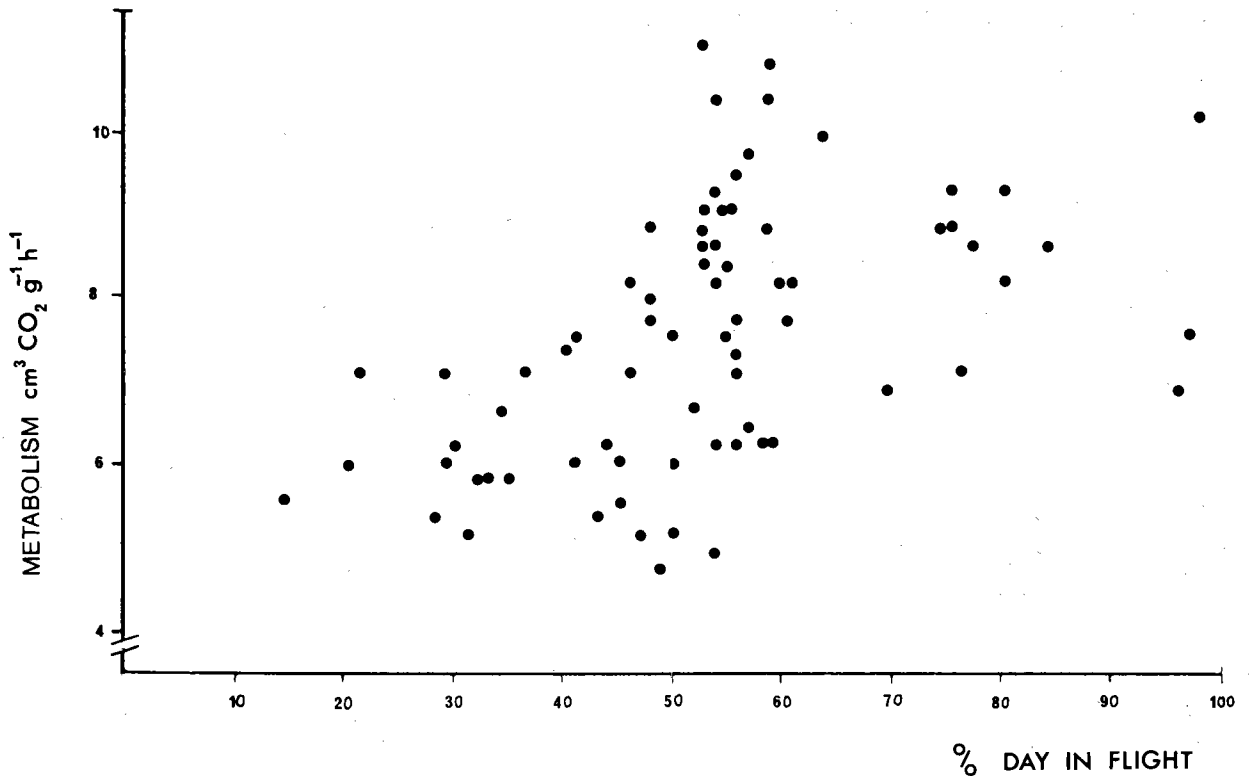


Fig. 5. Average daily metabolic rate (ADMR) plotted in relation to the proportion of the experimental period spent in flight (%FLY).  $r = 0.282$ ,  $P = 0.02$ .

in turn all closely interlinked with food abundance; on poor days birds generally left the vicinity of the colony to seek food, sometimes travelling over 1 km to find an insect concentration in the lee of a tree belt or by a nearby river. Under these conditions %FLAP was usually at a low level. Therefore, while the ultimate cause of the differences in ADMR are variations in food level, the proximate effect is via the intensity of flight metabolism; hence %FLAP was selected from two intercorrelated variables (%FLAP, foraging distance) for inclusion in a multiple regression analysis. Step-up multiple regression showed %FLY and %FLAP to be the only significant factors, together explaining 30 per cent of the variation in ADMR (Table 3). Substitution of foraging distance for %FLAP allowed over 40 per cent of the variation in ADMR to be explained, partly because of the high correlation between %FLAP and foraging distance ( $r = -0.534$ ,  $P < 0.001$ ), but equally because foraging distance was

probably a more accurate guide to average daily flight metabolism than that available from observations which only occupied between 30 and 60 minutes each day and thus inevitably failed to describe in full daily flight activity.

#### 3.4. FORAGING RATES

House Martins tend to bring food to the brood in "bouts" with each feed consisting of single large insect or much more commonly a bolus with many small items. The average bolus contained 0.27 kcal ( $\pm 0.09$  sd,  $n = 400$ ). At the end of a bout parents will typically leave the nest for a period much longer than the previous inter-feed interval, presumably to feed themselves. By simultaneously neck-collaring the brood (to prevent swallowing) and observing the time taken to gather food during a bout, food gathering rates under different circumstances could be derived. From these data in turn an upper level for the rate of food gathering was extracted (this corre-



Table 3. Multiple regression analysis of factors affecting average daily metabolic rate of House Martins. ADMR units are  $\text{cm}^3 \text{CO}_2 \text{g}^{-1} \text{h}^{-1}$

Independent variables	Partial regression coefficients ( $\pm$ s.e.)	Standard partial regression coefficient ( $\beta$ weights)	P
% observation period in flight (%FLY)	+ 0.042 $\pm$ 0.010	+ 0.441	0.001
% flight time in flapping flight (%FLAP)	+ 0.032 $\pm$ 0.015	+ 0.237	0.032
Regression constant	4.111		
$r^2 \times 100$	29.8%		
df1	2		
df2	63		
F	13.381		0.001

sponded to the most favourable 8.4 per cent of bouts, (Bryant in prep.)). Under these circumstances House Martins collected 3.15 metabolizable kcal in an hour. It is presumed that at such a gathering rate the physical attributes of the species (*i.e.* flight speed and manoeuvrability) and characteristics of the predator-prey interaction (*i.e.* search time, handling and recognition time) and any persistent intraspecific (Bryant 1979) or interspecific competitive effects become limiting.

### 3.5. THE ENERGY BUDGET OF THE HOUSE MARTIN

The variations found in levels of energy expenditure in this study and the differing requirements for the productive processes of body growth, egg laying and nestling growth made the budgeting of all breeding stages and circumstances a difficult task. For the present purpose the mid-growth stage of the nestlings has been selected for detailed examination, representing a point in the breeding cycle when the demands for reproduction are likely to be close to their highest level.

We could not distinguish between the mean ADMR for males and females; indeed our broods of four equaled about the bio-mass for which Hails and Bryant (1979) predicted overlap in ADMR for the sexes. Furthermore the correlation between members of pairs overall (Table 2) suggests that the sexes respond similarly to changing circumstances. Hence for this stage

they are treated as identical with a mean weight of 18.24 g and ADMR of  $8.17 \text{ cm}^3 \text{CO}_2 \text{g}^{-1} \text{h}^{-1}$  (Table 1, Fig. 3). This corresponds to an energy expenditure of  $22.58 \text{ kcal day}^{-1}$  per bird (given an R.Q. of 0.75, Hails 1977) (Fig. 6). In expending this energy they largely met their own requirements and delivered  $100.7 \pm 9.3$  (se) feeds to the brood. The small weight losses observed (Table 1) can partly be ascribed to depletion of the fat reserve because there was a tendency for the fat score to fall during experiments. The exact size of the loss however cannot yet be determined and this aspect must be omitted from the calculations.

Feeding studies showed that  $26.82 \text{ kcal d}^{-1}$  were delivered by each parent (bolus energy content  $\times$  no. feeds). Laboratory trials have demonstrated that nestling hirundines assimilate 70 per cent of the energy they consume (R.S. Guy & A. K. Turner's unpublished results yield a mean value of 70 per cent, range 65—74.5 per cent, for Swallows *Hirundo rustica*, Sand Martins *R. riparia* and House Martins). Therefore it may be calculated that  $37.55 \text{ kcal}$  ( $26.82 \times 2 \times 0.70$ ) are assimilated by a brood of four young and  $16.10 \text{ kcal}$  are voided as faeces. Direct measurements of the faeces produced by the broods of experimental birds (see Bryant & Gardiner 1979 for methods) yielded an average dry weight of  $4.32 \text{ g d}^{-1}$ , with an energy equivalent of  $15.19 \text{ kcal}$ . In addition an earlier study of the energetics of nestling growth in House Martins (Bryant & Gardiner 1979) has

## HOUSE MARTIN ENERGY BUDGET

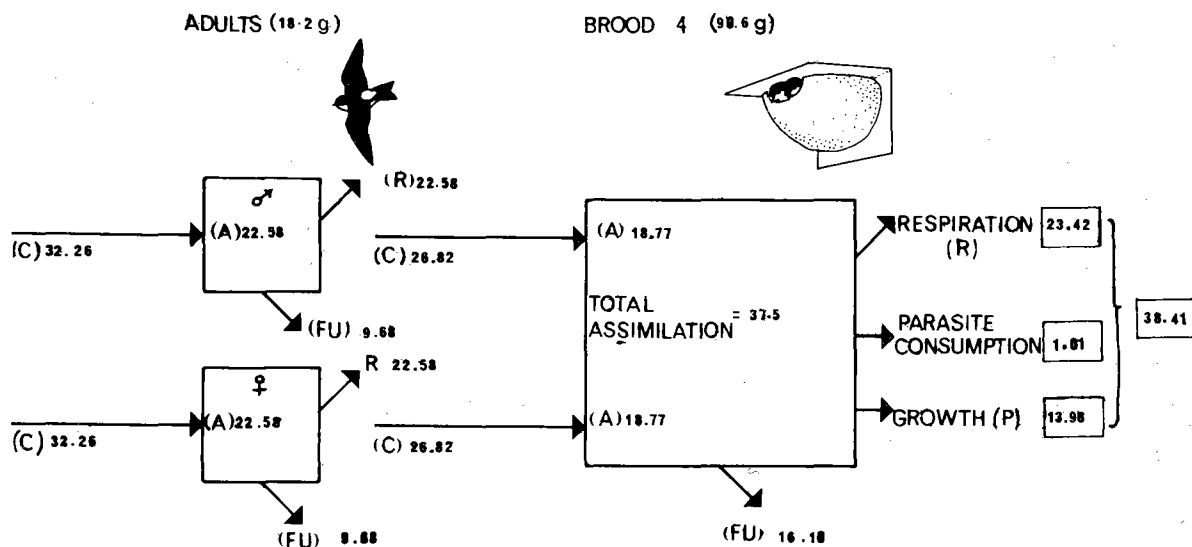


Fig. 6. The energy budget of the House Martin. All values are kcal d<sup>-1</sup>. C = consumption, A = assimilation (= metabolized energy), FU = faeces output, R = respiration. Boxed values on right hand side were obtained by Bryant & Gardiner (1979), unboxed values were obtained in this study and parasite consumption is from Guy (in prep.).

given similar values for assimilation (for broods of 4 aged 15 days) and faecal output: 37.40 kcal and 18.34 kcal respectively. Energy flow through the most important brood parasite, the ectoparasitic dipteran *Stenopteryx hirundinis*, has been determined by Guy (in prep.). He has shown that a normal population of the blood-sucking parasite consumes 1.01 kcal day<sup>-1</sup> (= 2.7% of brood assimilation). Because parasite populations were controlled in the present study, by removal of the overwintering puparia, the energy drain via the parasites would have been even less.

Overall, it may be concluded that the energy flow through the broods in this study conformed with results from a previous study (assimilation was only 3 per cent lower) and was consistent between two independent methods of deriving brood assimilation (6% difference in faecal output). In addition brood requirements were similar to the values predicted from the daily energy budget (DEB) equation of Kendeigh, *et al.* (1977).

The allocation of metabolized energy to adults

and brood led to the pair receiving 54.6 per cent of the daily harvest while the brood got 45.4 per cent.

#### 4. DISCUSSION

Observed levels of energy expenditure for breeding House Martins can be divided into two broad categories, the nestling stage with high ADMR and the other breeding stages with lower energy demands. During the pre-nestling stages mean values for ADMR ranged from 2.44–2.81 × BMR while during the nestling stage ADMR was at 3.59 × BMR; a similar figure (3.89) was given by Hails & Bryant (1979), based on measurements throughout the nestling period and a variety of brood sizes.

The total daily energy demand, however, will be the sum of adult maintenance requirements and any additional energy allocated to productive processes. The total daily demand during the nestling stage was thus the sum of adult needs and brood requirements whereas other stages

(except for laying females) involved only small investments in adult growth. For broods of four the total food gathered daily by each parent amounted to a metabolizable energy equivalent of  $6.57 \times \text{BMR}$  and for adults with exceptionally high maintenance costs (the highest 10%) the equivalent figure was  $7.87 \times \text{BMR}$ . Thus relative energy demands during rearing are on average more than  $2\times$  that for other stages and may rise to  $2.5\times$  or more when either foraging conditions are costly or brood requirements are high. Given this high energy demand during the nestling stage, energy limitations on breeding effort or success are likely to be most important at this time, provided environmental constraints remain constant. For early broods, however, conditions for laying may be poor (Bryant 1975a, 1979) and the effect of this on ADMR and hence energy as a limiting factor has yet to be determined. Modification of the stable isotope technique to allow its use without disturbing laying patterns is obviously a priority. The question of resource shortages apart from energy (Jones & Ward 1977) lie outside the scope of this study but a major challenge for future work is to identify limiting resources at each stage of breeding by conducting integrated studies of energy, protein and other nutrient requirements and availability.

Factors found to be correlated with ADMR fell into three categories; adult attributes, environment and activity. The significance of adult weight was largely spurious, due to heavy birds occurring at the low demand breeding stages (Fig. 3, Table 1). High adult weights at these stages may be linked to the probability of harsh conditions, leading to deposition of "insurance" fat reserves. Additionally, laying females are included in the sample and these are the heaviest of all breeding stages (Bryant 1975b). In contrast parents with young were light at the mid-growth stage, as a consequence of the earlier demands for nestling growth (Bryant 1979), and these light weights coincided with the most energy demanding of breeding stages measured.

Weather factors acted via an effect on food abundance and probably quality (Bryant 1975a). "Good" days were characterized by high values of ADMR and hence rather than poor conditions leading to greater difficulty with food gathering

and thence higher energy costs, the converse occurred. This positive association between food abundance and foraging effort apparently conformed to the predictive models of Evans (1977), Krebs (1979) and Norberg (1978).

Perhaps the most important finding of this study was the wide variability observed for birds performing similar activities (Fig. 3). Time-energy budget studies generally make extensive use of averaged values, often extrapolated from laboratory data, for various activities in the daily or annual cycles. Often implicit in these studies is the constancy of activity costs under changing environmental conditions. This was clearly not the case in this study, either for the data analysed as a whole or for the nestling stage analysed separately (Bryant & Westerterp, in prep.). Furthermore we found that detailed monitoring of flight activity improved the explanation of variation in ADMR, suggesting that precise time-energy budgeting is necessary rather than simply desirable in evaluating the energy costs of high-demand activities, itself a necessity if daily energy expenditure is to be estimated accurately in the absence of the doubly labelled water technique.

By combining the results of the foraging rate studies with the energetic studies the importance of energy as a limiting factor for breeding birds can be investigated. During incubation a mean  $\text{CO}_2$  output of  $6.401 \text{ cm}^3 \text{ g}^{-1} \text{ h}^{-1}$  was observed (Fig. 3). For an 18.88 g bird (Table 1) daily metabolized energy would be 18.32 kcal (if R.Q. = 0.75, Hails 1977). If foraging at the highest observed rate, a House Martin could gather 3.15 metabolizable kcal in one hour. As the average incubating bird spent 6.34 h away from the nest, mainly in the immediate vicinity of the colony, the maximum amount of energy which could be gathered in this time would be 19.95 kcal. This is only 6% in excess of requirements, leaving little margin for lower foraging rates on poorer days. It can be concluded that House Martins need to forage actively while away from the nest during incubation if the clutch is to be incubated normally. It might be inferred that the delicate balance of this budget means incubation would be a difficult time for House Martins especially during the unpredictable conditions of early

summer (Bryant 1975a, 1979). Evidently this is not so because 97 per cent of completed clutches hatch at least one youngster. Presumably the ability of eggs to survive chilling, especially in the early development stages, provides a flexibility which allows adult condition to be maintained at the small cost of lengthening (but not terminating) incubation. Hence, while the energy budget is finely balanced during incubation there is usually only a small time cost for operating a strategy which involves adults meeting their energy (and protein) demands before fulfilling a full incubation regime.

Similar calculations can be performed for the nestling rearing stage. The brood requires 53.64 kcal of which 37.5 kcal are metabolized. Of this each parent delivers 18.77 kcal and assimilates 22.58 itself. To meet both demands would require at least 13.15 h, foraging at the maximum rate. The average adult spent 14.15 h away from the nest, some of which was inevitably spent in food search and travel time. As for the incubation stage, there is also flexibility during the nestling stage. Feeding can take longer because daylength during the breeding season averages 16.26 h, and is even longer during the first broods. Furthermore both adults and young carry large fat stores which are used when current requirements cannot be met by foraging (Bryant 1979). Conversely, the early hours of the day appear to be rather unprofitable and poor weather may prevent full utilization of daylight hours. The common occurrence of weight losses among adults and young (especially for large broods, Bryant 1978, 1979) during unfavourable conditions are to be expected when at least 93 per cent of the normal flying time and 81 per cent of the mean daylength is required to meet the normal demands of the commonest brood size.

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#### 6. SUMMARY

The energy expenditure of breeding House Martins *Delichon urbica* was investigated using the doubly labelled water ( $D_2O^{18}$ ) technique. Average daily metabolic rate (ADMR) for 79 birds at all stages of breeding was examined for correlation with adult attributes, environmental conditions and time and activity budgets. Several significant correlations were identified, but in multiple regression analysis two were especially prominent (% observation period in flight and % flight time in flapping flight) and explained 30% of variability in ADMR. Energy expenditure for breeding adults was lowest for territorial males ( $2.44 \times BMR$ ) and highest for adults rearing broods ( $3.59 \times BMR$ ). Adults with young had the additional task of provisioning the brood and generally required twice the metabolizable energy of any other stage. Comparisons of feeding rates with food requirements showed that whilst on average birds were potentially in energy balance, adverse conditions could easily lead to imbalance because 81% daylength was required to meet the demands of the commonest brood size.

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