ENERGETICS OF FREE-LIVING HOUSE MARTINS (DELICHON URBICA) DURING BREEDING

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ABSTRACT

The D_2O^{18} technique is used to examine the daily energy expenditure of adult House Martins (Delichon urbica) raising broods of different size in order to extend the knowledge of the energetics of reproduction and to use energy expenditure as an estimate of the parental costs involved in reproduction.

The Average Daily Metabolic Rate (ADMR) of House Martins rearing young, ranges from 2.22 - 5.27 × SMR, which is a similar level to that found in many other homeotherms. In the aerial feeding House Martin morphological and behavioural adaptations for flight help to reduce the costs of foraging and thereby help to minimise daily energy expenditure.

The ADMR of male birds is positively correlated with nestling mass: this is probably a result of the rate at which food is delivered to the brood. Although the rate at which females feed the brood increased slightly with increasing nestling mass this is not reflected in their measured ADMR, which shows no correlation with brood mass. Experiments with artifically enlarged broods highlight the importance of the males' role in the fledging success of the brood.

The energy expended by both parents is higher during second brood rearing than during first, and the possible proximate factors bringing about the increase are discussed. This increase is also discussed in the context of reproductive strategies: increased reproductive effort at a time of decreased residual reproductive value may increase fitness and be the ultimate factor responsible for the higher energy expenditure during second brood rearing.

Parental energy invested in reproduction is examined and it is shown that male and female House Martins invest equal amounts of energy in rearing the mean brood size. It is suggested that this is a result of the monogamous co-operative breeding system found in this species and the attempt by each parent to minimise the cost of reproduction by reducing their own energy investment to a minimum level compatible with successful reproduction.

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CONTENTS

Page No.

1. INTRODUCTION

INTRODUCTION

The cause of changes in animal numbers has been the subject of much discussion over the past two decades (Andrewartha & Birch 1954; Wynne-Edwards 1962; Watson 1969; Lack 1954, 1966), with the emphasis in recent years on illuminating population processes by identifying the stage at which (Varly & Gradwell 1960, 1965; Cole 1954) and mechanisms by which populations are limited (Morris 1959; Slobodkin 19[illegible]ling 1963; 1964; den Boer & Gradwell 1971). One such population process is that of natality; and the examination of variation in breeding success amongst birds has played an important role in formulating some basic theories of population regulation (Wynne-Edwards 1962; Lack 1954; 1966). This thesis is concerned with the problem of why differences in natality may occur within a population, since even stable populations may show wide differences in the reproductive rates of its members (Snow 1958; Perrins 1965; Von Haartman 1967a, 1967b; Klomp 1970).

One approach to understanding the limits to reproductive output has been to examine the cost to the parent of a reproductive attempt, and this has formed the basis of much recent life-history theory (Williams 1966; Cody 1966; Schaffer 1971; Charnov & Krebs 1974). Variation in the cost which a parent organism incurs during reproduction may not only influence the success of the current reproductive attempt (Cody 1966) but also its future reproductive output by having an effect upon an organisms residual reproductive value (Fisher 1930; Williams 1966).

The approach to assessing the costs of reproduction has been to examine the ways in which the costs manifest themselves, mainly either as greater mortality or weight loss in breeding organisms when compared to non-breeding organisms (see reviews by Cody 1971; Ricklefs 1974; Stearns 1976). Although both of these approaches have identified a cost associated with breeding there are disadvantages to using either of them. Estimates of mortality require large samples of organisms to be monitored over a number of generations in order to place confidence in the results, which for vertebrate studies may take many years. Furthermore in many free-living organisms mortality occurs mainly over winter and it is often difficult to link this with previous reproductive effort. If measurements of weight loss are to be used they need to be positively identified as being a result of reproductive effort and separated from weight changes which might have occurred anyway (e.g. loss of migratory fat, gonadal recrudescence etc.).

In order to more fully understand factors affecting natality it is necessary to distinguish not only between breeding and non-breeding organisms, but also between those with a high or low reproductive commitment. Only a few studies to date have been able to identify differential costs associated with different levels of reproduction. Lack (1966) presents data for the Pied Flycatcher (Muscicapa hypoleuca) in which females raising large broods had a higher mortality in 5 out of 7 years. Hussel (1972) showed that female Snow Buntings (Plectrophenax nivalis) raising broods of 7 were 8% lighter at the end of the nestling period than those rearing broods of 4. Kluyver (in den Boer & Gradwell 1971) showed that the survival of adult Great Tits (Parus m. major) decreased steadily with increase in the number of young reared in one season.

These three studies all show the ways in which the extra work done, or energy expended, in rearing larger broods manifests itself.

Williams (1966) suggests that reproductive effort (Fisher 1930) could be quantified by measures such as gonadal mass produced, degree of sexual dimorphism of plumage or elaborateness of nest architecture, all of which are again estimates of energy expended in different activities, which may affect the reproductive process. Ricklefs (1974) stated that energetics can be related to evolutionary fitness by the influence of patterns of energy use on fecundity and survivorship, and that in time it will probably be possible to find suitable conversion factors to equate energy and fitness. In this thesis the approach will be that energy expenditure itself is a cost, and if quantified would serve as a method of estimating the costs of reproduction.

The energetics of the reproductive cycle in birds from gonadal development to nestling growth has been the subject of two very searching reviews (King 1973; Ricklefs 1974). Adequate information is available on the energy expended by the parents on gonadal development, egg formation and laying, incubation and the energetics of nestling growth; however there is very little data available on the energy expended by adult birds feeding and rearing nestlings. In nidicolous species it is likely that the nestling stage of the cycle will be the most costly for the adults, since in raising a brood of 5 or 6 young a parent bird may be required to provide food for a nestling mass equivalent to several times its own body weight, in addition to its own personal maintenance costs. The paucity of data during this stage results from the practical difficulties in measuring the energetics of foraging activity in free-living birds. Indirect estimates have been made using time budget techniques (Verner 1965; Schartz & Zimmerman 1971), but the only direct estimate of energy expenditure in a free-living bird is for a study of the Purple Martin

(*Progne subis*) (Utter 1971) and no attempt was made to correlate it with the level of reproduction.

The purpose of the present study was to make direct measurements of energy expenditure in adult birds during the nestling stage of the reproductive cycle of a nidicolous species. The ultimate aims were to (i) expand the present state of knowledge of the energetics of reproduction; (ii) investigate the role of energetic efficiency in predicting average reproductive output, and (iii) use energy expenditure as an approach to estimating parental costs associated with different levels of reproductive effort.

The species chosen for study was the House Martin (*Delichon urbica*); several features of the biology of this species made it apparently suitable for this type of study:-

i The species nests in colonies, can be encouraged to use nest boxes and can be handled regularly without desertion. This simplified data collection and the application of a direct technique to measure energy metabolism.

ii Since House Martins are aerial feeding birds the costs of foraging, especially when feeding nestlings, were initially considered likely to be higher than in other species, and therefore have a greater potential for exerting a limiting effect.

iii Much of the breeding biology and foraging strategy of the House Martin had previously been described both in Britain (Bryant 1973; 1975a, 1975b) and elsewhere (Lind 1960; Rheinwald & Gutscher 1969), which meant that time could be devoted largely to the development and application of a technique with which to measure energy expenditure in a free-living bird.

2. METHODS

2.1 SELECTION OF TECHNIQUE

The selection of a technique which would provide reliable estimates of free-living metabolism on a routine basis was of paramount importance in this study. Classical techniques involving calorimetric apparatus (Brody 1945) are completely unsuitable for measurements on unrestrained animals. As a guide to the approach of this problem those techniques which were initially considered as being suitable for the present problem are outlined in Appendix I, for a fuller description and for other techniques the reader is referred to Gessamen (1973).

The technique chosen for use in this study was the D_2O^{18} (doubly-labelled water) method of estimating CO_2 production.

2.2 DOUBLY-LABELLED WATER TECHNIQUE

2.2.1 Rationale of the Technique

Fundamental to the technique is the finding by Lifson et al (1949) that the Oxygen of body water is in isotopic equilibrium with the Oxygen of expired CO_2. The Oxygen of body water is also lost as water, both evaporated and excreted, whilst the Hydrogen is only lost as water. If the individual turnover rates of the two elements in body water can be measured, their difference will yield that amount of Oxygen which is lost as Carbon Dioxide. The two elements are conveniently labelled with the stable isotopes Deuterium and Oxygen-18 and their turnover rates measured by examining the difference in isotopic enrichments of samples of body water at the start and the end of an experimental period.

Thus the organism to be studied is enriched with the two isotopes either by being given labelled water to drink or by injection. After a suitable period for absorption and equilibration of the isotopes a sample of body water is taken, commonly blood but theoretically any water sample would serve. This first sample is analysed for the initial concentration of isotopes. After a pre-determined experimental period further body water samples are taken for analysis of the final level of isotopes. From the difference in isotopic enrichment in the initial and final body water samples the turnover rates of the elements of body water can be calculated. When these are embodied in an appropriate equation the total respiratory CO_2 produced during the experiment can be calculated.

2.2.2 Development and Previous Use

The D_2O^{18} technique has its origins in an investigation into intermediary metabolism and the fate of inspired Oxygen. Day & Sheel (1938) had inferred that inspired O_2 is expired as CO_2 and does not take part in the oxidative metabolism of carbon compounds. Lifson, Gordon, Visscher and Nier (1949) investigated the situation using O^{18} as a tracer for respiratory Oxygen, their results showed that:-

(a) the O_2 of respired CO_2 is in exchange equilibrium with the O_2 of body water;

(b) that utilized respiratory Oxygen is incorporated into body water.

After these findings the theory of a metabolism measuring technique was formulated and in 1955 Lifson, Gordon and McClintock labelled laboratory mice with D_2O^{18} and compared isotopic CO_2 production rates with classical methods of measuring the same. Their results were very favourable and they reported a mean absolute difference of 7% between the two methods. As a further test the method was then applied to a strain of hereditarily obese mice having a lowered metabolic rate, the results confirmed those that had been previously obtained (McClintock & Lifson 1957). The next test of the technique was carried out using rats (McClintock & Lifson 1958a) and the mean absolute difference between the D_2O^{18} and the van Slyke method of estimating CO_2 production was 3%. When tested under conditions of isotope re-entry using mice a 3% difference was again reported (McClintock and Lifson 1958b).

By analysing the dietary components of rats Lee and Lifson (1960) used the D_2O^{18} technique to estimate both total energy and material balance. A theoretical R.Q. was derived for the diet and by dividing this into the estimated CO_2 production a value for O_2 consumption was calculated. Food intake was estimated using CO_2 output and dietary composition, and water intake from the Deuterium turnover rate and mean body water content. By measuring each of these parameters during the course of the experiment, agreements of 4% for CO_2, 8% for O_2, 9% for water output and 4% for food intake were obtained. To eliminate one of the variables the experiment was repeated using fasting mice, again comparing isotopic with other measures mean absolute errors were 4% for CO_2, 5% for O_2, and 3% for water.

The close correspondence between the results of the D_2O^{18} method and classical methods, demonstrated in these studies, provided a sound basis for applying the technique to a field study, and Lefebvre (1964) used it to measure the energy expended during flight in racing pigeons (<u>Columbia livia</u>). The technique had not previously been applied to birds and in his validation studies Lefebvre found an average difference of 8% compared with the Van Slyke method of estimating CO_2 production.

A full description of the theory of the technique and its applications has been written by Lifson and McClintock (1966).

The emphasis in recent years has been the field application of the technique with Utter and Lefebvre (1970) measuring the energetics for free flight in the Purple Martin (Progne subis). Utter (1971) then proceeded to measure daily energy expenditures of Purple Martins and Mocking Birds (Mimus polyglottos) and compare the results with time-budget estimates; agreement between the two methods was within 10%.

The first field study involving mammals was carried out by Mullen (1970) on the heteromyid rodent Perognathus formosus. In validation studies prior to the field work, agreement with classical studies was reported as 6%. Further mammalian field studies were carried out on Dipodomys merriami (Mullen & Chew 1973), D. microps (Mullen 1971a) and Peromyscus crinilus (Mullen 1971b).

Most recently Little & Lifson (1975) carried out validation studies on two eastern chipmunks (Tamais striatus) and found agreement at 1% and 8%. The small sample size indicated the constraining effect of isotope cost in heavier organisms.

A variation of the technique using Tritium instead of Deuterium was employed by Nagy & Shoemaker (1975) in a study of the free-living lizard Sauromalus obesus. Although no validation studies were carried out, field metabolism measured in this way was within 11% of estimates involving dietary measures.

2.2.3 Simplifying Assumptions

Before the equation linking isotopic turnover rate to CO_2 production can be derived certain simplifying assumptions have to be made:

1) The first assumption is that the proportion of body water in the organism remains constant throughout the experimental period. Lee and Lifson (1960) derived equations to calculate CO_2 production when body water changes either linearly or exponentially with time, however before either can be applied it is necessary to determine the shape of the water-change curve. In the short experimental period used in this study (36-48 hours) body water changes were small as the animal was not deprived in any way. The average weight change of the birds sampled was +0.42g, and assuming this change to be entirely water, the maximum induced error would be -2.3%. However it is extremely unlikely that all the weight change was due to change in water content of the body.

The body water content of four adult House Martins (two males and two females) was measured by freeze-drying to constant weight the whole carcass. The mean water content was 64.% (± 4.6 s.d.), which compares with the Purple Martins (Progne subis) measured by Utter (1971) at 65.18%.

2) It is assumed that the concentration of D and O^{18} in water, and CO_2 lost from the organism, is the same as that attained in the body water. As it stands this assumption is invalid due to fractionation effects attributable to differences in the physical characteristics of the heavy isotopes. When any change of state occurs, e.g. from liquid to gas, the heavier isotopes tend to change state more slowly than the lighter isotopes and thus their concentration in each phase

differs. The important fractionations in the current context are:-

D_2O (gas) $\leftrightharpoons$ D_2O (liquid); D_2O^{18} (gas) $\leftrightharpoons$ H_2O^{18} (liquid);

CO_2^{18} (gas) $\leftrightharpoons$ H_2O^{18} (liquid).

The fractionation factors for each of these relationships are 0.93, 0.99, and 1.04 (Lifson et al 1955). When the concentration of the heavy isotopes in each phase are corrected using these fractionation factors they have been shown to be the same (Lifson et al 1949). These fractionation factors are therefore incorporated into the equation for the calculation of CO_2 production.

3) It is assumed that the introduced D and O^{18} enter all compartments of body water equally and at the same concentration. However it has been found (Lifson et al 1955; Lefebvre 1962) that the body water volume measured by dilution of the isotopes exceeds that volume measured by dessication. This is likely to be due to exchange of the isotopes with Hydrogen and Oxygen other than that in body water. Lifson et al (1955) measured the proportion of H_2O^{18} dilution : dessication volume as 1.06 and D_2O : dessication volume as 1.02 in mice, Lefebvre (1962) measured the former as 1.07 in pigeons. Lifson et al (1955) proposed that if this is ignored a 3% error in final CO_2 production occurs. However Lefebvre (1962) incorporated correction factors into his calculations and found no greater error in the results than in those which were uncorrected for true body water volume. Thus a correction factor for equilibration of isotopes other than with body water is not deemed necessary in the CO_2 calculation.

4) A fourth assumption is that the only loss of D and O^{18} from the body occurs via H_2O and CO_2. In assumption 3) it was shown that

the isotopes are incorporated in body substances other than water. However if they become incorporated in excretory products then elimination in a form other than water or CO_2 would occur. However if the incorporation occurred in the ratio of two D atoms : one O^{18} atom it would have no effect on the final CO_2 calculation only increase the apparent H_2O turnover rate. For example uric acid contains four 'H' atoms and three 'O' atoms, if all the H atoms were exchanged with D, and two of the O atoms, the result would be the apparent loss of two extra water molecules. Lifson et al (1955) corrected for urinary and fibre loss in mice and found only 1% difference with uncorrected values, Lefebvre (1964) did a similar correction and found no significant difference. The fact that exchange does not occur to any appreciable extent can be seen in the agreements within 9%, 3% and 8% between isotopic and direct measures of water intake and food intake respectively as cited in the last section.

5) A final assumption is that no D or O^{18} isotopes enter the animals body other than those initially introduced. In a free-living animal or one in a gas train where respiratory gases are removed this is quite valid. However Pinson and Langham (1957) have shown that tritiated water exchange occurs across both the respiratory and skin surfaces of laboratory rats at about equal rates. Thus any animal labelled with isotopes and in a confined space will experience some isotope re-entry in the form of water. Re-entry from ${CO_2}^{18}$ will not occur, and isotopes re-entering as water will not affect the CO_2 calculation, merely decrease the apparent body water turnover rate. McClintock & Lifson (1958 a & b) found no greater error induced in mice where isotope re-entry occurred.

In summarising these assumptions Lifson et al (1955) came to the conclusion that those errors introduced by body water changes, incomplete equilibration and isotope losses other than by H_2O and CO_2 have a self-cancelling effect (assumptions 1, 3 and 4). Assumption 5) whilst not completely valid has little effect upon the final CO_2 calculation. Errors introduced by assumption 2) can be minimized by incorporating the appropriate fractionation factors into the calculation of CO_2 production.

Having dealt with the simplifying assumptions and identified a need for incorporation of fractionation correction factors it is now possible to derive an equation to calculate CO_2 production.

2.2.4 Derivation of CO_2 Production Equation

On the basis of the foregoing assumptions the rate of water loss from an organism is equal to the fractional turnover rate of the Deuterium isotope multiplied by the total body water:-

$$rH_2O = K_D \bar{N} \qquad (1)$$

where rH_2O = rate of body water loss

K_D = fractional deuterium turnover rate

and $\bar{N}$ = body water content (mM).

Similarly the rate of water plus CO_2 loss is given by the fractional turnover rate of the O^{18} isotope multiplied by total body water:-

$$rH_2O + 2rCO_2 = K_o \bar{N} \qquad (2)$$

where rCO_2 = rate of CO_2 loss

K_o = O^{18} fractional turnover rate.

The factor 2 is incorporated into equation (2) because each mole of carbon dioxide contains the oxygen equivalent of two moles of water.

Subtracting (1) from (2) and solving for CO_2 yields:

$$r\,CO_2 = \frac{\bar{N}}{2}\,(K_O - K_D) \qquad (3)$$

The components K_O and K_D in equations (1) - (3) are the fractional turnover rates of the isotopes O^{18} and D respectively, they represent the decrease in isotope concentration in the body water during the experimental period and may be calculated according to the equation:-

$$K_{(O,\ D)} = \frac{\ln(S_i - S_t)}{\Delta t} \qquad (4)$$

where $K_{(O,\ D)}$ = fractional turnover rate of O^{18} or D

and S_i = initial isotope concentration

S_t = final isotope concentration

Δt = experimental time period (hours)

ln = natural logarithm.

The unit for S_i and S_t is that of the specific activity of the isotopes and is their excess in the body water above natural abundance. When dealing with stable isotopes the measure commonly used is Atom Percent Excess (APE) which is the percentage enrichment above natural abundance:-

APE = Enriched Abundance (%) - Natural Abundance (%)

In the discussion of the simplifying assumptions the need for incorporation of fractionation correction factors was identified. The important fractionations along with fractionation values are:-

D_2O (gas) $\leftrightharpoons$ D_2O (liquid) $f_1 = 0.93$

H_2O^{18} (gas) $\leftrightharpoons$ H_2O^{18} (liquid) $f_2 = 0.99$

CO_2^{18} (gas) $\leftrightharpoons$ H_2O^{18} (liquid) $f_3 = 1.04$

The correction factors are applied to equation (3) as follows:-

$$r\,CO_2 = \frac{\bar{N}}{2f_3}(K_O - K_D) - \left(\frac{f_2 - f_1}{2f_3}\right) rg \qquad (5)$$

where rg = rate of evaporative water loss (mM h^{-1}).

When the numerical values are substituted for the fractionations, equation (7) becomes

$$r\,CO_2 = \frac{\bar{N}}{2.08}(K_O - K_D) - 0.03\ rg \qquad (6)$$

In previous studies using birds, the evaporative water loss has been estimated at 50% of the total water-loss or 0.5 K_DN (Lefebvre 1962; Utter 1971). This was the value derived for mammals by Lifson et al (1955), Lefebvre (1962) discusses the possibility of evaporative losses in birds deviating from 50% of the total loss. However even if rg were estimated as the total loss K_DN, the magnitude of the error involved is less than 3%. In the absence of any better estimate of evaporative water loss in birds 0.5 K_DN was used here and the final equation used to calculate CO_2 production was:-

$$r\,CO_2 = \frac{\bar{N}}{2.08}(K_O - K_D) - 0.015\ K_DN \qquad (7)$$

For a more detailed discussion of the above derivation and simplifying assumptions the reader is referred to Lifson and McLintock (1966).

Before equation (7) can be used to calculate CO_2 production, the turnover rate of the two isotopes has to be accurately measured. The analytical techniques employed in the present study are somewhat different from those previously used, they are also adaptations of techniques more commonly used in a geological context. For these reasons there now follows a detailed discussion of the analysis of each of the isotopes.

2.2.5 Isotopic Analysis

The samples of body water used for analysis were taken as blood and sealed in glass capillaries, each sample was approximately 0.01 - 0.05 ml. (see section 2.3). The procedures followed during analysis of both isotopes were in principle the same, pure gas samples of the isotopes in question were prepared on a vacuum line and these gas samples were analysed using a mass-spectrometer.

1. Processing of Deuterium samples

Blood samples to be used for the analysis of the Deuterium isotope were converted to a mixture of H/D gases by distilling the water from the blood sample and reducing it. The high vacuum apparatus used to carry out this procedure is shown in Figure 2.1.

The capillary containing the blood sample was placed between the two forks of the capillary breaker at A. The capillary breaker was then opened to the vacuum manifold and evacuated whilst keeping the rest of the vacuum line isolated, the neck of the breaker was sparked with a high-frequency Tesla coil to aid removal of adsorbed gases. Care was taken to keep the spark away from the capillary to reduce the possibility of isotopic fractionation. When the pressure inside the line was lower then 10^{-4} mm.Hg, as measured by the thermocouple gauge at B, the vacuum manifold was isolated and the breaker opened to trap C whilst keeping the Uranium furnace isolated. This trap was surrounded by liquid Nitrogen (-160°C) and the tap of the breaker turned to break the capillary. In order to ensure complete evaporation of the water from the blood, the broken capillary and the breaker were heated to approximately 60-80°C with a hand held hot-air blower.

The distillation stage is extremely critical; if the distillation

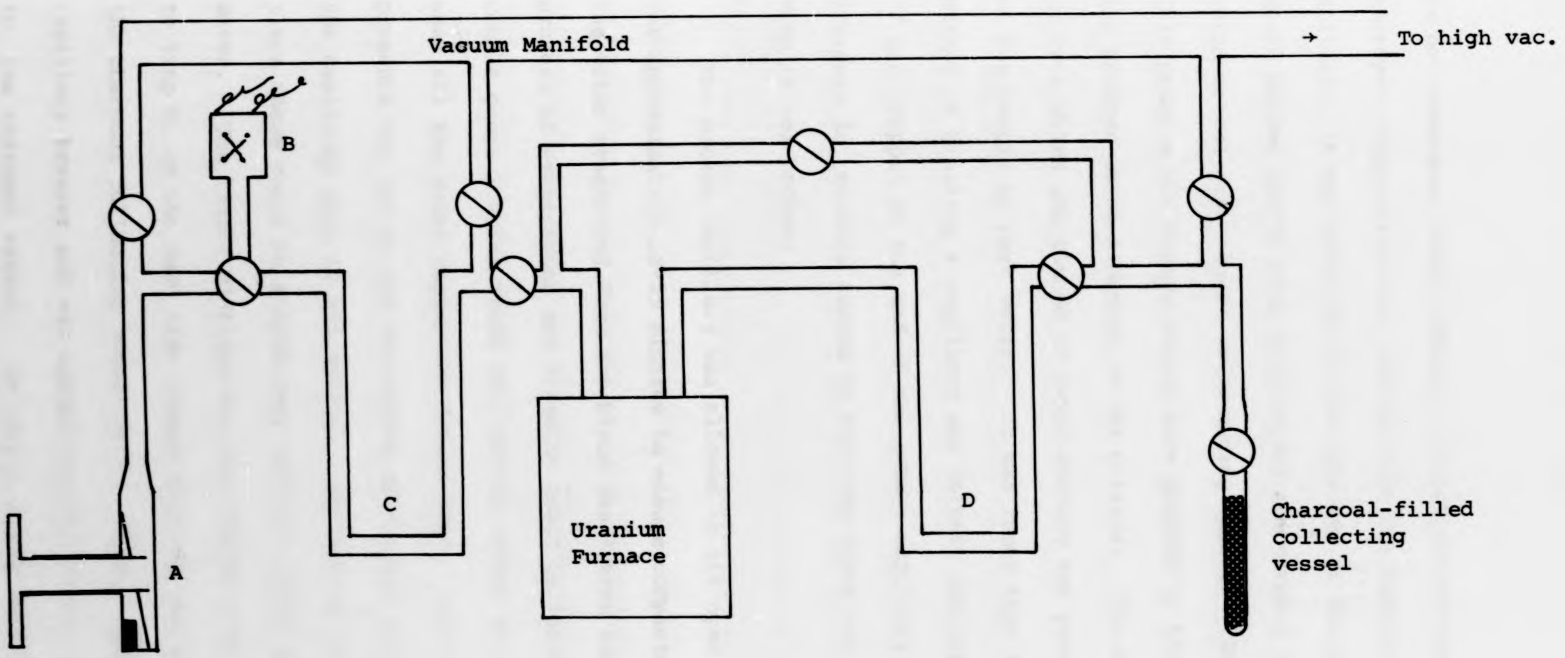


FIG. 2.1 Diagram of the high-vacuum line used for preparation of hydrogen-deuterium gas from blood water for analysis of deuterium isotope.

is not complete, large isotopic fractionations occur, the light H isotopes evaporating more readily than the heavier D isotopes. Initially it was often found that the end of the broken capillary would become sealed with dried blood and careful heating and cooling could reveal free liquid still moving inside. In order to overcome this problem the broken pieces were pounded by the metal slug inside the breaker using a magnet on the outside. The metal slug was made of iron which was tinned to avoid rusting and possible contamination of the sample by rust water. It was found that the most satisfactory method of breaking a capillary was to heat and expand the small amount of gas trapped at the end of the intact capillary. The consequent increase in pressure tended to blow the blood out of the capillary when it was broken.

The broken capillary was allowed to sit open to the first trap for approximately 10-15 minutes to ensure complete distillation. The water evaporated from the blood was frozen inside trap C, the process of evaporation and freezing could be followed using the thermocouple gauge B which would very nearly return to its original value when all the water vapour was frozen down. Any remaining increase in pressure was due to the non-condensible gases which were trapped in the capillary when it was sealed. By keeping the liquid Nitrogen in place these could be pumped away without losing any of the frozen water. The liquid Nitrogen was now removed from C and transferred to trap D, at the same time liquid Nitrogen was also placed around the charcoal collecting vessel at E. Trap C was isolated from the capillary breaker and was opened to the furnace, trap D and through to the charcoal vessel. As trap C slowly warmed to room temperature the water re-evaporated and passed through the furnace which contained

5-6g Uranium heated to 700°C. Here the Uranium reacted with the water:-

$$U + H_2O = UO + H_2$$

to produce hydrogen which was then absorbed by the charcoal at liquid nitrogen temperatures (-160°C). Any water which passed through the furnace unconverted, was frozen in trap D and converted by a second passage through the furnace. As a rule 90-100% of the water was converted after the first passage. If large amounts of water needed a second passage this indicated that a relatively large blood sample had been taken or that most of the Uranium in the furnace had become oxidised, in which case it was replaced (generally after approximately 90 extractions). It was found that whilst one sample was passing through the furnace the next could be loaded and pumped out, and whilst this was being broken a new collecting vessel placed on the other end. Using this technique a sample of gas could be prepared in approximately 35-40 minutes. Once the sample was completely collected in the charcoal, the tube was isolated and removed to be fitted onto the mass-spectrometer inlet manifold.

The Deuterium samples were generally at two levels of concentration, (i) those representing the first blood sample taken after injection and equilibration were the most concentrated at 0.0692 ± 0.01 A.P.E.; (ii) those representing the second blood sample, taken at the end of the experimental period which were the least concentrated, at 0.0242 ± 0.05 A.P.E.. The difference between the samples gave rise to problems concerning "memory" effects in the vacuum line, mostly attributable to the Uranium furnace. Memory is a phenomenon often experienced in mass-spectrometry where contamination from one sample carries over to the next. Thus the most concentrated (or 'heavy') samples may be made artificially 'light' if a less concentrated sample had passed through the vacuum line before it, and vice-versa. The memory experienced in the mass-spectrometer was negligible compared to the memory occurring in the vacuum line. To overcome the problem distilled water standards of the appropriate enrichment were used to prime the vacuum line and uranium furnace before blood samples were passed through. When changing from 'heavy' to 'light' gases on the mass-spectrometer a sample of normal abundance gas was flushed through.

The Hydrogen/Deuterium gas samples were taken from the vacuum line in the charcoal-filled collecting tube and transferred to the mass-spectrometer for analysis.

2. Processing of O^{18} samples.

The O^{18} blood samples were contained in capillaries prepared in exactly the same way as those used for Deuterium analysis. The vacuum line apparatus used for the processing of the O^{18} samples is shown in Fig. 2.2. The isotope was analysed as a CO_2 gas sample by reacting the blood water with BrF_5 to release O_2 which was converted to CO_2 by passage over a heated carbon rod.

The capillary was placed in the capillary breaker at A and evacuated as described for the analysis of the Deuterium isotope. The BrF_5 reservoir was opened to the expansion vessel B and the gas allowed to fill the vessel. The reservoir was closed and then with the rest of the vacuum line isolated the expansion vessel was opened to the nickel reaction vessel and the BrF_5 vapour was frozen down into the base by immersing the bottom 3 cm in liquid nitrogen. A period of 5-10 minutes was allowed for full condensation and then the liquid nitrogen bath raised to within 6 cm of the top of the vessel. The

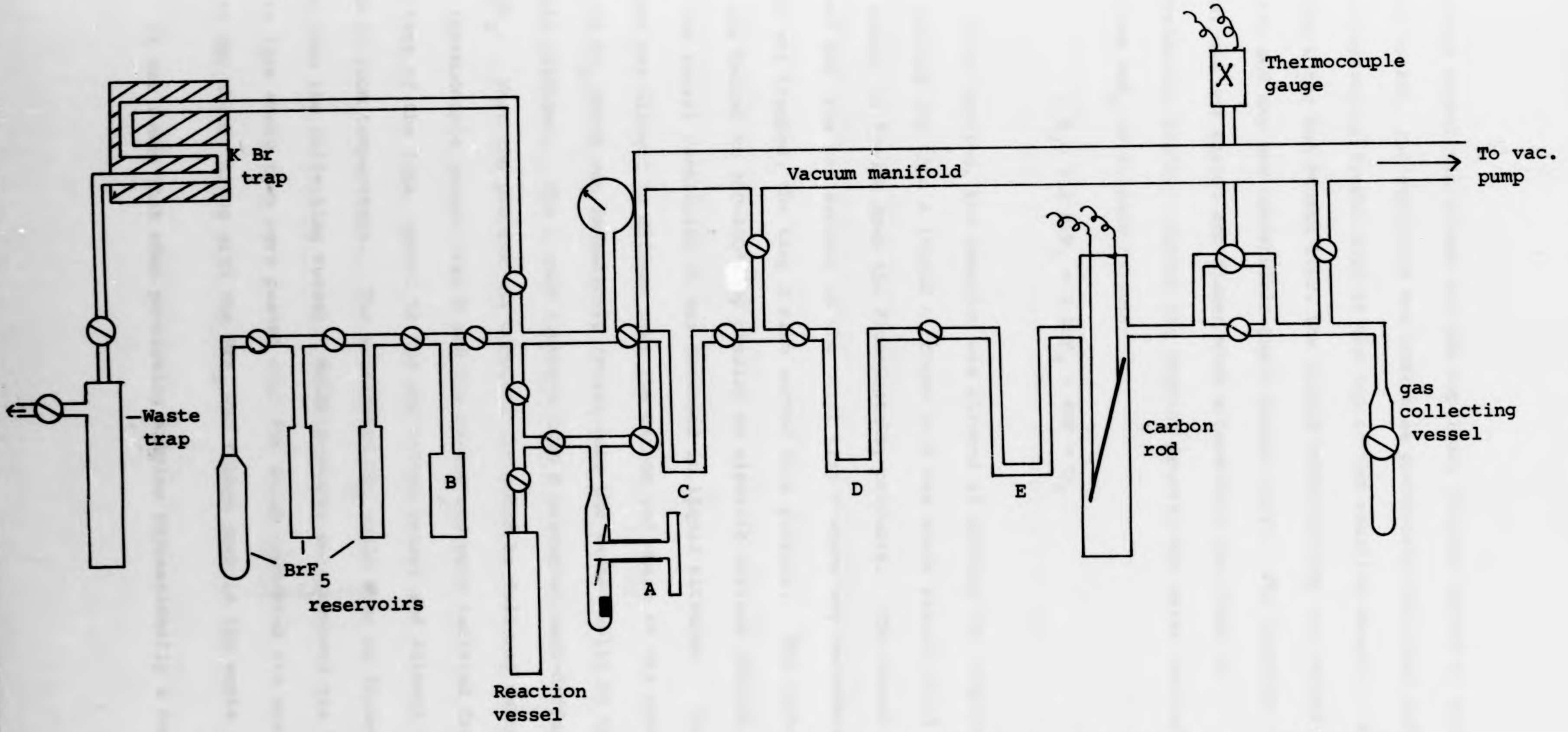


FIG. 2.2 Diagram of high-vacuum line for preparation of CO_2 gas from blood water for analysis of O^{18} isotope. The section of the line up to and including trap C was constructed of stainless steel, the remainder of pyrex glass.

expansion vessel was closed and the capillary breaker opened to the nickel vessel, the capillary was broken as previously described and the water vapour frozen down at the top of the reaction vessel. When all the water had frozen over, the liquid nitrogen trap was raised further and any non-condensible gases pumped away. The reaction vessel was now sealed and flamed with a hand-held gas flame to approximately 100°C. During the heating process the water reacted with the BrF_5 to release oxygen:-

$$2\ H_2O + 2\ BrF_5 = 2\ BrF_3 + 4HF + O_2$$

After heating, the reaction was allowed 15 minutes for completion and cooling and then a liquid nitrogen bath was again placed round the vessel to freeze down the fluorinated by-products. The vessel was opened and the gas exposed to the metal trap C where any uncondensed waste was trapped, the trap D also served this purpose. The carbon rod was heated to 300-400°C by passing an electric current through it, and the vessel containing it was immersed in liquid nitrogen. The oxygen was allowed to diffuse over the carbon rod where it was converted to CO_2 which was immediately frozen onto the vessel walls by the liquid nitrogen. The liquid nitrogen trap E prevented back-diffusion of CO_2. When the process was complete (it could be followed using the thermocouple gauge) trap E and the carbon rod were isolated from the rest of the line, opened to the collecting vessel and allowed to warm to room temperature. The sublimated CO_2 could then be frozen down into the collecting vessel. Waste products were removed via the waste line where they were passed over KBr which converted the waste HF to HBr which, along with the BrF_3 was frozen down in the waste trap.

It was found that when processing samples successionally a new capillary could be loaded whilst the previous one was reacting, at the same time yet another could be passed from the carbon rod to the collecting vessel. Using this method a sample could be processed in approximately 50 minutes. Memory problems experienced in the H/D line were negligible, but between samples the carbon rod was heated to red heat and opened to the vacuum pump, and more reagent was let into the reaction vessel which was re-heated. These two actions probably aided in eliminating any between-sample memory problems. The CO_2 samples were generally prepared in batches of six and then loaded onto the mass-spectrometer inlet manifold which held six sample tubes.

3. Analysis on the Mass-Spectrometer

The principles involved in analysing the two isotopes on the mass-spectrometer are very nearly identical. Since the analysis of hydrogen isotopes shows some irregularities it will be used by way of an example and the irregularities discussed.

The principle of operation of the mass-spectrometer is as follows, electrons emitted by a hot filament are accelerated by an electromagnetic field through one or more defining slits to form an electron beam. The electron beam is directed through a chamber containing the gas to be analysed at low pressure (ca. 10^{-4} mm Hg) and as a result there is produced within the beam a variety of ions. In the case of the analysis of Carbon Dioxide CO_2^+ ions are formed, and for hydrogen a variety of monatomic, diatomic and triatomic hydrogen ions are formed. These ions are drawn out in a direction perpendicular to the election beam by a small negative potential. The ions then pass through a series of collimating slits and the portion that remain are accelerated by an electric field to produce a ribbon of ions of very nearly constant energy. By directing the ribbon of ions through a magnetic field they are dispersed into an ionic spectrum, the place of each ion in the spectrum being dependent upon its mass, since the ions are of virtually constant energy, this spectrum is known as the mass spectrum. The mass spectrum falls upon the collector which consists of a narrow collimating slit with a collector plate behind, by which the current generated by ions of a particular mass can be detected and measured. By altering the ionic accelerating voltage the arc of curvature of the mass spectrum can be altered so that all the masses in the spectrum can be scanned individually if desired. The number of ions of a particular mass and charge formed at a fixed electron-beam intensity is a function of both the number of parent molecules in the unionized gas and their ionization efficiencies. If their ionization efficiencies differ corrections can be made and thus the current generated on the collector plate by the ions of a particular mass can be related to the number of molecules containing the ion in the parent gas.

In the case of hydrogen gas with low deuterium content (the type of gas important here) it is important to compare the mass 2 and mass 3 signals. In order to do this with minimum error the mass-spectrometer was equipped with double collecting plates so that both could be collected simultaneously. The mass 2 beam is primarily due to the H_2^+ ion with negligible contribution from the D^+ ion, the mass 3 beam is due to HD^+ ions and some H_3^+ ions. When analysing for the deuterium content of the gas it is only the HD^+ contribution to mass 3 which is of interest. It is assumed that the H_3^+ ion is formed by electron collision with H_2 or H which again collides with a neutral molecule. Thus the concentration of H_3^+ ions in the ribbon is proportional to the square of the pressure of the parent molecules, whereas the concentration of HD^+ ions is proportional to the pressure itself.

Thus it can be written that:-

$$I\ (\text{mass } 2) = a\, H_2^{+} p$$

$$I\ (\text{mass } 3) = a\, HD^{+} p + a\, H_3^{+} p^2$$

where: I = induced current on collector plate.

a = number of parent molecules.

p = pressure of gas in ionizing chamber.

Given the above relationships if I/p is plotted against p the current due to HD^+ ions only can be found by extrapolation to zero. In practice this is done by plotting the mass 2/mass 3 ratio against the pressure as measured by the H_2^+ ion signal, which is itself directly proportional to pressure.

The analysis of the O^{18} isotope was done as CO_2 gas, in this case the masses 44/46 were compared on a double collecting machine. The two masses are predominantly $C^{12}O^{16}O^{16}$ and $C^{12}O^{16}O^{18}$; the contribution of O^{17} is negligible and a C^{13} correction was applied to the machine results.

Since there are certain errors concerning discrimination and memory inherent in the operation of mass spectrometers, analysis was always done by comparing the signals of the unknown gas with those of a standard gas of known isotopic concentration.

2.3 FIELD TECHNIQUES

2.3.1 Location of House Martin Colonies

With future requirements in mind a survey was carried out of the Stirling region and the location of all the main House Martin colonies were mapped. The sites chosen for experimental purposes fulfilled most if not all of the following requirements:-

i. Colonies to be of reasonable size (> 8 nests).

ii. Nests to be easily accessible and replaceable with nest boxes.

iii. The siting of nests and flight paths of the adult birds to facilitate the operation of an efficient catching technique.

iv. Disturbance to nests and interference with associated apparatus to be negligible.

The sites chosen as a result of the survey were:-

a) Kippenross Home Farm, Dunblane, Perthshire, a mixed arable, beef and sheep farm situated 423 feet above sea level (map ref. NN794004) (approximately nine pairs decreasing to four in final year).

b) Cauldhame, Sherrifmuir, Perthshire, a large private house with associated fields and woodland, situated 997 feet above sea level (NN825011) (approximately nine pairs accessible, twenty inaccessible).

c) Naemoor Farm, Yetts of Muckart, Perthshire, a mixed dairy, arable farm situated 550 feet above sea level (NO016014) (approximately twenty-eight pairs, all accessible).

At Kippenross and Cauldhame natural House Martin nests were removed before the first season of the study, in their place removable nest boxes of a cement/sawdust composition were substituted. Naemoor had already been established as a study colony by D. M. Bryant, birds had been encouraged to nest in boxes from 1971 onwards. The nest boxes, when removed, had an open top to allow examination of the nest contents. Whenever birds built a natural nest they were left until lined and then removed, the lining transferred to a nest box and this fastened in exactly the same spot.

2.3.2 D_2O^{18} Field Protocol

(i) Capture of Adult Birds

The D_2O^{18} technique was only operated at Kippenross and Naemoor and at these study sites, nests were chosen where the adult bird returned to the nest by flying through an arch or opening. In practice this consisted of those nests situated underneath bridges or inside open fronted sheds. In both cases dropnet systems were devised to cover the archway, these nets were controlled by cords leading to a hide. From this hide the experimental nest and the flight path of the parents could be easily observed. When a parent bird returned to the nest the net was dropped over the entrance of the shed, (Figs. 2.3 and 2.4).

Between catches the nets were hoisted clear of the flight paths in order not to impede the bird's approach to the nest. Plastic ("Netlon") netting of the type used by gardners proved to be the most

FIG. 2.3 The yard at Naemoor Farm showing the open-fronted sheds inside which the House Martins nested. The birds were caught by dropping the nets which are suspended above the opening.

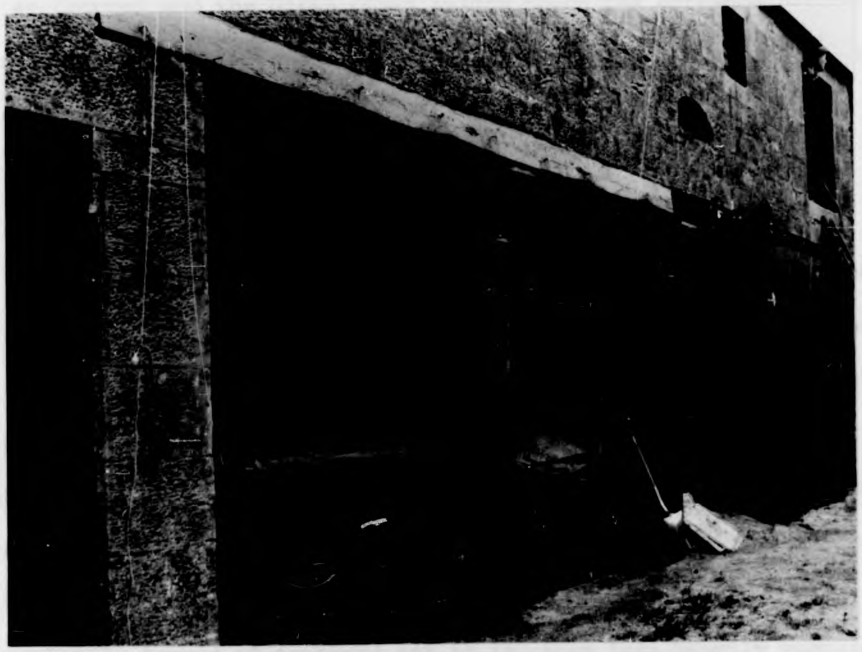


FIG. 2.4 **The yard at Naemoor Farm showing the catching nets in their dropped position.**

suitable type. It was cheaper and more readily available than mist netting and was more durable and involved less risk of injury to the birds. The net was left hoisted until the target bird was inside the nest, or perched at the entrance busily feeding young, the net was then dropped and the birds could seldom reach the entrance before it was completely covered. Using this method approximately 80% of the drops were successful in catching a bird.

(ii) Handling and Processing the Birds

Immediately after capture the bird was colour marked for identification purposes, the bird was weighed and sexed. Although there is no sexual dimorphism in the plumage of the House Martin the sexes can be discriminated in the breeding season by the development of the brood patch; that of the females extends high up over the rib cage and is devoid of feathers, whilst the male brood patch only covers the belly and lower rib cage. The male's brood patch is never completely devoid of feathers and it is often less heavily vascularised than that of the females (Bryant 1975b).

The volumes of O^{18} and D administered were calculated to bring the isotopic concentration in the birds to approximately 0.065 APE D and 0.18 APE O^{18}. The amounts required to do this were read from a calibration curve after weighing the bird. Isotopes were introduced as separate injections of aqueous solutions of 9.99% D_2O and 15.0% H_2O^{18}. A 17.06g bird (mean weight of birds injected) received 0.07 cm^3 of the D_2O solution and 0.14 cm^3 of the H_2O^{18} solution, a total of 0.21 cm^3 representing 1.92% of the total body water content of the bird. The sites of the injections, which were intraperitoneal are shown in Fig. 2.5. Since the amount of liquid injected was so small it was unnecessary to introduce it as a saline. The bird was then placed in

FIG. 2.5a An adult female House Martin during the breeding season, the feathers have been swabbed with alcohol to expose the brood patch. The isotopes were introduced by intraperitoneal injection at the sites marked with a cross (X) .

FIG. 2.5b Blood samples were taken by puncturing a leg vein and drawing the droplet of blood into small cappillaries.

a quiet darkened cage for approximately one hour. Preliminary experiments using budgerigars and canaries had shown that equilibration of the isotopes took approximately 45 minutes (see section 2.5.1). Lefebvre (1964) reported that in pigeons complete equilibration occurred within 60 minutes regardless of the method of injection (intravenous, intramuscular or intraperitoneal). Mullen (1970) found 2-2.5 hours was necessary for Perognathus formosus, whilst 30-40 minutes was found to be sufficient for Purple Martins (Utter & Lefebvre 1970).

Once isotopic equilibration had occurred the bird was removed from the cage and the initial blood samples were obtained. These were taken from a leg vein which runs close to the surface of the skin to the inside of the extensor muscle overlying the tarso-metatarsus. The vein was punctured using a 25 gauge needle and the drop of blood which welled to the surface was drawn inside a glass capillary. These capillaries had been prepared by drawing out a piece of 5 mm diameter pyrex tubing, they were then filled with heparin solution and oven dried, each one held approximately .01 - .05 cm^3. When the capillary was over half full it was removed from the drop of blood and shaken so that the blood droplet was held mid-way between the capillary ends. The end that had been in contact with the blood droplet was broken off and both ends were sealed by melting the glass in a very small, blue, oxy-propane flame. Sealing was instantaneous and great care was taken not to heat the blood inside as the evaporation and consequent condensation would have caused the isotopes to fractionate and induce errors in the final results. Six blood samples were taken in this fashion, allowing a maximum of three analyses of each isotope.

The flow of blood from the small wound could easily be stemmed by direct pressure, however, in the few cases where it appeared that bleeding might continue an alginate spray was used to promote clotting.

Before the bird was released the sexes were colour marked to aid identification in flight for the recapture. The second blood samples were taken in the same manner between 36 and 48 hours later, when the adult had a further six blood samples taken from it, was weighed and then released.

2.4 FIELD STUDIES

2.4.1 Breeding Biology Studies

A detailed account of the breeding biology of the House Martin in Britain has been given by Bryant (1975a). Studies of egg-laying, hatching, chick growth and fledging success were carried out during 1974. The results of these provided a basis for future application of the D_2O^{18} technique. The sites used were Kippenross and Cauldhame where nests were visited, on average, every second evening throughout the summer. Nest contents were recorded and young birds were weighed.

2.4.2 Average Daily Metabolic Rate (ADMR) Measurements

Since analysis time and expense are the limiting factors in the D_2O^{18} technique a very specific sampling regime had to be devised for the study. In total 26 adult birds rearing natural sized broods ranging from two to five nestlings were sampled; in addition the parents of three artificially enlarged broods, one of six and two of seven young were also measured. Measurements covered both first and second broods with the exception of those which had been experimentally enlarged which were all first broods.

Successful ADMR measurements were also carried out on three Swallows (Hirundo rustica) all females, rearing first broods of four and five nestlings and one second brood of three nestlings. The catching and processing of Swallows was carried out in exactly the same way as for House Martins. The body water content of H. rustica was not measured, but assumed the same as the House Martin.

2.4.3 Feeding Observations

Feeding rate observations were carried out on parent birds rearing broods of different sizes using visual and automatic recording during first and second brood rearing respectively.

(1) Visual Recording (First Broods)

The foraging rate of aerial feeding birds is dependent upon many factors, one important one being atmospheric conditions since these control the aerial food supply (Lack 1951; Bryant 1973). Thus in order to satisfactorily compare the feeding rate of different birds, observations should be carried out on each bird under uniform weather conditions. Similarly since the energy demand of the young changes as they grow, any record of adult feeding rates must be carried out on birds rearing broods at the same stage in the food demand curve. It has been shown that the food demand curve in House Martins reaches a plateau between nine and twenty days after hatching, after which it declines (D.M. Bryant, pers. comm.).

Taking these considerations into account, observations were carried out on broods which were on the plateau of the food demand curve, and all nests were observed during one day to ensure relatively constant atmospheric conditions. The nests observed were located in two separate places at Naemoor farm and all nests in each place were visible at the same time. The active day was divided into 30 minute intervals and observations made for this length of time at each place alternately. The adult birds had previously been colour-marked to distinguish the sexes, and the number of visits made by each parent bird to the nest in each 30 minute period were recorded.

The observations were made in two series:-

1. June 29th - July 2nd, 1976, covering 27.5 hours observations on six nests.

2. July 19th - July 23rd, 1976, covering 53 hours observations on twelve nests.

The atmospheric conditions were comparable during both sample series, both in terms of weather and food supply as measured using suction-trap catches. As an estimate of the amount of food delivered to the brood by the adults the faeces produced by the brood during the observation periods were collected by placing boards below each nest (Bryant 1972), they were freeze-dried and then weighed.

(2) Automatic recording (Second broods)

This was done by means of a nest-recording device, based on a design by Ward (1969) who used Tantalum-182 tags attached to the birds' legs and a scintillation detector placed six feet from the nest. Since the regulations controlling the use of radio-active materials in the field in Britain are strict a system had to be devised which involved a much lower level of radiation.

It was found that Iron-59 wire was the most suitable tag for use in the field, the relatively high emission meant that only small amounts needed to be used and the half-life of 45 days was of suitable length for the experimental period. High purity ("specpure") Iron wire was irradiated for 36 hours in a flux of 3×10^{12} n. cm^{-2} sec^{-1} in the nuclear reactor at the Scottish Universities' Research Reactor Centre, East Kilbride. At this flux Fe^{59} attains a specific activity of 54 $\mu Ci.g^{-1}$. The two sizes of tag used were 50 mg and 100 mg weights of the irradiated wire, which each gave emissions of 2.7 μCi and 5.4 μCi respectively. The lengths of wire were sheathed in shrink fit tubing to prevent rusting, they were attached to the birds' leg by strips of heavy duty self-adhesive tape and then covered in a layer of polystyrene cement. This assembly was light (< 200 mg), weather-proof and could be later removed with the least discomfort to the bird. When in position the tag did not hinder the birds' activities in any way.

For detection, a 1½" NaI crystal scintillation detector was placed 20 cm from the nest on an adjacent beam, see Fig. 2.6. This was connected by 25m of co-axial cable to a ratemeter and pen recorder, in this way the recording gear could be stored out of sight and sound of the nest, see Fig 2.7. A typical trace obtained by attaching a large and small tag to the male and female birds respectively is shown in Figure 2.8. Using this apparatus the activity of the birds could be monitored continuously 24 hours a day.

Two pairs of birds were treated in this way. Each pair had its brood size adjusted from two to five young and two days recordings were made at each brood size; all the nestlings were of an age corresponding to the plateau in the food demand curve.

FIG. 2.6 An adult House Martin perching at the entrance to the nest in order to feed its young. The NaI crystal and photomultiplier tube of the nest recorder are contained in the tube to the left of the nest box.

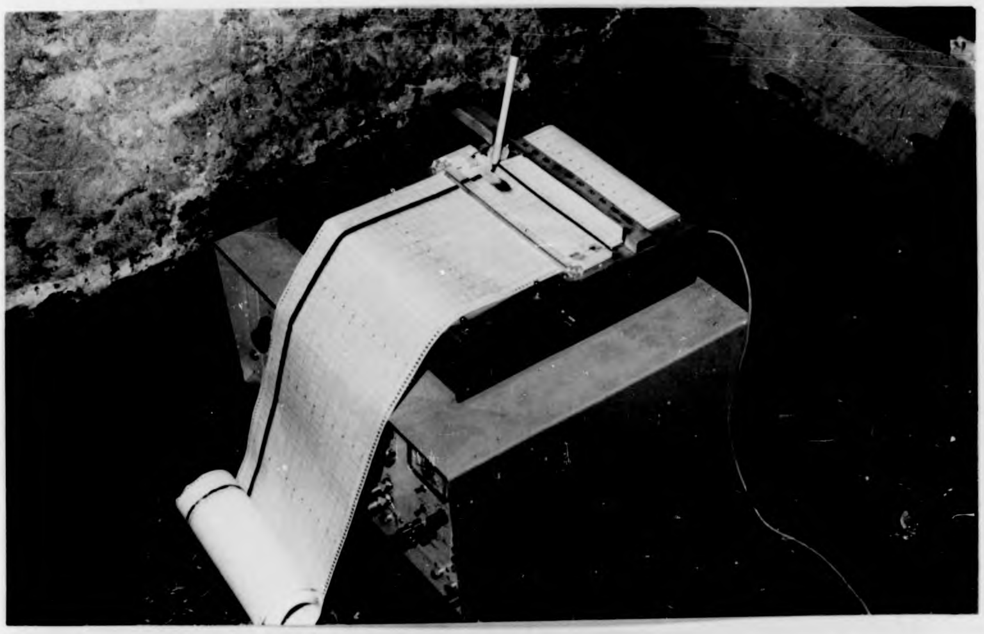


FIG. 2.7 The nest recorder in situ at the farm. The pen recorder is standing on top of a unit containing the E.H.T. supply, rate meter and amplifier.

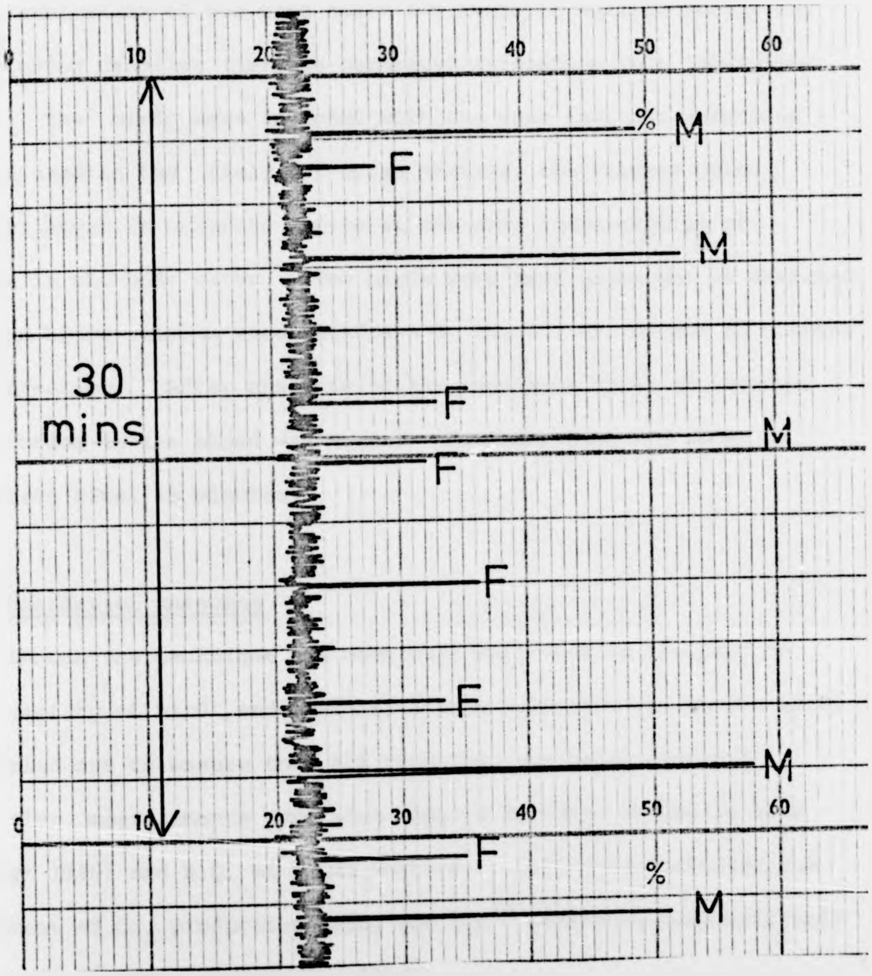


FIG. 2.8. Section of trace from the automatic nest recorder. 'M' denotes visit by male birds, 'F' denotes visit by female. (See text for explanation).

2.5 LABORATORY STUDIES

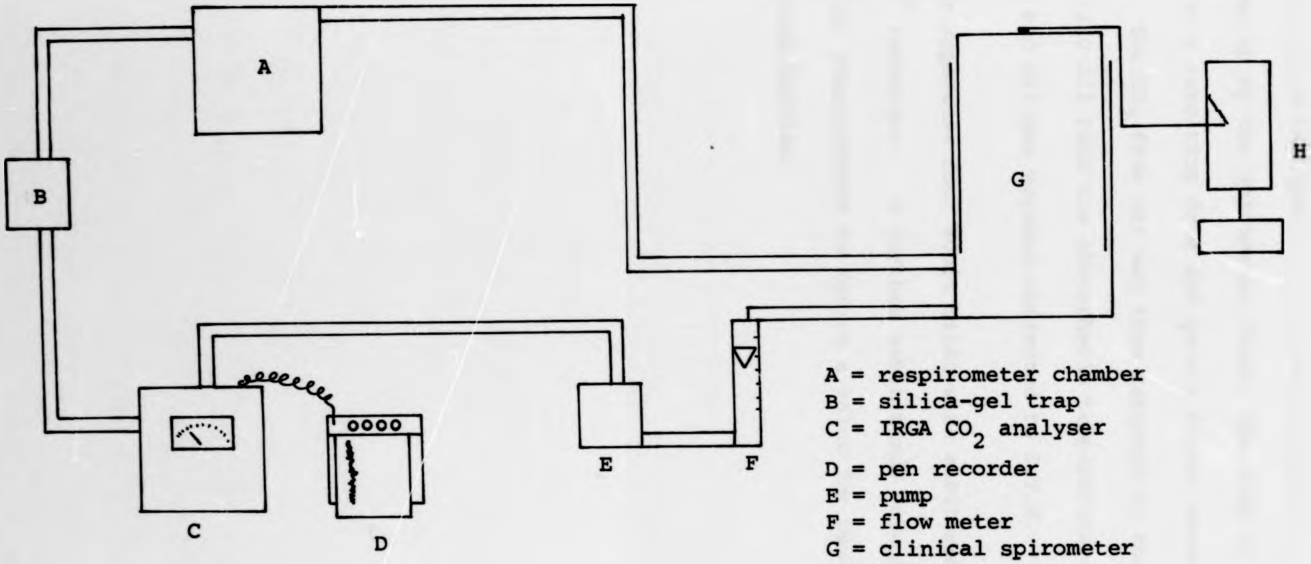
2.5.1 Isotopic Equilibration

Determination of the time taken for isotopic equilib ration was done by using Canaries (Serinus canarius) maintained in a laboratory aviary. The birds were injected with the same isotopic solutions as those used in the field for House Martins, the volumes being slightly larger in order to arrive at the same concentration of isotopes in the body water. The birds were kept quiescent in darkened cages and blood samples were withdrawn 5, 15, 30, 46, 60 and 90 minutes after injection. After analysis of the samples a curve of isotopic equilibration in the blood was drawn. Equilibration was shown to be complete after 45 minutes.

2.5.2 Validation Measures

Although the technique has been well validated in the past on a wide variety of birds and mammals, a less intensive validation study was carried out to ensure that the technique was being operated accurately; measurements were also made of Standard Metabolic Rate (Kendeigh 1970) and R.Q. of House Martins. Validation involves the measurement of CO_2 production using the D_2O^{18} technique simultaneously with one of the more classical methods.

A respirometer was constructed which could simultaneously measure CO_2 production and O_2 uptake (Figure 2.9). The bird was placed in the respirometer chamber at A, the air was extracted and passed through a silica-gel drying trap. It was then filtered before passing through an infra-red gas analyser manufactured by Mine Safety Appliances (MSA) Ltd., here the percentage CO_2 concentration was determined and recorded on a pen recorder. The gas then passed through the circulating pump and flow meter into a clinical spirometer, the chamber of



A = respirometer chamber
B = silica-gel trap
C = IRGA CO_2 analyser
D = pen recorder
E = pump
F = flow meter
G = clinical spirometer
H = recording drum

FIG. 2.9 Schematic diagram of respirometer train used in the laboratory studies which contained soda-lime to absorb CO_2. The reduction in pressure resulting from the absorption of O_2 by the bird and CO_2 by the soda-lime, was taken up by the spirometer float, the drop of the float was recorded on a revolving drum and gave a direct measure of O_2 consumption. The CO_2 free air was then returned to the respirometer chamber. During all runs the atmospheric temperature and pressure were recorded and all gas volumes corrected to S.T.P.

Using the apparatus four adult birds were monitored in conjunction with the D_2O^{18} technique. A further seven birds were monitored without isotopic measurements to derive a value for resting metabolism and R.Q. in House Martins.

3. RESULTS

3.1 BREEDING BIOLOGY

3.1.1 Clutch and Brood Size

Of the studies made at Cauldhame and Kippenross the overall mean clutch size was 3.53 (±0.84 s.d.) for first clutches and 2.75 (±0.96 s.d.) for second clutches. The mean brood size of the two sites was 3.35 (±1.13 s.d.) n=23 for first broods and 2.67 (±0.93 s.d.) n=13 for second broods. There was no significant difference in the mean clutch or brood size at either of these sites. Although clutch and brood size measurements were not carried out at Naemoor in this study the mean brood size averaged from 1970 to 1976 was 3.52 (±1.00 s.d.) n=144 for first broods and 2.92 (±0.84 s.d.) n=110 for second broods, (D.M. Bryant, pers. comm.). The larger sized broods at Naemoor resulting from the greater number of large clutches laid there. House Martins exhibit the phenomenon of clutch and brood size recession during the breeding season (Bryant 1975a); Naemoor was the largest and most well established of the three colonies and breeding began there earlier each year than at Cauldhame or Kippenross and thus contained a higher proportion of the large broods.

3.1.2 Nestling Development

Nestling development was monitored by recording individual nestling weight, at approximately 1930 hours each evening; by calculating the mean weight of all nestlings on each day after hatching a typical growth curve was constructed (Figure 3.1). Weight increase was sigmoidal up to the sixteenth day when it reached a peak and subsequently declined until fledging. The phenomenon of weight recession has been recorded in other hirundines (Peterson 1955; Edson 1930), but in few other passerines (Ricklefs 1968).

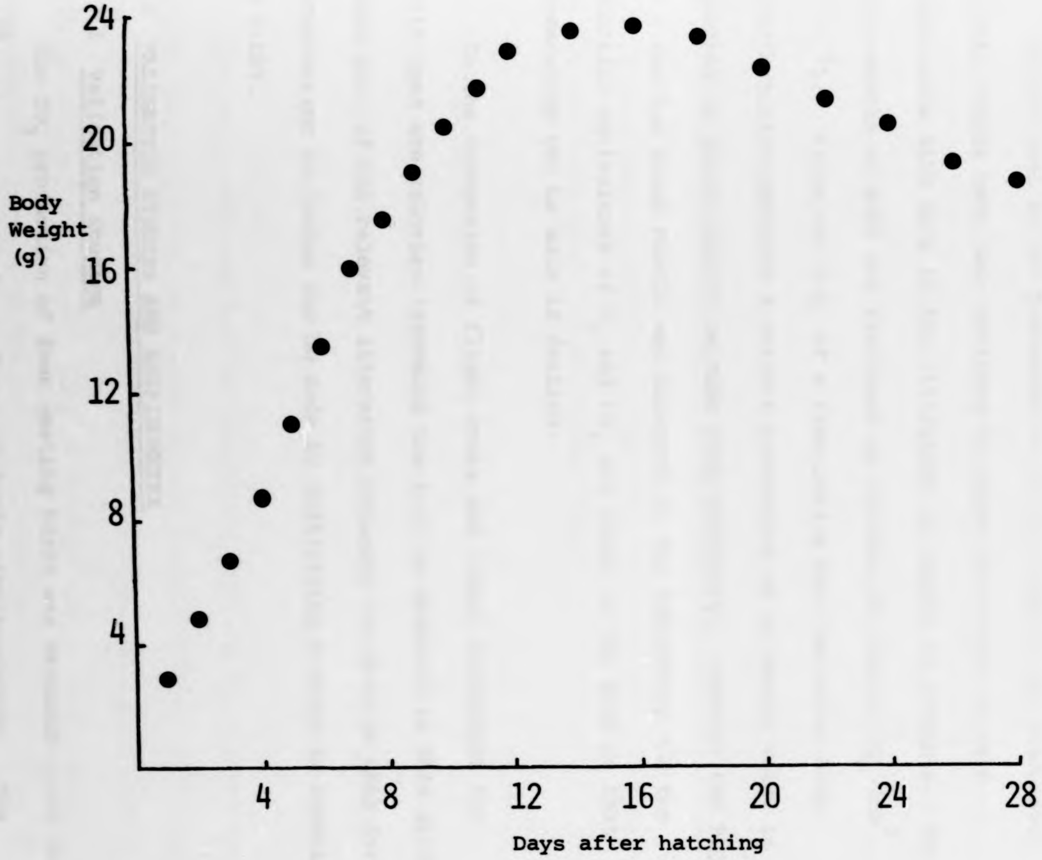


FIG. 3.1 Growth curve of nestling House Martins

3.1.3 Adult Weights

The mean weight of 17 adult male House Martins was 18.2 ± 1.3g and that of 21 adult females 17.5 ± 1.1g, this difference was not significant ($P > 0.1$); the mean weight of all adults was 17.81g ($n = 38$).

3.2 UNITS

Units used in the presentation of the results and discussion in this thesis have been designed to allow the reader to make comparisons with data in the literature as easily as possible. The measurements of ADMR are presented as volumes of expired CO_2 ($cm^3 . g^{-1} . h^{-1}$). Since the R.Q. of a free-living bird has never been satisfactorily measured a correct conversion to an energy value in calories or joules cannot be made with certainty. However the R.Q. of a resting House Martin was measured in the laboratory and the calorific equivalents of O_2 and CO_2 are given in the text so that conversions can be made if desired.

In the discussion of flight costs and energy investment the units used are calories (assuming the R.Q. as measured in this study), since much of the relevant literature presents the data in this form. A conversion to joules can be made by multiplying a value in calories by 4.187.

3.3 VALIDATION STUDIES AND RESPIROMETRY

3.3.1 Validation Studies

The CO_2 production of four resting birds was measured using the D_2O^{18} technique and infra-red gas analysis simultaneously. The mean absolute difference between the two methods was 6.64% and the total algebraic difference + 3.37% ($\frac{\text{gaseous - isotopic}}{\text{gaseous}}$ %) (Table 3.1).

Validation figures from eight other studies have been reported in the literature with mean absolute errors ranging from 3% to 12.4% (Table 3.2), the mean of these independently derived absolute errors is 7.07%. Thus it would appear that the D_2O^{18} technique as executed in this study involved a similar error to that previously reported.

3.3.2 R.Q. Measurement

The R.Q. of seven birds in which CO_2 production and O_2 uptake were monitored simultaneously, ranged from 0.72 - 0.79 with a mean of 0.75 (Table 3.3). This is a similar range to that obtained by Mellen & Hill (1955) (in Kleiber 1961, p.90) from fasting birds (also Farner & King, 1974). Since this is not a nitrogen-free measure (i.e. corrected for protein metabolism) very little can be stated about the metabolic substrate being utilised.

Caloric equivalent of O_2 at this R.Q. is 4.729 kcal. litre^{-1}, and for CO_2 6.319 kcal. litre^{-1} (Brody 1945).

3.3.3 Resting Metabolism Measurements

The conditions of measuring resting metabolism in this study followed the definition of standard metabolism (SMR) as presented by Kendeigh (1970) i.e. at complete rest in a post-absorptive state.

The values derived for the rate of CO_2 production of House Martins at rest in a respirometer chamber appear to fall into two categories (Tables 3.1 and 3.3). The CO_2 production of two birds was 3.35 and 3.42 $cm^3.CO_2.g^{-1}.h^{-1}$, with a mean of 3.39 $cm^3.CO_2.g^{-1}.h^{-1}$, whilst the remainder gave results in the range 1.25-2.49 $cm^3.CO_2.g^{-1}.h^{-1}$ with a mean of 1.87 $cm^3.CO_2.g^{-1}.h^{-1}$. From visual observations made at the time of the measurements it would appear that the two birds with

TABLE 3.1

CO_2 production of resting House Martins measured using gas analysis and isotopic (D_2O^{18}) methods and a comparison of the two.

Bird	Weight (g)	Barometric Pressure	t°C	Δt(h)	cm^3 CO_2 $g^{-1}.h^{-1}$	cm^3 CO_2 at S.T.P.	Isotopic $CO_2.g^{-1}h^{-1}$	% diff.
A	17.58	770.0	22.0	26.67	3.57	3.35	3.55	+ 5.97
B	15.60	775.0	23.0	18.75	1.92	1.77	1.68	- 5.08
C	17.15	753.7	24.0	23.25	2.28	2.07	2.04	- 1.45
D	16.00	754.2	23.2	16.75	1.95	1.78	2.03	+14.04
				Mean algebraic difference				+ 3.37
				Mean absolute difference				6.64

TABLE 3.2

Reported differences between D_2O^{18} method of measuring CO_2 production and other methods.

Reference	Mean Absolute Diff. %	Mean Algebraic Diff. %	Species (no. of samples)
Lefebvre 1962	8	-6	Columbia livia (10)
Little & Lifson 1975	8 & 1		Tamais striatus (2)
Lifson et al 1955	7	-3	Mus musculus (15)
Lee and Lifson 1960	4	+2	Rattus norvegicus (7)
McLintock et al 1958a	3		Mus musculus (5)
McLintock et al 1958b	12.4	+9	Perognathus formosus (8)
Present study	6.64	+3.37	Delichon urbica (4)

TABLE 3.3

Simultaneous measurement of CO_2 production and O_2 uptake of House Martins at rest in a respirometer chamber

Bird	Weight (g)	Barometric Press. (mm)	Temp. °C	Δt (h.)	CO_2 $cm^3.g^{-1}.h^{-1}$	CO_2 correct to S.T.P.	O_2 $cm^3.g^{-1}.h^{-1}$	O_2 correct to S.T.P.	R.Q.*
1	17.15	753.75	24.0	23.25[1]	2.28	2.07	2.95	2.68	0.77
2	17.0	755.75	24.0	13.75[1]	1.38	1.25	1.75	1.59	0.79
3	16.0	754.2	23.2	16.75[1]	1.95	1.78	2.71	2.47	0.72
4	17.5	768.5	21.5	6.25	1.98	1.85	2.68	2.51	0.74
5	19.31	755.5	22.0	6.92	3.73	3.42	4.91	4.52	0.76
6	16.95	767.25	23.5	7.5	2.69	2.49	3.64	3.38	0.74
7	18.35	755.8	23.0	7.58	2.09	1.91	2.79	2.55	0.75
								Mean =	0.75

* R.Q. is calculated from the volumes of CO_2 and O_2 at S.T.P.

[1] measurements made overnight

higher resting metabolism did not fall into a completely quiescent state whilst the measurements were carried out, but remained awake and alert. The latter group with the lower range of CO_2 production adjusted well to the respirometer and were either asleep or sitting quietly throughout most of the measurements.

Thus it is likely that the value of 1.87 $cm^3\ CO_2.g^{-1}.h^{-1}$ as exhibited by the latter group is the most accurate estimate of the metabolic level of a House Martin at rest in the nest at night. The higher estimate of 3.39 $cm^3.CO_2.g^{-1}.h^{-1}$ is probably more useful as a measure of the metabolic rate of a House Martin perching at the nest or on wires during the day, where the bird is not flying but remaining alert.

3.4 FIELD METABOLISM MEASUREMENTS

Factors which may have influenced the Average Daily Metabolic Rates of the adult free-living House Martins, monitored using the D_2O technique, may be categorized as follows:-

a. Procedural differences between each measurement.

b. Environmental conditions prevailing at the time of measurement.

c. Reproductive commitment of each bird at the time of measurement.

d. Differences in the physical attributes of each bird.

A more detailed discussion of each of these variables can be found in Appendix II.

In this third section the measured ADMR's will be analysed in respect of each of the variables; in doing so each sex will be treated independently where appropriate.

3.4.1 Analysis of Factors Affecting AMDR[1]

Although the majority of the birds sampled reared their broods to successful fledging the pair in nestbox C in 1976 were an exception. This pair was one of the experimental pairs which had the brood artificially enlarged from three to seven young and although the D_2O^{18} measurements were carried out whilst all seven young were still alive it was clear they were undernourished and shortly after the experiments two of the brood died. Since this pair were an obvious anomaly all the results gathered from them (D_2O^{18}, feeding rates etc.) were excluded from the main analysis and are considered as a special case in a later section.

1. Procedural Variables

Although the experimental period (Δt) ranged from 21 to 52 hours this difference in itself did not influence the results (Fig. 3.2), the correlation coefficient between ADMR and Δt was $r = -0.12$ ($p > 0.1$). However as explained earlier, variation in Δt also resulted in different proportions of rest and activity being included in the final ADMR. Since the birds were roosting for the approximate seven-hour period of darkness each night the ADMR was corrected for any period of inactivity by assuming a resting metabolic level of 1.87 cc. $CO_2.g^{-1}.h^{-1}$ (as measured in the respirometer) during roosting. The relationship between this "active" metabolic level and ADMR was very consistent (Fig. 3.3) and the relationship between the two described by the equation:

$$\text{ADMR} = 0.72 \times \text{Active Metabolism} + 0.73, \; r = 0.95 \; (p < 0.001)$$

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[1] Raw data may be found in Appendix III

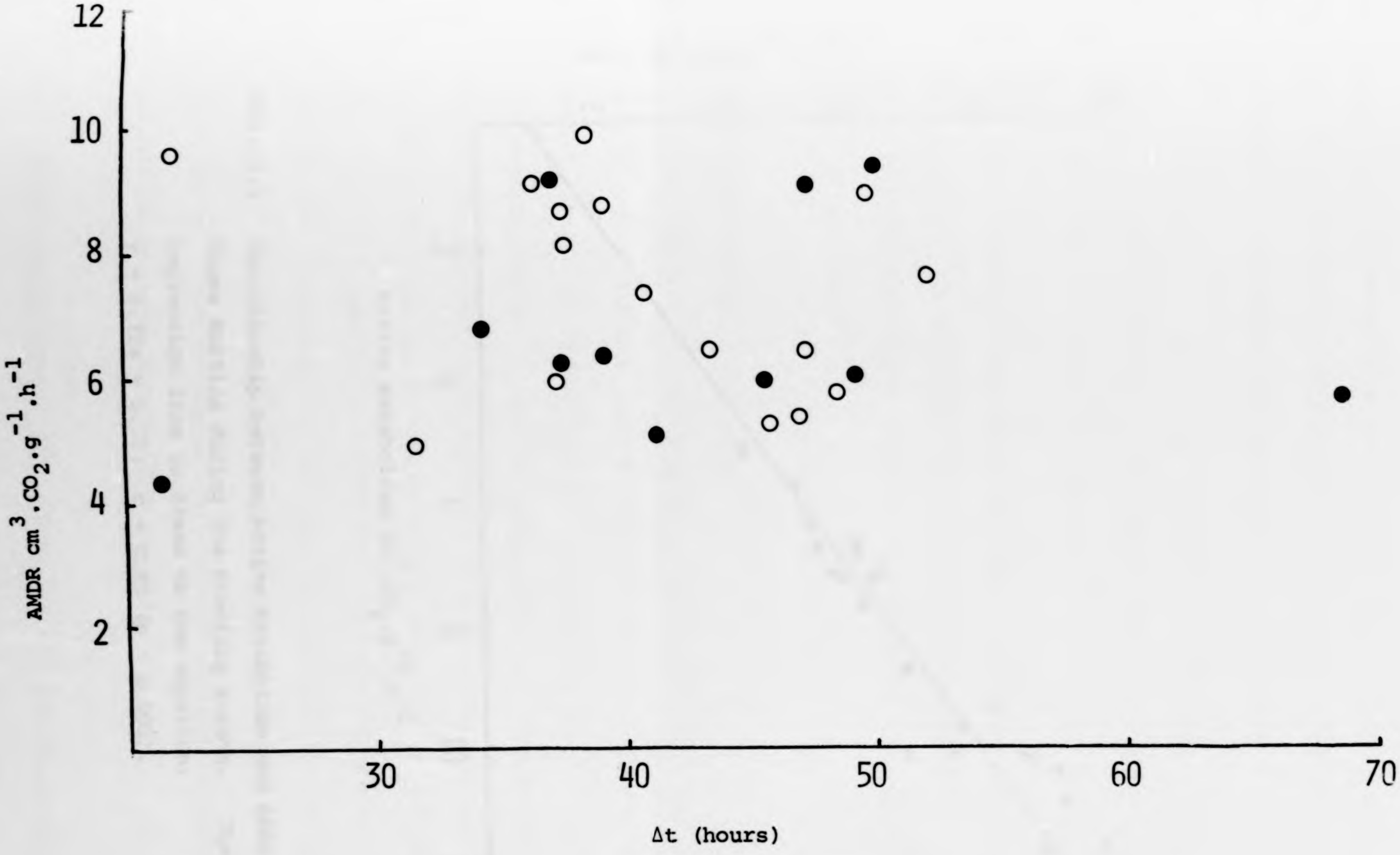

FIG. 3.2 Relationship between ADMR and length of experimental period (Δt) for House Martins, when ADMR is measured using the D_2O^{18} technique.

● = males
○ = females

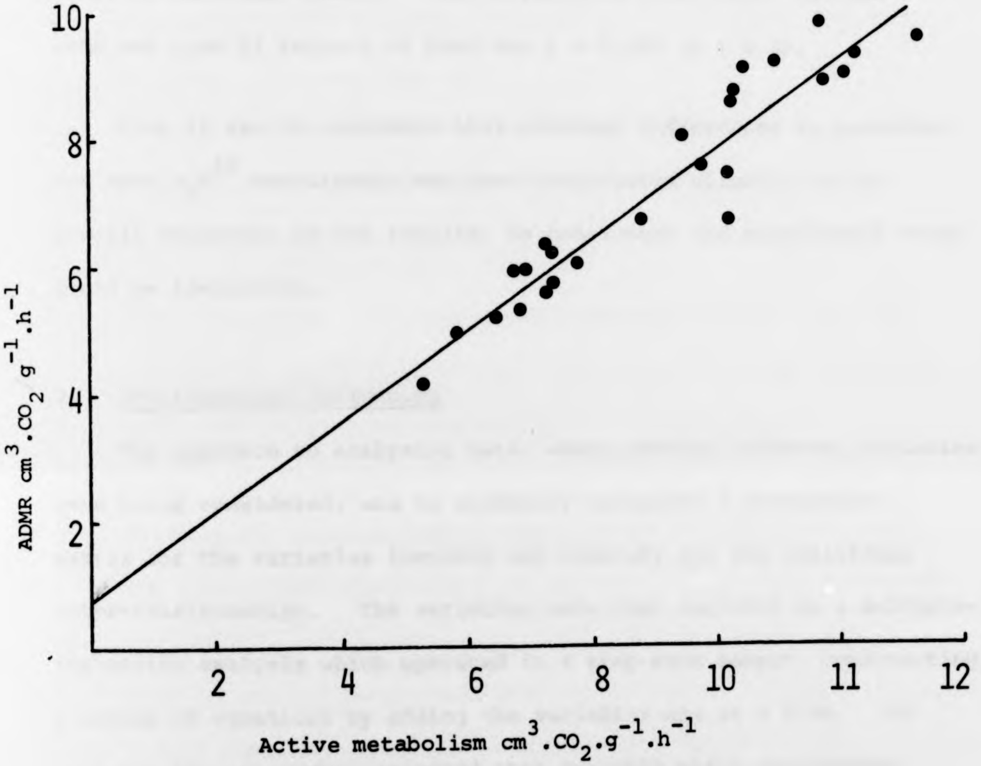

FIG. 3.3 Relationship between Active metabolism and ADMR for House Martins during the breeding season. The regression line is drawn to the equation: $y = 0.72x + 0.73$; $r = 0.95$ ($p < 0.001$).

Since the two metabolism measurements were so closely correlated, it was considered preferable to retain the data in its original form, i.e. ADMR comprising both day and night metabolism.

There was no significant effect of variation in timing of the start of each experiment. The correlation coefficient between ADMR and time of release of bird was $r = 0.069$ ($p > 0.1$).

Thus it can be concluded that although differences in procedure for each D_2O^{18} measurement may have contributed slightly to the overall variation in the results, no consistent and significant trend could be identified.

2. Environmental Influences

The approach to analysing data, where several different variables were being considered, was to initially calculate a correlation matrix for the variables involved and identify all the individual inter-relationships. The variables were then included in a multiple-regression analysis which operated in a step-wise manner, constructing a series of equations by adding the variables one at a time. At any step the programme selected that variable which contributed most to the explanation of the residual variance in the dependent variable. In this way the programme built up a multiple-regression equation of those variables which were of greatest significance. (Significance level chosen was $p \leq 0.05$).

(a) Relationship Between ADMR of Male Birds and the Environment

Single correlation coefficients between male ADMR and environmental variables suggested that rainfall and day length were two variables likely to be of some importance (Table 3.4). When all the variables were included in a step-wise multiple regression analysis the most significant variables proved to be rainfall, maximum temperature and day length (Table 3.5); they accounted for 91.97% ($r^2 \times 100$) of the variation in the data. The standardised partial regression coefficients (β weights) indicated that maximum temperature was the most important variable followed by day length and rainfall in that order; all were significant at less than 1%. It is notable that although food abundance did not form a significant element when included in the equation it had the highest β weight of those variables not included.

Thus, as maximum temperature and rainfall increase, the ADMR of male birds increased whereas the relationship with day length was a negative one; ADMR decreased as day length increased.

(b) Relationship Between ADMR of Female Birds and the Environment

From preliminary examination of the data, using simple correlation coefficients, it appeared that there were no significant relationships between female ADMR and environmental variables (Table 3.6). This conclusion was confirmed when the variables were included in a multiple regression analysis since none of the environmental variables could be used singly or combined to form a significant regression describing the ADMR of female birds.

3. Reproductive Commitment Variables

(a) Males

There are basically only two reproductive commitment variables that need to be considered for each sex: brood mass and brood number (i.e. 1st or 2nd brood). Considering single regression coefficients with the ADMR of male birds, metabolic brood weight

TABLE 3.4

Matrix of Correlation coefficients for environmental variables at the time of measurement of ADMR in male House Martins during the breeding season.

	Food Abund. (Log. suct. trap catch)	Daylength (hours)	Wind (Beaufort No.)	Rainfall (in)	Min. Temp. (°C)	Max Temp. (°C)
ADMR	0.05	-0.63*	-0.39	0.75**	0.25	0.10
Max temp	0.60*	0.46	-0.04	-0.28	0.52	
Min temp	0.46	0.22	-0.44	-0.01		
Rainfall	-0.11	-0.43	-0.48			
Wind	-0.29	0.08				
Day length	0.09					

* $p \leq 0.05$

** $p \leq 0.01$

TABLE 3.5

Multiple regression analysis of the effect of environmental variables on the ADMR of adult male House Martins during the breeding season.

	Multiple Regression Coefficient	Standardised Partial Regression Coefficient	Cumulative Coefficient of Determination		
Variable	b	β.Wt.	$r^2 \times 100$	F	P
Rainfall	0.718	0.649	57.6%	24.63	<0.01
Max temp	0.296	0.557	68.7%	18.16	<0.01
Day length	-0.691	-0.587	91.9%	17.37	<0.01

Constant = 10.80

Multiple r = 0.95

Multiple regression variance ratio: F = 22.918 ($p < 0.01$)

TABLE 3.6

Matrix of Correlation coefficients between environmental variables of the time of measuring the ADMR of female House Martins during the breeding season

	Food Abund. (Log suction trap catch)	Daylength (hours)	Wind (Beaufort No.)	Rainfall (in)	Min. Temp (°C)	Max Temp (°C)
ADMR	-0.06	-0.42	0.25	0.02	-0.10	-.29
Max Temp	0.55*	0.14	-0.22	-0.21	-0.01	
Min Temp	0.23	0.18	-0.22	0.11		
Rainfall	0.22	0.04	0.24			
Wind	-0.19	0.06				
Day length	0.01					

* $p \leq 0.05$

TABLE 3.7

Multiple regression analysis of the effect of reproductive commitment variables on the ADMR of male House Martins

	Multiple Regression Coefficient	Standardised Partial Regression Coefficient	Cumulative Coefficient of Determination		
Variable	b	β.Wt.	$r^2 \times 100$	F	P
Metabolic brood weight	0.248	0.795	52.4%	62.29	<0.001
Brood number	2.323	0.643	93.3%	142.67	<0.001

Constant = 0.431

Multiple r = 0.96

Multiple regression variation ratio : F = 48.78 ($p < 0.001$)

shows the strongest relationship with $r = 0.72$ ($p < 0.01$) whilst for brood number, $r = 0.55$ ($p < 0.05$). When included in a multiple regression equation the two accounted for 93.3% of the variation in the data, with brood weight contributing most to the explanation (Table 3.7).

Male birds therefore showed an increase in ADMR from first to second broods and also with increasing brood weight.

(b) Females

Of the two variables only brood number was significantly correlated with ADMR of female birds ($r = 0.54$: $p < 0.05$). In the same way as the male birds, the relationship was a positive one indicating a higher ADMR at the time of rearing second broods. The equation relating brood number to ADMR of females accounted for 29.8% of the variation in the data (Table 3.8).

Comparison of responseof male and female to Reproductive Commitment Variables

Some sexual differences were again apparent when considering reproductive commitment; the ADMR of male birds showed a positive relationship with metabolic brood weight, although both shared a common feature in having a high ADMR at the time of second brood rearing (Fig. 3.4).

The relationship between ADMR and metabolic brood weight for males rearing first broods was:-

$$\text{ADMR} = 0.23\ (\text{brood weight})^{0.66} + 3.01,\ r = 0.96\ (p < 0.001)$$

and for second broods

$$\text{ADMR} = 0.36\ (\text{brood weight})^{0.66} + 3.64,\ r = 0.98\ (p = 0.06)$$

An analysis of covariance indicated that the regression constants of these equations differed significantly ($p > 0.001$) whilst the regression coefficients did not.

The mean ADMR of female birds raising first and second broods respectively differed significantly ($t = 2.42$; $p < 0.05$).

4. Relationship Between Power Requirements for Flight and ADMR

Power required for flight was calculated after Pennycuick (1972) (see Appendix II).

(a) Males

The single correlation coefficient between ADMR of male birds and power requirement for flight was not significant at the 5% level ($r = -0.39$: $p > 0.1$). Since there were too few observations ($n = 5$) to include in a multiple regression analysis it must be concluded that there was no significant relationship between the two.

(b) Females

The single correlation coefficient between ADMR of female birds and power requirement was $r = 0.33$ ($p > 0.1$) (Fig. 3.5). However when included in a multiple regression analysis, brood number and power requirement together accounted for 84.05% of the variation in female ADMR data, the standardised partial regression coefficients (β weights) indicated that power requirements were of lesser importance than brood number (Table 3.9). Thus it would appear that when the brood number differences were accounted for, those females with the largest power requirements for flight had the highest ADMR

TABLE 3.8

Regression equation relating brood number to ADMR of female House Martins

$$\text{ADMR} = 4.898 + 2.025 \times \text{Brood Number}$$

$r = 0.54$

$F = 5.535$ ($p < 0.05$)

$r^2 \times 100 = 29.8\%$

TABLE 3.9

Multiple regression analysis of the relationship between brood number and power requirements for flight and ADMR of female House Martins during the breeding season

	Multiple Regression Coefficients	Standardised Partial Regression Coefficients	Cumulative Coefficients of Determination		
Variable	b	β.Wt.	$r^2 \times 100$	F	P
Brood Number	3.249	0.881	55.5%	27.42	< 0.01
Power requirements	15.747	0.551	84.1%	10.72	< 0.05

Constant = - 6.49

Multiple r = 0.91

Multiple regression variance ratio $F = 15.81$ ($p < 0.01$)

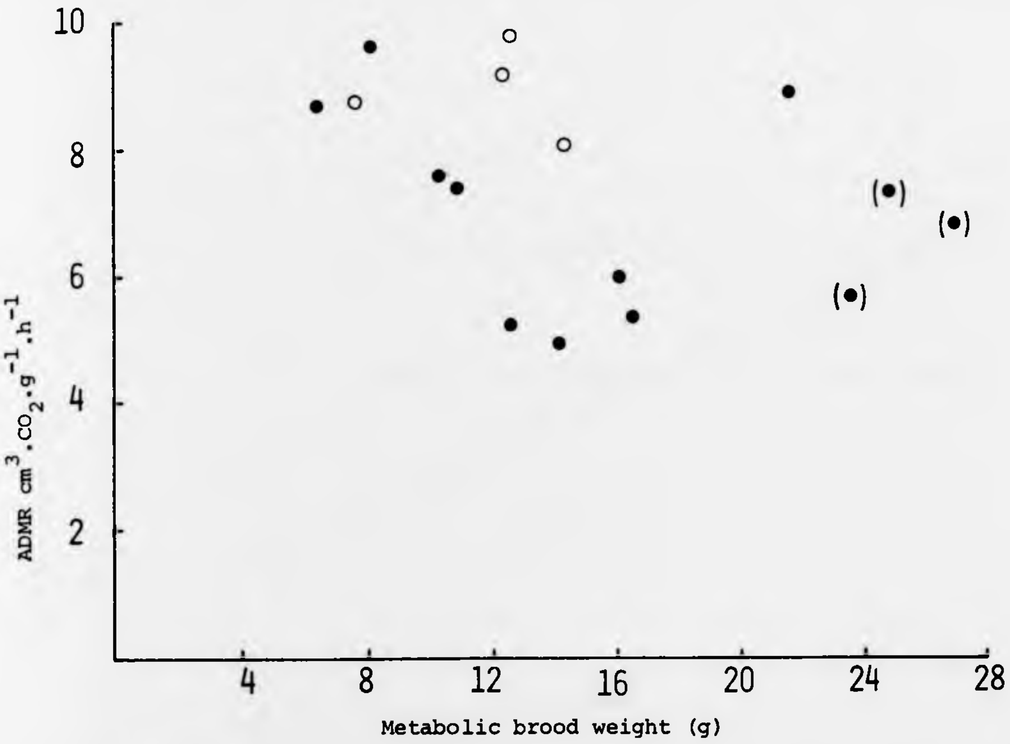

FIG. 3.4 (a)

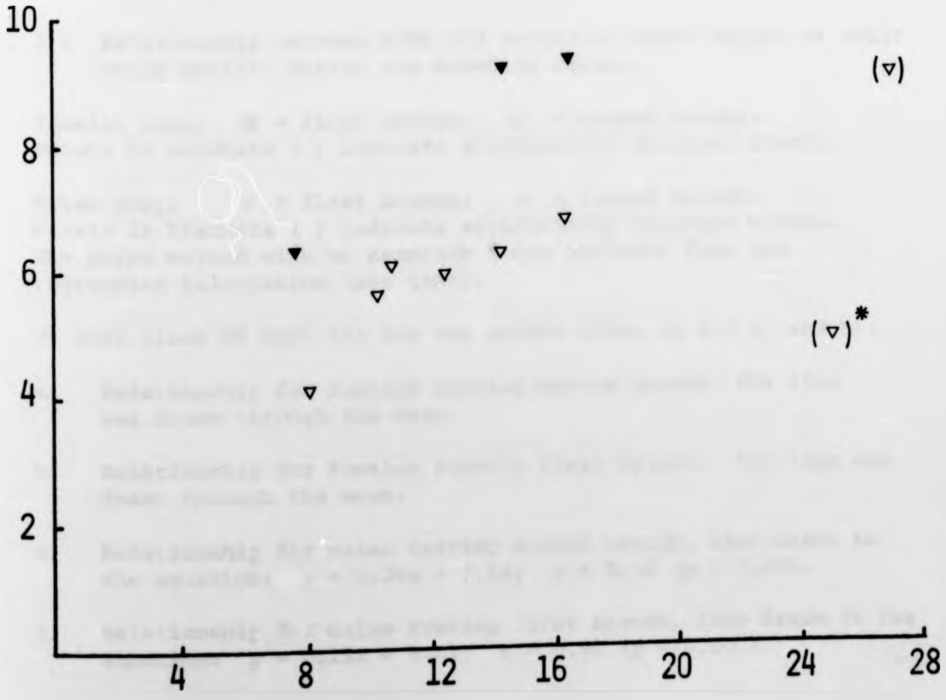

FIG. 3.4 (b)

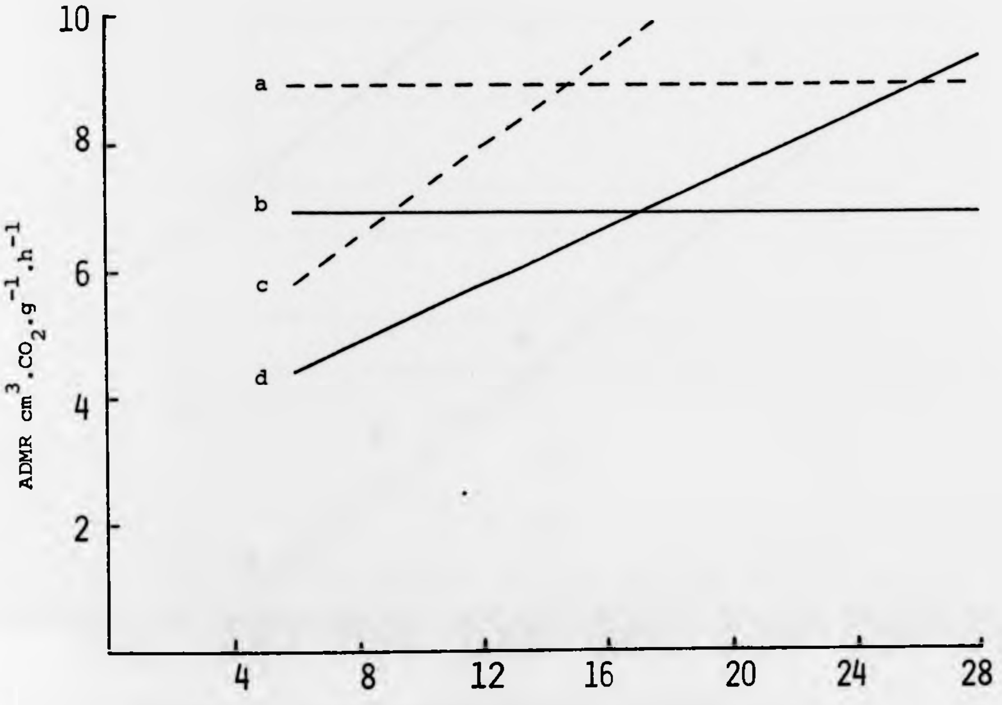

FIG. 3.4 (c)

FIG. 3.4 Relationship between ADMR and metabolic brood weight of adult House Martins during the breeding season.

a) Females only; ● = first broods; ○ = second broods; Points in brackets ( ) indicate artificially enlarged broods.

b) Males only; ▽ = first broods; ▼ = second broods; Points in brackets ( ) indicate artificially enlarged broods. The point marked with an asterisk * was excluded from the regression calculation (see text).

c) To show lines of best fit for the points shown in 3.4 a) and b):

a. Relationship for females rearing second broods, the line was drawn through the mean.

b. Relationship for females rearing first broods; the line was drawn through the mean.

c. Relationship for males rearing second broods, line drawn to the equation: $y = 0.36x + 3.64$; $r = 0.98$ ($p > 0.06$).

d. Relationship for males rearing first broods, line drawn to the equation: $y = 0.23x + 3.01$; $r = 0.96$ ($p > 0.001$).

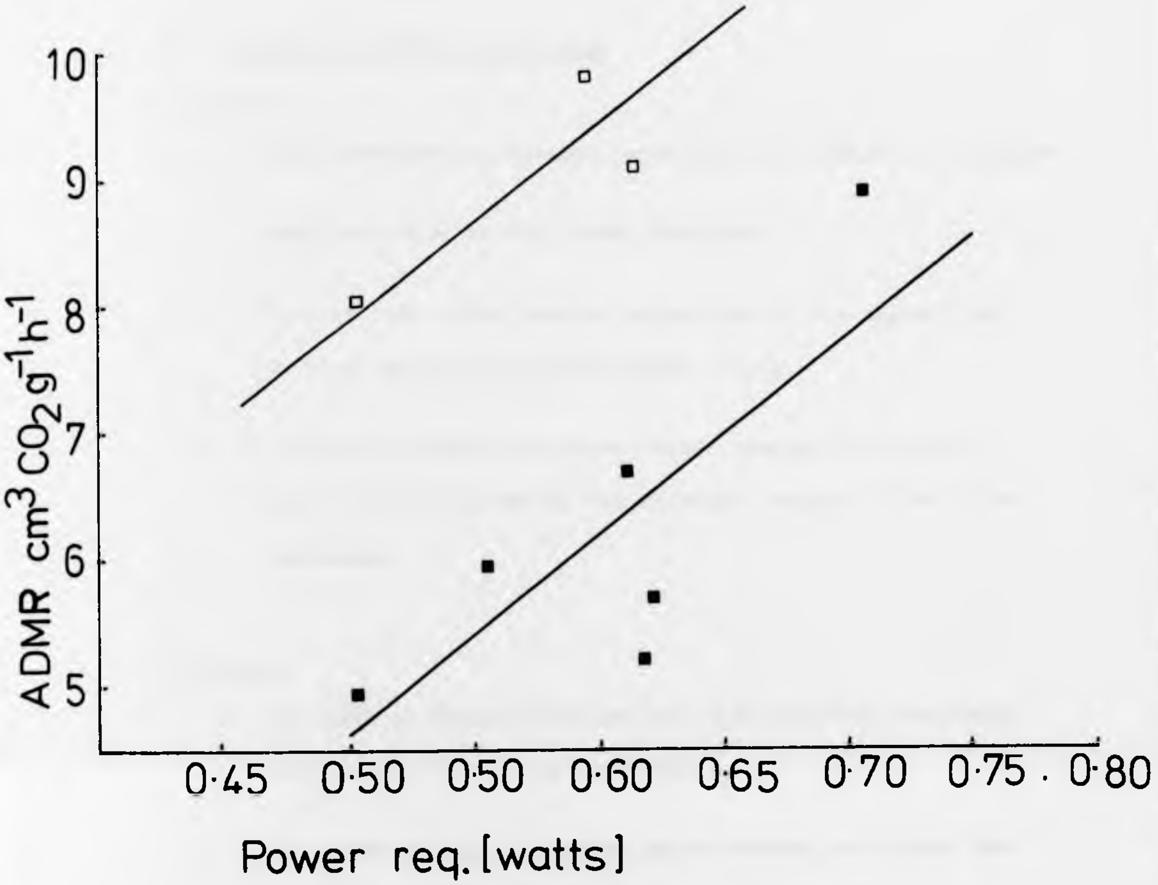

FIG. 3.5 Relationship between ADMR and power required for flight calculated after Pennycuick (1972) for female House Martins during the breeding season; partial regression lines drawn to the equation:-

ADMR = Brood number × 3.25 + Power req. × 15.75 - 6.49

■—■ = first broods

□—□ = second broods

3.4.2 Summary of ADMR Relationships

(a) Males

i ADMR increased as maximum temperature and rainfall increased.

ii ADMR increased as day length decreased.

iii ADMR of male birds rearing second broods was higher than that of male birds rearing first broods.

iv During both first and second brood rearing the ADMR of male birds increased as the metabolic weight of the brood increased.

(b) Females

i The ADMR of female birds was not significantly correlated with any environmental variables.

ii The ADMR of females rearing second broods was higher than that of females rearing first broods.

iii Unlike male birds the ADMR of female birds did not show any relationship with the metabolic weight of the brood.

iv As the power required for flight increased so the ADMR of female birds increased.

3.4.3 ADMR of Free-living Swallows (H. rustica)

The ADMR of a female Swallow raising a first brood of four nestlings was 4.14 $cm^3.CO_2.g^{-1}.h^{-1}$, and the ADMR of the same bird rearing a second brood of three nestlings was 6.23 $cm^3.CO_2.g^{-1}.h^{-1}$. The ADMR of another female rearing a first brood of five nestlings was 10.58 $cm^3.CO_2.g^{-1}.h^{-1}$.

Although these data were too few to carry out the same detailed analysis as for the House Martin the first bird showed a second-brood increase in ADMR comparable to the House Martin. The data were also useful in estimating the cost of flight in this species (see section 4.2).

3.5 FEEDING RATE MEASUREMENTS

3.5.1 Adult Attendance

Feeding rate measurements were carried out during first brood rearing using visual observations and during second brood rearing using nest recording equipment. The reproductive and environmental variables that were used in the analysis of free-living metabolism were used to examine variations in feeding rates. Due to the different techniques used in each case the data for first and second broods were examined independently.

(1) First Broods

No rainfall was recorded on any of the days that the feeding observations of first broods were carried out and since the observations were done on consecutive days day length changes were negligible.

The rate (feeds h^{-1}) of feeding first broods by male birds was positively correlated with metabolic brood weight ($r = 0.74$; $p = 0.001$) and negatively correlated with minimum temperature ($r = -0.30$; $p = 0.02$). These two variables were also correlated in the same way with the feeding rate of female birds ($r = 0.56$; $p = 0.001$ for metabolic brood weight and $r = -0.46$; $p = 0.001$ for minimum temperature) (Table 3.10). When included in a step-wise multiple regression analysis only brood weight formed a significant equation relation to the feeding rate of male birds, whilst both minimum temperature and brood weight

TABLE 3.10

Matrix of correlation coefficients for variables pertaining to the rate that male and female House Martins deliver food to first broods.

	Metabolic Brood Wt. (g)	Min. Temp (°C)	Max. Temp (°C)	Wind (Beaufort)	Female feeds (no. h^{-1})
Male feeds	0.74 ***	-0.30 *	0.2	-0.01	0.61 ***
Female feeds	0.56 ***	-0.46 ***	0.24	-0.04	
Wind (Beaufort)	-0.08	0.14	-0.33 *		
Max Temp (°C)	0.23	-0.32 *			
Min Temp (°C)	-0.15				

* $p \leq 0.05$

** $p \leq 0.01$

*** $p \leq 0.001$

formed a significant equation relating to the feeding rate of female birds, (Tables 3.11 and 3.12).

Thus it would appear that both males and females increase their rate of feeding as the metabolic weight of first broods increases (Fig. 3.6). However the rate of increase is higher for the males than it is for the females, so that although the male initially delivers fewer feeds than the female to the newly hatched brood he delivers more feeds to the young once they have a metabolic weight greater than 13.0g. An analysis of covariance showed that the two regression coefficients differed significantly ($p < 0.001$).

(2) Second Broods

As with first brood measurements day length changes over the observation period were negligible and so were excluded from the analysis, however rainfall was recorded on certain days and thus was included.

The number of feeds h^{-1} delivered by male birds to second broods was correlated with metabolic brood weight ($r = 0.69$; $p = 0.004$) and rainfall ($r = -0.44$; $p = 0.06$), whilst that of female birds was correlated with minimum temperature ($r = -0.57$; $p = 0.02$) and rainfall ($r = -0.42$; $p = 0.077$) (Table 3.13). However when these variables were included in a step-wise multiple regression analysis, only metabolic brood weight formed a significant relationship with the feeding rate of male birds and only minimum temperature produced a significant equation relating to the feeding rate of female birds (Table 3.14). The relationship between the feeding rate of each sex and metabolic brood weight is shown in Figure 3.7.

TABLE 3.11

Regression equation relating the metabolic weight of the brood to the rate of food delivery by male House Martins

Feeds per hour = 0.575 × met. bd. wt - 0.573

$r = 0.739$

$r^2 \times 100 = 54.72\%$

$F = 54.38$ ($p < 0.001$)

TABLE 3.12

Multiple regression analysis of environmental and reproductive variables and their relationship to the rate of food delivery to the brood by female House Martins

	Multiple Regression Coefficient	Standardised Partial Regression Coefficient	Cumulative Coefficient of Determination		
Variable	b	β.Wt.	$r^2 \times 100$	F	P
Met. Brood Weight	0.294	0.501	31.5%	20.09	<0.001
Minimum temp.	-1.086	-0.388	46.2%	12.06	<0.01

Constant = 19.59

Multiple r = 0.68

Regression equation variance ratio $F = 18.92$ ($p < 0.001$)

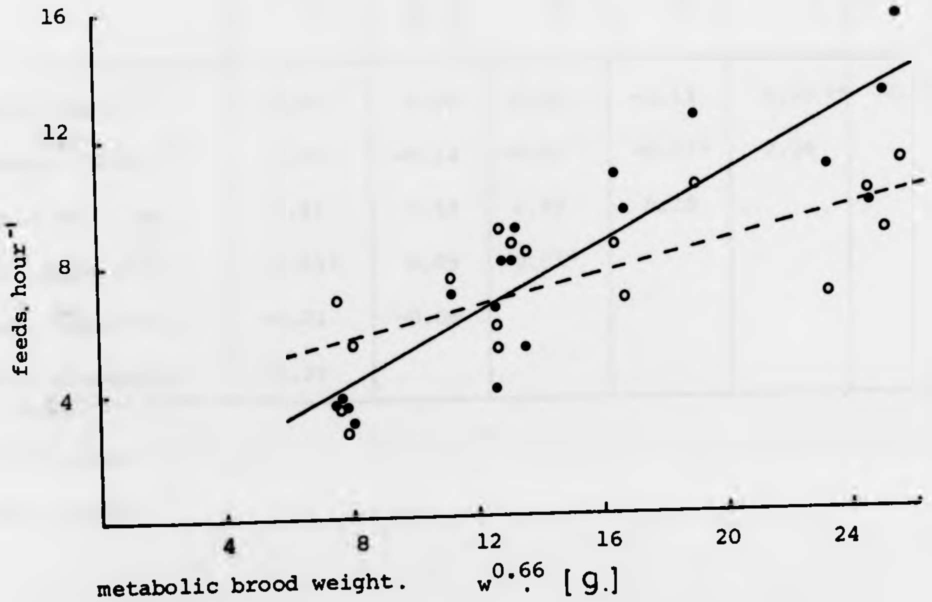

FIG. 3.6 Relationship between feeding rate and metabolic brood weight for male and female House Martins raising first broods.

●——● = males;
$y = 0.54x - 0.17$; $r = 0.89$, $p < 0.001$

o----o = females;
$g = 0.25x + 3.68$; $r = 0.69$, $p < 0.001$

TABLE 3.13

Matrix of correlation coefficients for conditions prevailing at the time male and female House Martins are feeding second broods

	Rainfall (in.)	Wind Speed (Beaufort)	Max Temp (°C)	Min Temp (°C)	Metabolic Bd. Wt. (g)	Female feeds (No. h^{-1})
Male feeds h^{-1}	-0.45	0.06	0.18	-0.13	0.69**	0.49
Female feeds h^{-1}	-0.42	-0.12	-0.32	-0.57*	0.04	
met.b.wt. (g)	-0.41	0.44	0.23	0.18		
Min. Temp (°C)	0.51*	0.09	0.51*			
Max. Temp.(°C)	-0.21	-0.06				
Wind (Beaufort)	-0.29					

* $p \leq 0.05$

** $p \leq 0.01$

TABLE 3.14

Regression equations linking the rate that food is delivered to the nest by male and female House Martins to the most significant variable.

Feeds per hour by male = Metabolic brood weight × 0.84 - 5.78

$r = 0.69$

$r^2 \times 100 = 48.4\%$

$F = 10.32$ ($p < 0.01$)

Feeds per hour by female = Minimum temp × -0.619 + 12.37

$r = 0.57$

$r^2 \times 100 = 33.1\%$

$F = 5.44$ ($p < 0.05$)

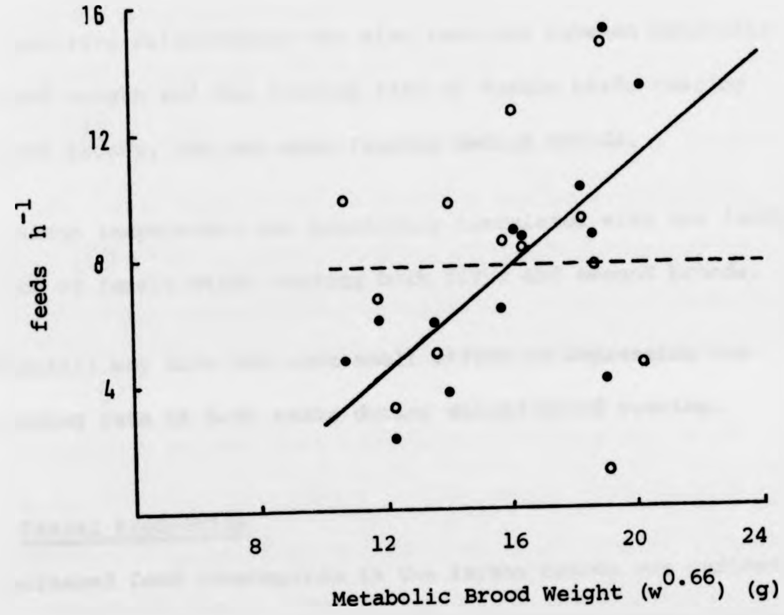

FIG. 3.7 Relationship between feeding rate and brood weight for male and female House Martins raising second broods of adjusted sizes (see text)

●—● = males $y = 0.84x - 5.77$
$r = 0.69$ ($p < 0.01$)

o----o = females line drawn through mean

3. Summary of Feeding Rate Measurements

i A positive linear relationship between metabolic brood weight and feeding rate was recorded for male birds feeding both first and second broods. An analysis of co-variance showed that there was no significant difference in either the regression coefficients or constants of the equations describing the relationship for first and second broods.

ii A positive relationship was also recorded between metabolic brood weight and the feeding rate of female birds rearing first broods, but not when feeding second broods.

iii Minimum temperature was negatively correlated with the feeding rate of female birds rearing both first and second broods.

iv Rainfall may have had some small effect in depressing the feeding rate of both sexes during second brood rearing.

3.5.2 Faecal Production

Increased food consumption in the larger broods was indicated by increased faecal production. The relationship between dry weight of faeces produced in 24 hours and metabolic brood weight was linear and described by the equation:-

$$\text{Dry weight faeces (g)} = 0.33 \times \text{metabolic brood weight} - 0.34$$

$$r = 0.86 \ (p < 0.001)$$

3.6 EXPERIMENTAL BROODS

For the purposes of measuring the ADMR's of parent birds, three broods were artificially enlarged above the normal size. Measurements of faecal production and feeding rates were also made on these three broods. Brood sizes were also manipulated to investigate the feeding rate relationships of second broods.

3.6.1 ADMR of Adults rearing experimentally enlarged broods

Three experimental broods of larger than normal size were set up:-

1. Nest A enlarged from 4 to 6 young
2. Nest B enlarged from 5 to 7 young
3. Nest C enlarged from 3 to 7 young

Of these nests the young in A and B were all raised successfully but in nest C only five or the seven young survived to fledging. The growth curves of the young from A and B were similar to those of young from natural sized broods, whereas the young from nest C were very much lighter at almost every stage in the nestling cycle.

Measurements of ADMR were successfully carried out on all the birds except the male from nest A. The results from nests A and B were similar to those which may have been predicted from birds rearing natural broods. However the ADMR of the male bird from nest C was 41% lower than that predicted from the regression line for male birds rearing first broods.

Likewise the measurement of the feeding rate of those birds from nests A and B and the female from C were in agreement with data gathered from natural sized broods, but the feeding rate of the male bird from nest C was 22% lower than expected. To confirm the undernourished condition of the brood the average daily faecal production was 32% lower than that of other broods of similar size.

The brood of nest B was raised by parent birds each of which was 2+ years old, this pair laid the largest initial clutch size and successfully reared the largest number of young. The brood in nest A was raised by a 2+ year old female paired with a 1+ year old male bird, this pair laid a medium sized initial clutch of four eggs and successfully reared six young. The brood in nest C was raised by a pair of 1+ year old birds, they laid the smallest initial clutch of eggs and the experimentally enlarged brood suffered a 28% mortality which appeared to be due to undernourishment resulting from the male bird not contributing enough to the breeding effort.

Because of this anomalous behaviour of the male bird from nest C and the death of the nestlings the data from this nest were omitted from the earlier analyses.

3.6.2 Feeding Rate of Manipulated Second Broods

The males feeding the two manipulated second broods responded to increased brood size in a similar manner to those feeding natural sized first broods. However the females did not respond in a similar manner, they showed no relationship between feeding rate and metabolic brood weight (see section 3.5 for analysis of data).

4. DISCUSSION

4.1 Energetic Cost of Free Existence

One of the most detailed studies of the daily energy expenditure of free-living birds is that of Utter (1971). Using both time budget and D_2O^{18} techniques he estimated the ADMR's of Purple Martins (*Progne subis*) and Mocking birds (*Mimmus polyglottos*). In comparing his data with those of previous studies (summarised in Table 4.1) he concluded that when a homeotherm successfully maintains itself within its niche it does so at a level of energy expenditure between 1.6 and 2.6 times its SMR. When doing more work than simple self-maintenance this ratio will be increased accordingly, e.g. whilst feeding young during reproduction the ratio may be 3-4 × SMR.

In the present study, the ADMR of House Martins feeding young, ranged from 2.22 - 5.27 × SMR with a mean of 3.89 × SMR, this concurs with Utter's conclusion for an adult homeotherm feeding young.

Utter took this consistency to indicate that in the filling of niches by homeotherms, evolution must have operated within the constraints of a limit placed on the average intensity of work performed during a day. However in preference to a concept of a pre-determined level of energy expenditure it could be possible that evolution has favoured the energetically most efficient individuals of each species. If this is so then for homeotherms at least, the average level of energy expenditure at which a favourable balance between energy harvested and energy expended is maintained at about 2 - 3 × SMR (3 - 4 × SMR when breeding). Support for this hypothesis is outlined below.

In order to maintain itself an organism must be able to gain more energy from foraging than it expends during the foraging process

TABLE 4.1

Relationship Between ADMR and SMR for a variety of Avian Species

Author	Bird	Conditions	ADMR/SMR
Owen 1969, 1970	Anas discors	Caged in outdoor pens	1.8
"	"	With flight costs calculated by Utter	2.4
Keskpaik 1968	H. rustica D. urbica	Daily existence	2.0-2.6
Pearson 1954	Calypte anna	Immediate post breeding	3.5-4.7
Schmid 1965	Zenaida macroura	Crop intake	3.3
Graber 1962	Strigidae spp.	Pellet analysis during breeding	3.1-6.1
Odum 1962	Ammodranus sandwichensis		3.5
Kale 1965	Cistothorus palustris	Time budget	2.1
Utter 1971	Progne subis	Not feeding young	2.1-2.5
"	"	Feeding young	2.9-3.4
"	Mimus polyglottos	Not feeding young	1.7-2.1
"	"	Feeding young	2.7-3.0
Shartz & Zimmerman 1971	Spiza americana	Time budget	1.41
Ebbinge, Canters & Drent 1975	Branta leucopsis	Food intake (free living)	2.2

(Rapport & Turner 1975). Any excess energy gained may be utilized for maintenance during non-foraging periods. When energy requirements are increased e.g. during moult, courtship, and reproduction, the organism must be able to gather more energy to meet the increase. An immediate solution would be to devote more time to foraging, and if this is done at the expense of resting time an increase in daily energy expenditure occurs. A sufficient time however must remain free from foraging for other essential activities such as incubation, inter- and intra-specific competition, courtship and predator evasion. If an organism is at the limit of the time it may spend in foraging, increased energy requirements can only be met by increasing foraging efficiency (ratio of energy gained : energy lost) (Lawton 1973). Thus evolved the theory of optimal foraging (Emlen 1966; Krebs 1973).

When adult birds are feeding young the requirement for increased foraging efficiency is probably greatest since the majority of day light hours will probably be utilised. If the adults minimise the associated costs their fitness (in the sense of Fisher (1930)) will be increased, partly because the survival chances of the offspring will be increased, as the adult would have a certain surplus of time and energy to devote to the brood when adverse conditions occur (e.g. during bad weather, presence of predator etc.). Furthermore in minimising the work done in carrying out essential duties the adult is likely to increase its own survival chances (Stearns 1976) and thus increase the probability of future reproduction. In this way those organisms which can minimise their daily energy expenditure (ADMR), whilst carrying out all other activities at maximum efficiency, are likely to be favoured by natural selection. For those organisms examined to date the minimum amount of energy required to do this seems to be between 2-3 × SMR for non-reproductive activities and 3-4 × SMR for reproductive activities.

The adaptations which allow organisms to work at this level are varied, and Utter's (1971) work highlighted an interesting consequence of different life-styles. He estimated the ADMR of Purple Martins feeding young at 2.9-3.4 × SMR, and of Mockingbirds at 2.7-3.0 × SMR. Mockingbirds forage primarily for insects on the ground occasionally taking flying insects by short flights. When this is contrasted with the apparently energetically demanding aerial feeding behaviour of the Purple Martin it is notable that the work done by both species is similar, and serves to emphasis some remarkable adaptations for flight found in Hirundines, which are discussed in the next section.

4.2 Energetic Cost of Flight in Hirundines

4.2.1 Flight costs estimated from present study

The cost of flight alone was not measured directly in the present study (c.f. Utter and Lefebvre 1970), however a fairly accurate approximation can be made in two ways:-

a) As explained earlier (Chapter 3.4.1) the measured ADMR's can have the roosting component removed and each converted into an "active" metabolic rate. During first brood rearing at least, birds were not observed at rest away from the nest, thus it can be concluded that the adults were flying continuously whilst away from the nest, thus the calculated active metabolic rate will be a fairly reliable estimate of flight cost in the House Martin.

The mean active metabolism for all birds measured is 9.04 $cm^3.CO_2.g^{-1}.h^{-1}$ ($0.037\ k.cal.g^{-1}.h^{-1}$) which is 4.83 × SMR. There are however, some disadvantages with this estimate. Some of the birds (males) which were sampled increased their energy expenditure as the metabolic weight of the brood they were feeding increased. Furthermore it is an estimate based on birds which were taking insects and this predation involves twisting and turning flight as well as active pursuit. Although House Martins utilise a certain amount of gliding flight during foraging which is likely to reduce the cost gliding has also been observed in more direct flight during migration (Lyuleeva in Bykhovski 1973) and is a characteristic of House Martin flight not restricted to the breeding season. It is felt that because of costs of foraging the estimate of flight metabolism using this method is probably a maximum.

Using the same method the active metabolism of two female Swallows measured in this study averaged 0.059 $k.cal.g^{-1}.h^{-1}$.

b) A second method could utilise the relationship between active metabolism of male birds and the metabolic weight of the brood. The regression constant of this relationship theoretically represents the active metabolism of male birds without a reproductive commitment. It is felt however that the relationship should not be linearly extrapolated below the brood masses that were sampled. This is because the cost to the bird of feeding a very small brood mass is unlikely to be much different from self maintenance and flight because only a very small amount of food has to be delivered to the nest at this time. The metabolism estimates at the lower end of the range of measurements are therefore likely to be a minimum estimate of the cost of flight in a House Martin.

The lowest six estimates of active metabolism have a mean of 6.34 $cm^3.CO_2.g^{-1}.h^{-1}$ (0.04 $k.cal.g^{-1}.h^{-1}$) which is 3.39 × SMR.

Using the above two methods of estimation, the flight costs of House Martins in the present study fall in a range between 0.04-0.057 $k.cal.g^{-1}.h^{-1}$ which is 3.39-4.83 × SMR.

Although both of these estimates involve slightly more resting time than that spent at roost at night, it is felt that this is balanced somewhat by the extra energy expended by a breeding bird.

4.2.2 Flight Costs of Hirundines from Other Studies

Utter and Lefebvre (1970) measured the cost of continuous flight in the Purple Martin (Progne subis), using the D_2O^{18} technique, at 0.069 $k.cal.g^{-1}.h^{-1}$ (5.7 × SMR). Birds were captured and removed from their nest site, loaded with D_2O^{18} and metabolism measured during the period of homing flight.

The cost of flight has also been estimated by material balance studies for continuous flight in House Martins and Swallows (Hirundo rustica) (Lyuleeva 1970). The birds were removed from the nest site and their bills tied closed with cotton and the resulting weight loss during homing flight was converted to a calorific value of 0.045 $k.cal.g^{-1}.h^{-1}$ (3.0 × SMR) for House Martins and 0.057 k.cal. $g^{-1}.h^{-1}$ for Swallows (3.8 × SMR).

Keskpaik (1968) used four methods to calculate the energy expenditure of flight in House Martins:

i. extrapolating from O_2 consumption immediately after flight = 0.035 $k.cal.g^{-1}.h^{-1}$ (2.12 × SMR)

ii. using weight loss during flight = 0.043 $k.cal.g^{-1}.h^{-1}$ (2.67 × SMR)

iii. using heat loss estimates = 0.049 $k.cal.g^{-1}.h^{-1}$ (3.06 × SMR)

iv. using a theoretical model = 0.050 $k.cal.g^{-1}.h^{-1}$ (3.12 × SMR)

The estimate for the Purple Martins is slightly higher than the range for House Martins in the present study. This is perhaps unexpected as a Purple Martin has a body weight nearly three times that of a House Martin and when a variety of data is assembled flight cost per gram decreases as weight increases (Table 4.2 Figure 4.1). However this may be due to structural differences between the birds (see next section).

The absolute estimates of flight cost in House Martins, from the Russian studies (Lyuleeva 1970; Keskpaik 1968), are in agreement with the range of values derived in the present study. The relationship of Keskpaik's values to SMR are somewhat lower than those of Lyuleeva and the present study, however since very little information is available on the methodology of this work, the basis of discrepancy cannot be identified. Using the value of SMR from the present study, Keskpaik's recalculated data lies in the range 2.91-4.3 × SMR.

The material balance studies have been criticised (Berger & Hart in Farner & King 1974) since the calorific equivalent of weight loss is a difficult parameter to quantify. However the estimates derived using this method agree well with those of the D_2O^{18} technique and the three alternative methods of Keskpaik. The number of birds handled in perfecting the material balance study is very impressive (Dolnik and Gavrilov in Bykhovski, 1973) and measures of times and distances involved were very precise. Farner (1970) considered that the Russian results were probably the most reliable of material balance studies.

TABLE 4.2

Estimates of Flight Costs in a Variety of Avian Species

No	Source	Bird	Wt (g)	k.cal. $g^{-1}h^{-1}$
1	Lasiewski 1963	Calyte costae	3.0	0.198
2	Berger & Hart 1974	Amazilia fimbriata	5.5	0.206
3	Hainsworth & Wolf 1969	Eulampis jugularis	8.3	0.205
4	Dolnik & Gavrilov	Spinus spinus	12.5	0.205
5	"	Fringilla coelebs	22.0	0.176
6	"	"	22.5	0.152
7	"	Fringilla montifringilla	23.3	0.170
8	"	Pyrrhula pyrrhula	29.5	0.1634
9	Tucker 1968	Melopsittacus und.	35.0	0.097
10	Berger et al 1970	Carpodacus erytherinus	60.0	0.160
11	Johnston & McFarlane 1967	Pluvialis dominica	140.0	0.055
12	Tucker 1972	L. atricilla	350.0	0.047
13	Lefebvre 1964	Columbia livia	384.0	0.056
14	Berger et al 1970	L. delawarensis	410.0	0.045
15	Dolnik & Gavrilov	L. marinus	800.0	0.039
16	"	Anas platyrhynchos	1000.0	0.038
17	"	A. rubripes	1026.0	0.038
18	Lyuleeva 1970	Apus apus	40.5	0.039
19	Utter & Lefebvre 1970	Progne subis	51.0	0.066
20	Lyuleeva 1970	H. rustica	17.8	.0647
21	"	D. urbica	20.5	.045
22	Keskpaik 1968	D. urbica	19.0	0.034- 0.050
23	Present study	D. urbica	17.81	0.038- 0.057
24	"	H. rustica	18.99	0.059

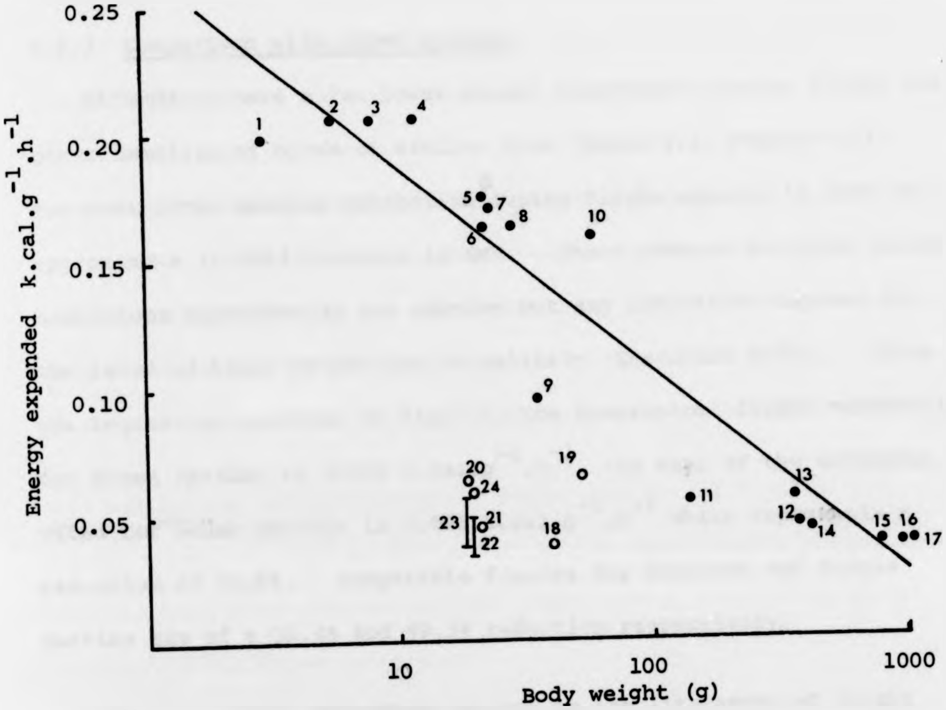

FIG. 4.1 Relationship between energy expended in flight and body weight for a range of birds. The regression line is drawn to the equation $y=0.265-0.079\log x$; points 18 (Swift) and 19 to 24 (hirundines) were excluded from the regression calculation. All numbers refer to references given in Table 5.2

In conclusion the cost of flight as estimated from three species of hirundine lies in the range 0.035 - 0.069 $k.cal.g^{-1}.h^{-1}$ which is approximately 2.9 - 5.7 × SMR.

4.2.3 Comparison with other species

Hirundines have a far lower energy expenditure during flight than other families of birds of similar size (Table 4.2, Figure 4.1). For most other species metabolism during flight appears to show an approximate 12-fold increase in SMR. Exact reasons for this fairly consistent relationship are unknown but any limitation imposed by the level of basal metabolism is unlikely (Greenwalt 1975). Using the regression equation of Fig.4.1, the theoretical flight metabolism for House Martins is 0.164 $k.cal.g^{-1}.h^{-1}$, the mean of the estimates cited for House Martins is 0.045 $k.cal.g^{-1}.h^{-1}$ which represents a reduction of 72.6%. Comparable figures for Swallows and Purple Martins are of a 62.4% and 49.3% reduction respectively.

There are only two other reports in the literature of flight metabolisms which are as low as those of the hirundines. Firstly the Swift (Apus apus) has been estimated at 0.039 $k.cal.g^{-1}.h^{-1}$ (Lyuleeva 1970) which is 5.4 × SMR. Like the hirundines Swifts are specially adapted for flight and depend for their food supply upon flying insects. Secondly in the Black Poll Warbler (Dendroica striata) flight energy was estimated at 4.1 × SMR (Nisbet et al 1963). However this figure has been criticised (Raveling and Lefebvre 1967) due to certain assumptions made in the methodology, and although species differences may exist (Farner 1970), Dolnik et al (in Bykhovski 1973) recalculated Nisbet's own data and arrived at 7.7 × SMR. Due to this controversy this data was excluded from Table 4.2.

There are a great many morphological and physiological adaptations to a certain mode of life or feeding behaviour in birds; it therefore perhaps comes as no surprise that aerial feeding birds like hirundines and swifts have a far lower energy cost of flight compared with other groups with different methods of food gathering. However the exact nature of the adaptation which allows flight at such little cost is not clear. Increased flight efficiency may occur as a result of physiological adaptations at the metabolic level, although measurements of SMR do not suggest this since they lie very close to theoretical predictions related to their weight (Lasiewski and Dawson 1967). Behavioural and morphological differences are more likely to account for most of the reduction in flight energy expenditure.

Pennycuick (1969) identified three ways in which birds must expend energy in order to fly and it can be shown that hirundines have morphological characteristics which tend to reduce the power required in all three categories.

i. Induced Power

This is the power that a bird must produce in order to support its own weight by continuously accelerating air downwards, the upward reaction on the wings being equal to the rate at which downward momentum is imparted to the air. The power required is proportional to the disc area, which is basically the almost circular area swept by the wings. It has been shown (Greenwalt 1975) that hirundines have a greater wing area than other birds of the same size. The wing loading in hirundines (weight supported by a unit area of wing) is half that of the Troglodytidae and approximately two thirds that of groups like the Turdidae and Corvidae. Thus by having relatively large wings the Hirundines can reduce the induced power required for flight.

ii. Parasite Power

This is the power required to overcome the drag caused by non-lifting parts, which is essentially the drag caused by the body. Pennycuick showed that drag was proportional to the "equivalent flat plate" area of the body, which can be described as a function of the body weight. Streamlining reduces this drag considerably (Pennycuick 1968); a pigeon has a flat plate area of approximately 36 cm^2 but its drag measured in a wind tunnel corresponds to a flat plate of 15.5 cm^2. In profile the body of a hirundine has a shape very similar to that of an aerofoil; the extremely short neck allows the cone-shaped head to be set into the wider thorax with the abdomen and tail tapering behind. The streamlining features are much more refined than in the pigeon and thus the equivalent flat plate area of a hirundine must be relatively smaller. This reduction in flat plate area will reduce the power required to overcome parasite drag.

iii. Profile Power

This is the most difficult of Pennycuick's (1969) categories to calculate. It is the power required to overcome the drag created by the wings as they are flapping. Since hirundines have been shown to have a large wing area relative to their weight they may possibly be at a disadvantage when providing profile power. However the aspect ratio ($wingspan^2 \div$ wing area) of hirundines, and also of swifts, is high, the wings tending towards a sickle-shape. A high aspect ratio tends to reduce the profile drag end hence the power required to overcome it. Brown (in Marshall 1966) states that wings with high aspect ratios may be better equipped to meet the contradictory requirements of gliding and flapping but may be too clumsy or fragile in many habitats. Since hirundines usually exploit open air spaces a large, high aspect ratio wing would seem to be eminently suitable. Brown goes on to pose the questions: are small species with their (generally) low aspect ratio wings less efficient at flight, and is it their confined habitat that precludes a more efficient wing shape? The present energetics data seem to confirm that the small species with low aspect ratio wings are less efficient at flight than their hirundine counterparts. Greenwalt (1975) also came to a similar conclusion when comparing the power requirements of the Swallow and Wren. In reference to the second question it is very likely that a confined habitat tends to result in small wings. Although high aspect ratio wings would undoubtedly lower the cost of flight for a woodland species, it would be very much encumbered when trying to manouevre through trees and bushes. Since most small woodland species escape from aerial predators by flying quickly into the heart of the nearest thicket any reduction in manoeuverability would place them at a selective disadvantage.

As well as these morphological characteristics, aerial feeders also employ behavioural tactics, utilizing gliding flight to reduce flight costs. Gliding flight is achieved at much lower cost than active flight (Pennycuick 1972) and its extended use must reduce the total cost of remaining airborne for long periods. The low wing loading and high aspect ratio of hirundines and swifts favours gliding flight (Pennycuick 1972) and it has been said (Ramel 1960) that they are the smallest birds to employ it. It is worth noting that there is a continuum of gliding flight utilization within the group, Swifts and House Martins gliding the most, Sand Martins next and Swallows employ gliding flight the least (D. R. Waugh, pers. comm.). From Fig. 4.1 it can be calculated that House Martins and Swifts have the greatest reduction in flight cost of 72%, whilst Swallows (H. rustica) are 62% lower than other birds of that size. Unfortunately there is no data on the flight characteristics of the Purple Martin (Progne subis) as it appears to have only a 49% reduction in flight cost. However differences may also exist in the detailed morphology of the Purple Martin since it is very much larger than any of the European hirundines.

A useful exercise to shed more light on this matter would be to observe a range of hirundines and compare their relevant dimensions and flight characteristics, with the theoretical predictions of Pennycuick (1968, 1969, 1972) and Greenwalt (1975).

4.3 Energetics of the House Martin During the Breeding Season

4.3.1 Factors affecting the ADMR of House Martins during the breeding season

In the results section (i) environmental variables, (ii) reproductive commitment variables and (iii) the physical attributes of the adults were all dealt with separately for the purposes of statistical analysis. This distinction was maintained in order to simplify the presentation of the data. However the chosen independent variables are in practice not independent and some interactions inevitably occur. The variables should be considered in the form of a hierarchy in which they can be most realistically incorporated into the multiple regression analysis in order to demonstrate the underlying trends:

1) The primary variable is that of physical attributes; variations in weight occur during the breeding season, especially in the laying female (Bryant 1975b) but the mean value is related to the basic skeletal size on which muscle blocks are inserted and in which organs are contained (Evans & Smith 1975). Likewise wing-length is essentially an estimate of the length of the supporting bones even though growth and wearing cause fluctuations in length (von Balen 1967). In the analysis the most satisfactory way of expressing the basic physical attributes of a bird, for the purposes of an energetics approach, was to calculate the power required for flight given the weight and wing-length of the bird at the time of measurement. In this way a figure could be calculated, which incorporated both weight and size, which was related to the activity into which the bird channeled a large part of its energy (Pennycuick 1972).

2) The second variable to be included is that of reproductive commitment, this may or may not be related to the physical attributes (this point will be examined later). Commitment in this context refers to the size of brood the birds were rearing and the stage in the seasonal cycle, i.e. whether it was a first brood or a second brood.

3) The final variable is that of the environmental conditions prevailing at the time of measurement. Earlier in the cycle the environment could have had an effect on commitment; House Martins have been shown to suspend the laying of an egg if food availability falls below a certain threshold, (Bryant 1975a) and it is possible that this may be associated with the laying of a small clutch on some occasions. However at the time the ADMR measurements were made the birds would have to accommodate the prevailing environmental

conditions in order to bring the brood to which they had already committed themselves to successful fledging. This variable was included in order to discover if any response to environment was reflected in the daily energy expenditure.

This order of priority could ideally be given to the variables by carrying out a step-wise multiple-regression analysis in which the regression equation was constrained to include the variables in the pre-determined order. In this way the relative importance of each variable could be assessed, for each sex, whilst in its theoretically, and presumably ecologically, correct position.

However, due to shortage of data on the physical attributes of all the birds sampled, modifications to this approach, as described in the sections below, were found to be necessary.

A. MALES

Insufficient data was available on the physical attributes of the male birds sampled and thus had to be excluded from the analysis. A step-wise multiple-regression analysis was carried out to describe the ADMR of male birds by firstly including the reproductive commitment variables (metabolic brood weight and brood number) and secondly, those environmental variables which had been identified as being important. All these variables were entered in their previously identified order of importance i.e. (1) metabolic brood weight, (2) brood number, (3) maximum temperature, (4) day length and finally (5) rainfall.

The first two components accounted for 93.3% of the variation in the male data and were significant at the 1% level, indicating the overriding importance of reproductive variables on male ADMR. The inclusion of maximum temperature did not account for any of the residual variation. When day length was added in the next step it accounted for 2.2% of the remaining variation but reduced the importance of brood number to the point that it was insignificant (Table 4.3).

The conflict between day length and brood number merits discussion since there was clearly some interaction between the two variables. The correlation coefficient between the two was $r = -0.97$ ($p < 0.001$), which undoubtedly accounts for the observed conflict in the multiple regression analysis, and was due to the fact that second broods are raised during the shorter days of late summer. Thus the results of the multiple regression analysis must be used with some discretion.

It is possible that there was a causal relationship between day length and increased ADMR during second brood rearing. Such a relationship could arise if the shorter days necessitated foraging being completed in a shorter space of time, resulting in a higher cost of foraging flight due to a lack of time for resting. However since it was found that there was no difference in the hourly feeding rate of first and second broods it would appear that if time was limited during second brood rearing it was not reflected in increased feeding intensity. Since this is the case it can be assumed that the costs per hour were no higher during the shorter days of second brood rearing.

Although day length was well correlated with ADMR for males rearing second broods ($r = 0.9917$; $p > 0.5$) the correlation was based on only three data points; there was no significant single correlation between day length and ADMR in males raising first broods ($r = 0.15$),

TABLE 4.3

Step-wise Multiple Regression Analysis of Relationship between ADMR of Male House Martins and Various Variables Measured During Breeding Season

	Variable	b	β.Wt	r^2 × 100% for each var.	F	P
Step 1	Brood Weight	0.24	0.79	52.49	65.29	<0.001
	Brood Number	2.32	0.64	40.81	42.67	<0.001
Step 2	Brood Weight	0.25	0.79	52.49	45.33	<0.001
	Brood Number	2.31	0.64	40.81	30.95	<0.01
	Max. Temp.	-0.003	-0.007	0.004	0.003	N.S.
Step 3	Brood Weight	0.21	0.67	52.49	27.25	<0.01
	Brood Number	-0.39	-0.10	40.81	0.05	N.S.
	Max. Temp.	0.06	0.12	0.004	0.79	N.S.
	Day length	-0.95	-0.81	2.26	2.56	N.S.

TABLE 4.4

Step-wise Multiple Regression Analysis of Relationship Between ADMR of Male House Martins and Various Variables Measured During Breeding Season

	Multiple Regression Coefficient	Standardised Partial Regression Coefficient	Coefficient of Determination		
Variable	b	β Wt.	r^2 × 100% for each var.	F	P
Brood Weight	0.18	0.59	52.49	6.98	<0.05
Brood Number	2.11	0.58	40.81	22.12	<0.01
Maximum Temp.	0.06	0.13	0.004	0.51	N.S.
Rainfall	0.25	0.23	1.23	1.13	N.S.

Constant = -0.17

Multiple r^2 = 0.94

Regression F = 21.67 ($P < 0.01$)

or females raising first broods ($r = -0.04$), second broods ($r = 0.68$; $p > 0.1$), or all the female data combined ($r = 0.23$). Thus there was no significant effect of day length within each of the brood groups. For these reasons it was considered that the apparent effect of day length emerging from the multiple regression analysis was spurious and simply due to its correlation with brood number.

Since more time is spent roosting during the longer nights of second brood rearing the effect of reduction in day length, using time-budget calculations, should be to reduce ADMR by as much as 35% rather than increase it. Pimm (1976) also came to the conclusion that decreased photoperiod should decrease energy costs because of decreased time spent in activity. Although Lack (1954) proposed a global model for variation in clutch size based on day length, the relationship has been shown to be a complex mixture of temperature, brood size, food abundance and foraging time (Royama 1969).

When day length was omitted from the multiple regression analysis brood number re-assumed its importance (Table 4.4) whilst the remaining environmental variables were not affected.

Thus it would seem that the ADMR of male birds was most closely correlated with brood mass in both first and second broods, and that the level of energy expenditure was higher for any given brood mass during second brood rearing. Environmental variables appeared to play very little part in determining the ADMR of male birds.

B. FEMALES

Since physical attribute measurements were available for only a sample of the female birds the regression analysis was initially carried out with the reproductive commitment variables included first and environmental variables included second in the equation. Although previously when environmental factors were considered on their own none were found to be of importance in determining ADMR there remained the possibility of an interaction between reproductive commitment and environmental variables. However this possibility was not confirmed by this further analysis, and brood number was confirmed as the only significant variable determining female ADMR.

The analysis was now repeated on that sample of data for which power requirement calculations could be carried out. It was found that power requirements accounted for some 31% of the variation unaccounted for by brood number, so that between them, brood number and power requirements accounted for 84.1% of the variation in the female data (Table 3.9). The data for weight and wing length of the females was limited, (n = 9) and so the power requirement calculations hold for only a sample taken from the original birds for which ADMR's were measured. It was assumed that the same relationship held for those birds for which Pmin could not be calculated.

C. Summary of Factors Affecting ADMR

When all the measured variables were considered together in their correct context the ADMR of male birds during the breeding season was more sensitive to changes in these variables than that of female birds. Females increased the amount of energy expended on second broods and those birds with greater power requirements had a correspondingly greater energy expenditure, however their ADMR was not correlated with brood mass or any of the environmental variables. On the other hand the ADMR of male birds was not only higher during second brood rearing but also correlated with brood mass and to a very much lesser (non-significant) extent certain environmental variables.

4.3.2 Relationship Between Adult Energy Expenditure and Brood Nutrition

It has been shown that as the broods increased in size they produced increasing amounts of faeces and received increasing numbers of feeds. Clearly the greater the amount of food delivered to the young (measured as parental feeding visits) resulted from the greater total food requirements (measured as faecal production). Faecal production was only measured on natural sized, first broods, where both the male and female increased the rate at which they delivered food to the nest as the brood grew. (For this reason the following calculations are carried out on the first brood data only, in order to demonstrate the relationships involved). It is possible to calculate approximately the amount of food delivered by the parents in one feeding visit by using the appropriate regression equations:-

$$\text{feeds } h^{-1} \text{ by male} = 0.57 \times (\text{Brood wt.})^{.66} - 0.57$$

$$\text{feeds } h^{-1} \text{ by female} = 0.25 \times (\text{Brood wt.})^{.66} + 3.68$$

$$\text{g. dry weight of faeces} = 0.33 \times (\text{Brood wt.})^{.66} - 0.34$$

For a brood with a metabolic weight of 8.0g (the lower size limit of broods studied) the male and female together fed the brood on average 9.67 times per hour. Over a 17 hour day (pers. obs.) this would amount to 164.4 feeds. The same brood would have produced 2.3g. dry weight of faeces during one day which amounted to 13.9 mg faeces per feed. Assuming an assimilation efficiency of 60% (Myrcha, Pinowski & Tomek 1972) this is equivalent to 34.9 mg dry weight of food delivered at each feed.

The same calculation when applied to a metabolic brood weight of 27.0g (the upper size limit of broods sampled) gave a figure of 49.91 mg dry weight of food delivered per feed. The absolute value of these figures are in reasonable agreement with those derived by D. Waugh (pers. comm.) who made direct measurements of the weight of food bolus delivered by adult Swallows Hirundo rustica which averaged 78.24 mg (± 32.05 s.d.). It would therefore appear that birds rearing larger broods delivered more food per visit than those rearing smaller broods, which in turn implies that they had a greater foraging efficiency. Because of the way the data was derived (i.e. involving a range of different pairs of birds) it is not possible to distinguish whether parent birds increased their foraging efficiency as the brood grew, or whether those birds with a high foraging efficiency reared larger broods than those birds with a lower one.

Another approach to the problem was to compare the increment in ADMR of male birds with the increment in feeding rate. By using the regression equation for male birds rearing first broods:-

$$\text{ADMR } (\text{cm}^3\ \text{CO}_2.\text{g}^{-1}.\text{h}^{-1}) = 0.23\ (\text{Brood wt})^{0.66} + 3.01$$

it can be calculated that the CO_2 production of a male bird rearing a brood with a metabolic weight of 8.0g is 4.85 $cm^3.g^{-1}.h^{-1}$. As calculated above he would feed the brood 4.03 times per hour, giving a CO_2 production of 1.20 $cm^3.g^{-1}.feed^{-1}.h^{-1}$. By the same method a male bird rearing a brood with a metabolic weight of 27g would produce 9.22 $cm^3.CO_2.g^{-1}.h^{-1}$ which is 0.62 $cm^3.CO_2.g^{-1}.feed^{-1}.h^{-1}$. Thus it appears that there was a reduction in energy expended per feed of approximately 50% when feeding a larger brood. However this calculation needs a certain amount of modification since much of the energy expended each day was used for personal maintenance and it is that increment devoted to the larger brood only that is required for the calculation. A useful figure to take for personal maintenance cost would be that point where the regression line of ADMR vs Metabolic brood weight for first broods intercepts the Y axis (Fig. 3.4), which is equivalent to a brood weight of zero and is 3.01 $cm^3.CO_2.g^{-1}.h^{-1}$. Subtracting this amount, the CO_2 production attributable to care of the brood was 1.84 and 6.21 $cm^3.g^{-1}.h^{-1}$ for the two brood sizes chosen. These gave figures of 0.46 and 0.41 $cm^3.CO_2.g^{-1}.feed^{-1}.h^{-1}$ for the amount of CO_2 produced, and thus energy expended, by the male on each feed. Thus from an energetic viewpoint there is some indication that those birds feeding the larger broods were operating at least as efficiently, if not slightly more efficiently, than birds feeding smaller broods. This again leads to the conclusion that since the larger broods required more energy the foraging efficiency of the adults rearing them must have been higher. As explained earlier no distinction can be made between the possibility of either (i) a change in foraging efficiency of the adult as the brood grew, or (ii) a difference in adult foraging efficiencies linked to the size of brood they produced.

The fact that the increment in ADMR was very similar to the increment in feeding rate from the lower to the upper size limit of those broods examined also implies that it was the increase in feeding rate which accounted for much of the increase in ADMR of male birds. More specifically it is likely to be the energetic cost of almost continuous hunting added to the energy expended travelling from the feeding grounds to the nest, which increases as feeding rate increases.

The slight increase in the rate at which female birds fed increasing weights of first broods was not reflected in the energetic data. It is possible either that the increment was too small to be detected by the D_2O^{18} technique, or that any relationship with feeding rate was swamped by the physical attribute relationship. The latter case, however, should have been identified by the multiple regression analysis.

In conclusion, it has been shown that the increase in male energy expenditure in large broods was mainly accounted for by the increase in the number of feeds delivered to the brood. The increase in feeding rate ultimately manifested itself in increased feacal production by the brood. There was some indication that those birds rearing large broods had a higher foraging efficiency than birds feeding small broods.

4.3,3 Experimental Broods

A. Experimentally enlarged broods

In the previous section it was concluded that it was the increase in feeding rate which gave rise to the increase in ADMR by the male birds. Further evidence for this conclusion was provided in the experimental brood C where the male had a reduced feeding rate which was reflected in a lower ADMR, whereas the rest of the birds which were feeding experimentally enlarged broods had both feeding rates and ADMRs which were similar to those predicted using the regression equations derived from normal sized broods.

The feeding rate response shown by the males and females in the present study was very similar to that recorded by Purchon (1947) in the European Swallow (*Hirundo r. rustica*). Likewise the pattern of mortality in the experimental broods was very similar to mortality recorded in that same study. Purchon (1947) studied two natural broods of four; the nests were sited close to each other on the same stairway and the eggs hatched within eight days of each other. In the first brood the male steadily increased the rate at which he fed the brood whilst the female increased only marginally, as the brood grew, and all four nestlings fledged successfully. In the second brood the feeding rate of the male bird never exceeded that of the female which in turn was similar to the female of the first brood; all the nestlings had died by the eleventh day after hatching. The difference in nesting success and its correlation with the male feeding behaviour is quite striking in these data. Purchon attributed the nestling mortality to the effect of bad weather upon the younger brood. However his data show that only three days of the nestling period were thus affected, only one day showed a serious decline in feeding rate attributable to the weather (and this six days before the brood died), and only on two days did the bad weather occur consecutively. Furthermore there is data available to suggest that hirundine nestlings are more resistant to short periods of food shortage since they have between three and four times as much lipid, per unit lean weight, stored in their bodies as other passerine nestlings (D.M. Bryant, pers. comm.).

From the similarity between the correlation of nestling mortality and male behaviour in Purchon's study and the present one it would appear to be vital to the survival of the brood that the male increases his feeding rate as the brood grows. A similar relationship has been identified in Common and Arctic Terns (Sterna hirundo, S. paradisaea) where the amount of food delivered by the male bird during the first four nestling days is correlated with the total brood weight, the weight of the last chick to hatch and the fledging success of the last chick (Nisbet 1973). The importance of this increased feeding in relation to parental energy investment in the brood will be discussed later.

It was notable in the experimental broods in this study that it was the two one-year old birds which laid the smallest initial clutch and failed to raise all the young in the experimentally enlarged brood. The pair in which a one-year old male was paired to a two-year old female laid a medium sized clutch of four and successfully reared six young. The oldest pair of two-year old birds laid five eggs initially and successfully reared seven young. Although the sample is only from a small number of nests the results tend to suggest that older birds not only are initially more productive, but when put under pressure by providing them with abnormally large broods they are more likely to raise them successfully. The results from these few experimentally enlarged broods thus open an avenue for future research into the effect of age and experience on the reproductive performance of House Martins.

B. Feeding rate of manipulated brood sizes

In order to investigate the relationship between feeding rate and brood size in second broods two nests were manipulated to contain between two and five nestlings over a period of six days. The male birds responded to the altered brood size by adjusting the rate at which they fed the brood accordingly. Their response was exactly as predicted from data for male birds feeding the natural sized first broods and suggests that it is ultimately a response to nestling hunger via the gaping and begging of the brood.

The females on the other hand didnot respond to a change in brood size at all, but maintained constant feeding at a rate appropriate to the natural size of her brood. This lack of flexibility of response is somewhat similar to the ADMR relationship and would suggest that female House Martins are somehow conditioned to a set reproductive effort which once initiated they adhere to. Females feeding first broods showed a slight increase in feeding rate as the brood grew; this is probably because the measurements were made using natural sized broods and the increase was in response to a gradual increase in their own brood, a response not evoked by the gross changes of the manipulated broods.

4.3.4 Seasonal Increase in Energy Expenditure by Adult House Martins

Higher ADMR's were measured for both sexes during second brood rearing. The elevation in energy expenditure can best be judged by considering a constant brood size of 3.29 (the overall mean brood size). The combined adult (male plus female) ADMR for a first brood of 3.29 would be 14.05 $cm^3.CO_2.g^{-1}.h^{-1}$, and for a second brood of the same size 18.97 $cm^3.CO_2.g^{-1}.h^{-1}$ this represents an increase of 35.02% in the energy expended on broods of this size, reared as second broods. However the average increase was less than this since House Martins exhibit a seasonal decline in clutch size. The combined adult ADMR for the mean first brood size of 3.52 was 14.23 $cm^3.CO_2.g^{-1}.h^{-1}$ and for the mean second brood size of 2.92 it was 18.49 $cm^3.CO_2.g^{-1}.h^{-1}$ which represents an increase of 29.94% in the energy expended on first broods. Thus, whilst the reduction in second clutch size ultimately affected the total energy expended by the adults it only partly compensated the extra work done in rearing second broods.

Possible reasons for the elevated energy expenditure during second brood rearing are discussed below.

i. Extra metabolic loads

Increased metabolism may be required later in the season due to either:

a) premigratory fat deposition

b) lower ambient temperature.

a) The weight of adult birds sampled during first brood rearing (17.9g) showed no significant difference to those sampled during second brood rearing (17.6g), and it is likely that any substantial fat deposition would be reflected in a body weight increase. Furthermore, it has been shown (Bryant 1975b) that there is no evidence of substantial weight increase, indicative of fat accumulation, in adults before the second brood young have fledged.

b) The mean minimum temperature during the rearing of second brood young was only 1.1°C lower than during first brood rearing. Such a decrease could cause at most a 4% increase in metabolism in a resting House Martin (King and Farner in Marshall 1961; Keskpaik & Lyuleeva 1968). Also much of the energy expenditure can be attributed to the time spent in flight, when energy expenditure is partly or fully independent of temperature (King in Paynter 1974).

For these reasons it was concluded that any extra energy required during second brood rearing to form premigratory fat deposits or combat lower temperatures could not account for the total elevation in daily energy expenditure.

ii. Nestling Demand

It is possible that the increased metabolism during second brood rearing is a response to the immediate food demand of the nestlings which could have been higher in second broods. The second brood demands may have been unusually high, or feeding conditions for the adults unusually poor, during the late summer of 1975 when the second brood measurements were taken.

There is no evidence however to support the suggestion that conditions during second brood rearing were unusually poor; during the year in question ambient temperatures were above average and rainfall below average. In a concurrent study the aerial food supply was monitored by means of a 40 ft. Rothamstead suction trap (Bryant 1975a; Johnson 1950; Taylor & Palmer 1972) and food levels were little different from conditions in earlier years (D. R. Waugh pers. comm.); at all times food availability was above the threshold required for normal nestling growth (Bryant 1973).

Food consumption of first brood nestlings was estimated by measuring the dry weight of faeces produced in 24 hours (Section 3.5). The mean first brood size of 3.52 produced approximately 5.78g dry weight of faeces per day at their peak weight, whilst the mean second brood size of 2.92 produced approximately 5.07g dry weight of faeces per day. Thus the reduction in brood size should have resulted in a decrease in feeding demand of some 12%. Since the brood is effectively buffered against changes in ambient temperature by the nest and its lining, it is unlikely that any reduction in ambient temperature could have increased the second brood food demands above that of first broods. Although this argument is based upon data collected from first broods, recent information has confirmed that second brood faecal production for constant nestling biomass is no greater than that of first broods (D. M. Bryant, pers. comm.).

The rate of feeding of first and second broods was monitored by recording adult attendance at the nest. There was no significant difference in the number of feeds per hour delivered to first and second broods of equivalent size.

Thus it is unlikely that the increased energy metabolism measured in birds rearing second broods was due to increased energy demand by the brood.

iii. Adult Energy Reserves

The third possibility concerns the relationship between body reserves and reproductive effort of adult birds. Jones & Ward (1976) showed that in the Red-Billed Quelea (*Quelea quelea*) lipid and protein stores reach a peak in both males and females before egg formation. The stores were then depleted as the female formed eggs and as the male constructed the nest; during incubation both parents re-established the lipid and protein stores. It was suggested that it was the level of body reserves which determined whether breeding would occur or not and the subsequent rate of utilisation of the reserves which at least partly determined the realised clutch size in this species. Since the authors were primarily interested in the egg-laying stage their data for the nestling stage of the reproductive cycle is limited. However some data is presented which shows that in *Ouela q. lathami* the males deplete fat stores, and the females deplete both fat and protein stores, whilst in *Quelea q. intermedia* the males deplete and then re-establish their protein reserves, during the time they are feeding the nestlings. The authors suggest that if at the end of the nestling period the parents can reach peak condition quickly then the reproductive cycle may begin again immediately, otherwise time must be taken to re-establish the breeding condition. The re-establishment of reserves during incubation would appear to be in preparation for the costs of feeding the brood when it has hatched, and the subsequent decline of reserves is an indication of the demands placed upon parent birds.

In a double-brooded species such as the House Martin it is possible that more energy would need to be expended on second broods if body reserves were depleted during the rearing of first broods and were not replaced, because utilising body reserves would presumably reduce the amount of foraging required to meet personal energy costs. Thus if such reserves were absent then more extensive foraging would be required to meet personal costs.

Evidence for depletion of energy reserves in hirundines is scarce at the present time. Peterson (1955) showed that both male and female Bank Swallows (Riparia riparia) lost weight during the nestling stage. Male House Martins show no significant decline in weight whilst feeding nestlings but females lose 2.49g from the fifth to twenty-fourth day after the brood has hatched (Bryant 1975b). If this weight loss were all fat it would be equivalent to 6.21% of the bird's energy requirements over the 19 day period. Thus if such reserves were not available during second brood rearing the female would have to work 6.21% harder in order to compensate for them. In the present study the mean weight of those adults sampled whilst rearing second broods was 0.3g lighter than those rearing first broods. Although this difference was not statistically significant it may possibly indicate an absence of energy reserves during second brood rearing.

The first eggs of House Martin second clutches are laid seven days after the first brood young have fledged (Bryant 1975a). Since the eggs take six days from initiation to laying (Bryant 1971) this leaves only one day between the fledging of the final nestling of first brood young and initiation of second clutch eggs. Unless the female begins to form pre-laying energy stores during the last few nestling days of the first brood, she will not have any reserves with which to begin second broods. Since the male bird increases his ADMR as the brood grows his energy expenditure in most cases will be higher than that of the female in the days immediately prior to fledging of the first brood. The males may also take the largest share of the feeding of young birds once they have left the nest, since the female is laying the second clutch and doing 66% of their incubation at this time. In this way the males may also begin second brood rearing with depleted energy reserves.

However unless their energy reserves have been driven to an exceptionally low level (and weight data does not suggest this (Bryant 1975b)) re-establishment should be able to take place during second clutch incubation. Quelea are able to re-establish their reserves during eleven days of incubation (Jones & Ward 1976), and pre-migratory fattening can occur in Sedge Warblers (Acrocephalus schoenobaenus) at a rate of $0.4 g.day^{-1}$, and in the Whitethroat (Sylvia communis) at $0.7 g.day^{-1}$ (Fry, Ash & Ferguson-Lees 1970). Furthermore House Martins can deposit egg material at a rate of $1.72 g\ day^{-1}$ during egg formation, thus the fourteen days of incubation should provide ample time in which to re-establish 2.4g of reserves, even allowing for any activities associated with first brood young.

Thus, until further work is carried out to establish whether House Martins form and utilise reserves in the same way as Quelea; and also to estimate the demands placed upon parents by first brood fledged young, this suggestion must remain in a hypothetical form. It is felt that the hypothesis cannot be further examined until the appropriate investigations have been carried out; but overall it is unlikely that the depletion of energy reserves accounts for more than a small part of the additional energy expended on second broods.

iv. Food Supply

The final possibility which may result in greater energy being expended on second broods pertains to changes in the aerial food supply. It has already been stated that quantitative changes in aerial insect abundance are unlikely to have any effect upon the foraging energetics of the birds, but qualitative changes also occur. First broods are fed mainly on Aphidoidea and small Diptera (Bryant 1973), whereas second broods are fed on the stronger flying (Lewis + Taylor 1967) Bibionidae and larger Schizophora; the change in food taken reflecting a change in the composition of aerial insects available (Bryant 1973). A similar late season switch to larger prey has also been noted in the Swallow (Hirundo rustica) (D. R. Waugh, pers. comm.). This switch to larger more mobile prey means that foraging techniques which are energetically more expensive have to be employed. The associated increase in the cost of feeding presumably reduces foraging efficiency and could account for much of the increase in energy expenditure.

Another change in the aerial insect food supply which may occur relates to its availability to the birds. Whilst the overall abundance of insects as measured by the suction trap may be at a constant level throughout the breeding season, certain atmospheric conditions such as wind coupled with low temperatures may cause the insects to more frequently accumulate in shelter belts in late summer. Thus because the birds tend to seek out aggregations of insects they forage more frequently in shelter belts than open spaces during second brood rearing (D. M. Bryant pers. comm., D.R. Waugh, pers. comm.). When feeding at these stations House Martins employ a greater proportion of flapping than gliding flight (D. R. Waugh, pers. comm), presumably due to the lack of fast moving airstreams upon which to glide (Pennycuick 1972), and limited space within which they must manouevre to exploit the concentrated food supply. Thus although foraging in shelter belts probably results in a higher rate of prey capture per unit time, it is likely to result in a lower foraging efficiency, due to the extra energy expended in using a greater proportion of energetically more expensive flapping flight (Pennycuick 1972), and could contribute to the explanation of increased energy expended on second broods.

4.3.5 Utilisation of Energy as a Reproductive Strategy

Having established that more energy is committed to rearing an average second brood than first brood, and having suggested areas in which this energy is expended, it is nowvaluable to consider how this pattern of energy deployment has evolved in the House Martin.

All the activities of an organism may be considered in terms of their effect upon that organism's "reproductive value", which is the age-specific expectation of all present and future offspring (Fisher 1930), and at age x is designated by the symbol V_x. The current investment in reproduction at age x is known as the "reproductive effort" designated E_x (Fisher 1930). Under many circumstances increased E_x might be expected to increase V_x, and if so is likely to be favoured by natural selection. On the other hand any actions which tend to depress V_x are likely to be selected against. It has been pointed out, however, that a high level of commitment to reproduction may result in a cost, such as increased parental mortality, which could ultimately lower V_x (Williams 1966). By this means the most productive clutch size in iteroparous bird species may involve a parental effort which shortens the reproductive span and hence lowers V_x. Thus the optimal clutch size may not be the most productive clutch size (Lack 1954, 1966) but one which is smaller, involving a lower E_x but which increases V_x (Charnov & Krebs 1974).

It has been suggested that in order to maximise lifetime reproductive success, E_x should be deployed in inverse proportion to residual reproductive value V_x* (age-specific expectation of future offspring i.e. V_x-current offspring) (Pianka & Parker 1975). Thus an organism with a high residual reproductive value would be expected to invest less in current reproduction than another organism with a lower expectation of future offspring. There is evidence to suggest that successful reproduction induces a cost to the organism which has the result of lowering V_x* (Lack 1954; Williams 1966; Cody 1966, 1971; Stearns 1976 (review)). Organisms with semelparous ("big-bang") reproduction maximise their current reproductive effort which reduces their residual reproductive value to zero. Iteroparous species on the other hand have the opportunity to strike a balance between E_x and V_x*. In the optimal case for iteroparous species E_x may be low early in the life history, subsequently E_x would increase in accordance with the concurrent decline in V_x^* (Gadgil & Bossert 1970). However it has also been argued that an optimal strategy can involve an initial rise and subsequent decline in E_x (Emlen 1970) or the converse (Fagen 1972). Thus on a life-history basis the costs and benefits of different levels of E_x are controversial, and if they are to be assessed it is useful to work in a context where theoretical ambiguity does not exist. Such a situation exists in multi-brooded species where the changes in V_x^* within the breeding season are more marked than changes throughout the reproductive span (Pianka & Parker 1975), especially if the age-specific mortality rate is constant. Thus in order to test the predictions of life-history theory it is useful to examine the changes in E_x within the breeding season of a multi-brooded species, and compare them with the associated change in V_x^*.

Reproductive effort (E_x) has proved a difficult parameter to quantify. In salmon it has been estimated as the length of river which the fish need to swim in order to spawn (Schaffer & Elson 1975). A more quantitative approach in organisms without post-natal or post-hatching care has been to compare the ratio of reproductive tissue to total somatic tissue. Using this latter approach the agamid lizard Amphibolurus isolepsis has been shown to devote more effort to second than first clutches which was linked to a decline in V_x^* (Pianka & Parker 1975). Most birds however show extensive post hatching care and in species with altricial young, effort is directed mainly towards supplying food for maintenance and growth of the young (Ricklefs 1974). It would seem therefore that the measurement of ADMR as made in this study would be a suitable assessment of E_x since the measurements are of parental energy expenditure during the period of intensive post-hatching care.

On initial analysis it would seem that the increment in energy expenditure during second brood rearing measured in the present study parallels the situation found in Amphibolurus isolepsis described above. It is necessary however to calculate the change in $V_x{}^*$ in the House Martin within the breeding season for confirmation of this conclusion.

During the breeding season House Martin mortality between laying of first and second clutches is approximately 5% (personal observation) and can be assumed constant. Outside the breeding season adult mortality has been shown to range from 36% to 60% for various European sites (Rheinwald & Gutscher 1969), and preliminary analysis of British data puts it at 56.2% (D.M. Bryant, pers. comm.). Most small passerines have a constant age-specific mortality from the first year of breeding (Lack 1954), and for the House Martin expectation of further life for a breeding individual is 1.28 years; no adult House Martins at the study colony were more than four years old. Using these data $V_x{}^*$ can be calculated from the following equation:-

$$V_x{}^* = \sum_{x=0}^{\omega} \ell_x(\ell_{x_1} \times M_1 + \ell_{x_2} \times M_2)$$

where ℓ_x = age-specific survivorship

ℓ_{x_1} = survivorship to produce first brood

ℓ_{x_2} = survivorship to second brood

M_1 = first brood fecundity

M_2 = second brood fecundity

ω = age of last breeding

V_x* is high at the start of the breeding season during first brood rearing and low during second brood rearing. If the individual survives over winter V_x* assumes its high value at the start of the next season and the pattern is repeated until death (Fig. 4.2). Thus since E_x has been measured as higher during second brood rearing when V_x* is low it does seem as though E_x is deployed in inverse proportion to V_x*.

[It must be noted that Figure 4.2 is perhaps a simplification of the true situation since reproductive effort may change with age, in that older birds may lay larger clutches, which in itself may affect mortality. However the relationship between V_x* during first and second brood rearing will be largely unaltered and changes in V_x* within the season will still be greater than life-time changes. Until more data is available on the clutch size of birds of known age, the model must remain in its present form.]

The possible proximate factors bringing about the relationship have been discussed earlier, and although it is difficult to identify specifically the fate of the extra energy expended on second broods it is relatively unimportant exactly which factor or combination of factors is responsible. What is important is that if this application of a hypothesis of life-history strategy is correct, then the optimal distribution of E_x must have resulted in increased fitness in order to be selected for in the population.

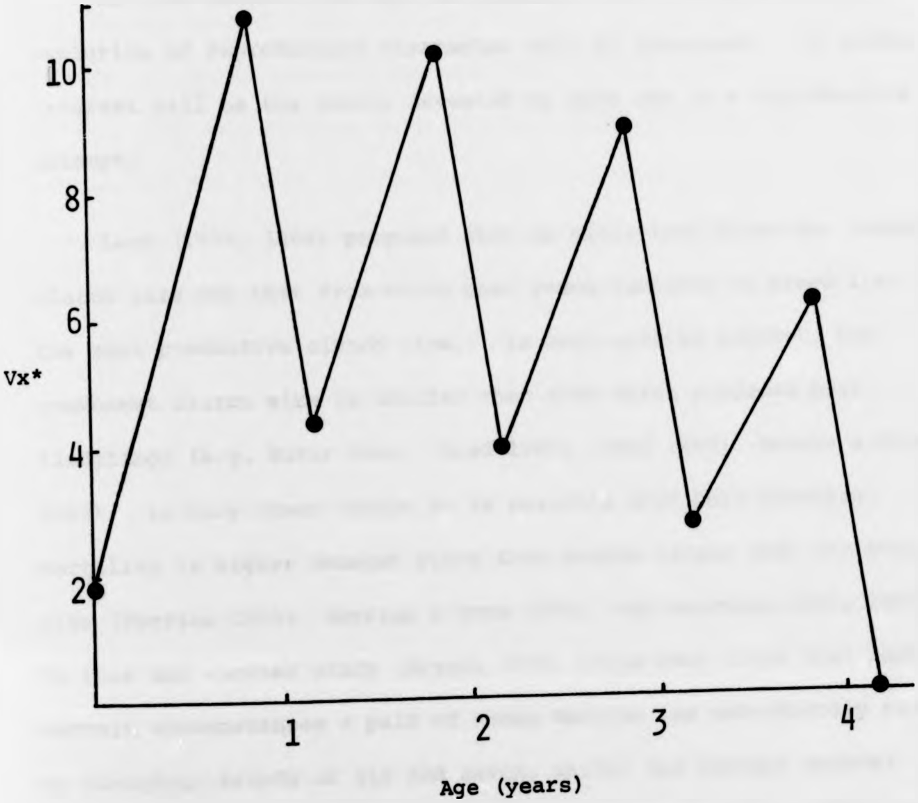

FIG. 4.2 Change in residual reproductive value (Vx*) with age in adult House Martins. Points have been calculated up to the maximum known age of birds at the study colony.

4.4 Energetics of Parental Investment in Reproduction

In this section the role of energetic considerations in the evolution of reproductive strategies will be discussed. Of prime interest will be the energy invested by each sex in a reproductive attempt.

Lack (1954, 1966) proposed that in nidicolous birds the commonest clutch size was that from which most young survived to breed i.e. the most productive clutch size. In many species however, the commonest clutch size is smaller than that which produces most fledglings (e.g. Tutor 1962; Ward 1965; Cavé 1968; Harris & Plumb 1965); in many cases though it is possible that post fledging mortality is higher amongst young from broods larger than the average size (Perrins 1965; Perrins & Moss 1975; von Haartman 1954, 1967a). In this and another study (Bryant 1972) it has been shown that under certain circumstances a pair of House Martins can successfully raise to fledging broods of six and seven, whilst the largest natural clutch size is five and the mean between three and four; there is no published data on post-fledging survival from large broods in this species, however Bryant (1975) indicates that there are no substantial differences in peak nestling weights which might indicate a higher mortality amongst large broods (cf.Perrins 1965). It has been proposed (Charnov & Krebs 1974) that the optimal clutch size in many birds may be smaller than the most productive, because it is the size which maximises lifetime productivity, rather than seasonal productivity of the parents that increases fitness. Cody (1966) suggested that time and energy are limited resources, especially during reproduction, and if this possibility is considered along with the various clutch-size hypotheses, it could be proposed that energy is utilized at its maximum efficiency at the mean brood size.

In the present study the mean daily metabolic level of adults feeding young was measured for each sex feeding a range of brood-sizes. The measurements were made on adults feeding broods which ranged from five days old to fledging at around 28 days. The cumulative energetic investment for a particular brood can be calculated by taking the mean daily brood weight (using growth curve Fig. 3.1), converting to the metabolic brood weight (brood weight$^{0.66}$) and for male birds the ADMR can be calculated using the regression equation in Fig. 3.4, assuming a body weight of 17.81g (mean body weight of all birds sampled) and an R.Q. of 0.75 (as measured in the laboratory). For female birds, which do not increase their ADMR with increasing brood size the cumulative investment is constant (Fig. 4.3). The intercept of the regression lines of energy invested by each sex in rearing broods of different size occurs for first broods at a brood size of 3.71, which is very close to the observed mean first brood size of 3.53. Similarly for second broods the intercept is 3.05, again very close to the observed mean second brood size of 2.93. This suggests a possible link between the average reproductive output (represented by mean brood size) and energetic investment in the brood.

The period that these calculations are based upon represents only 24 days out of a cycle lasting nearly 50 days; and if energetic investment is to be considered fully, the cumulative energy expenditure during the entire reproductive cycle should be assessed. This involves dividing the reproductive cycle into its component phases and ascribing an energetic cost to each phase. The energy expended during the entire reproductive cycle has never been accurately measured for a wild bird, although many studies have taken different parts of

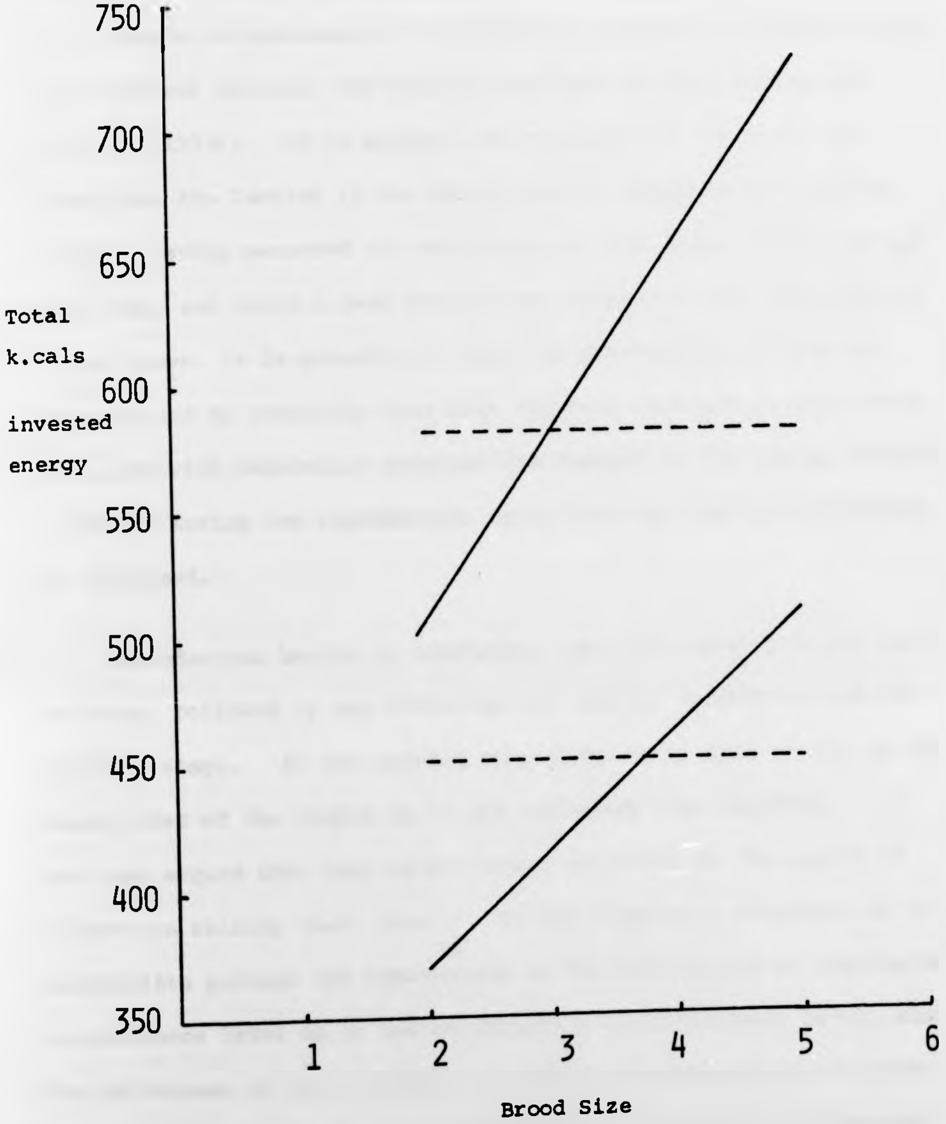

FIG. 4.3 Total energy invested during the nestling period by Parent House Martins when producing broods of different size. Lower first broods, upper second broods.

—— = male

---- = female

the cycle and examined them closely. The available results tend to be a mixture of measurements and estimates covering different stages for different species, all recently reviewed by King (1973) and Ricklefs (1974). It is evident that the part of the cycle for which data are lacking is the energetics of adults whilst rearing young. Having measured the energetics of this phase using the D_2O^{18} technique, and since a good deal of the biology of the House Martin is now known, it is possible to take the conclusions of King and Ricklefs and by combining them with the data gathered in this study, calculate with reasonable accuracy the changes in the energy expended by adults during the reproductive cycle from egg laying to fledging of the brood.

Reproduction begins by courtship, nest-site selection and nest-building, followed by egg-formation and laying, incubation and the nestling stage. At the present time there is no data at all on the energy cost of the stages up to and including nest building. It has been argued that they exert little influence on the succes of parents in raising their young. On the other hand selection of the appropriate partner and cementation of the bond may be of considerable significance later on in the reproductive cycle (Trivers 1972), also the efficiency of nest building may affect the energetics of incubation, brooding and nestling thermoregulation (Ricklefs & Hainsworth 1969; Calder 1974). Thus when considering investment the initial stages of the cycle may be important. However in the complete absence of data it must be omitted from present calculations.

The rest of the cycle can be conveniently divided into four phases:-

i egg formation

ii incubation

iii 1st - 4th nestling day

iv 5th - 28th nestling day

A distinction is made for the first four nestling days as this period was not covered by the D_2O^{18} measurements. The method of estimating the daily energy expenditure during each of the phases is described in Appendix IV.

The estimated daily energy expenditure during the complete reproductive cycle for males and females producing broods of two and five young (the extremes of natural brood sizes) is shown in Fig. 4.4. In deriving the figure it was assumed that embryo and nestling mortality was nil. Females show an increase in energy expenditure of about 2 $k.cal.day^{-1}$ at the time of egg formation, a cost not experienced by the male. During the incubation phase and first four nestling days the daily energy expenditure of each parent is relatively low, since a large percentage of their time is spent sitting on the nest. During the nestling stage, as previously discussed, there is no change in female energy expenditure with brood size, but a large change in that of the males.

Presented in this way energy expenditure would appear to be a useful way to measure the cost of reproduction to the adults, throughout the majority of the cycle. The only exception being the incubation period where it could be argued, that the true cost is perhaps not well represented since the female in doing most of the incubation would appear to suffer a lower cost than the male. On an energetics basis alone this is correct; however since the female devotes more time to incubation than the male, it is possible that

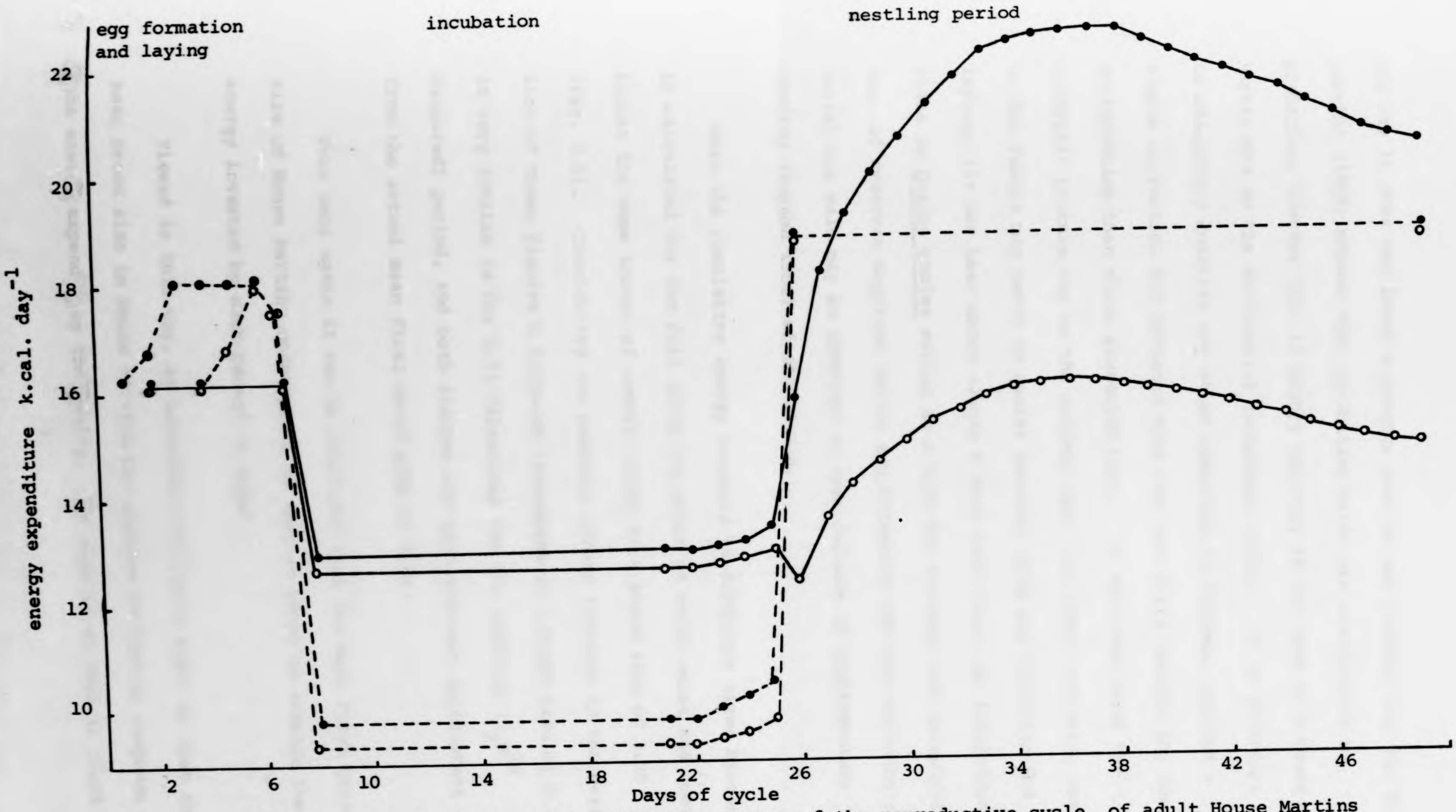

FIG. 4.4 Daily energy expenditure, during different stages of the reproductive cycle, of adult House Martins producing broods of 2 and 5 young;

open circles brood of 2; closed circles brood of 5; ---- female; —— male;

she may in some way incur a greater cost to her fitness than the male. Perrins (1965) showed that incubating birds are susceptible to predation, however this is highly unlikely in the case of a House Martin due to the enclosed, inaccessible nests. It is difficult to adequately quantify any other reduction in fitness, because a simple correction for invested time does not yield results any more enlightening than those presented here. On the other hand the energetic picture may be the correct one; the lower energetic cost to the female may serve to assist recovery from egg formation and laying, (it has been shown (Jones & Ward 1969) that the incubation phase in Quelea quelea serves as a time for recovery and re-establishment of reserves depleted during egg formation and nest building); whilst the male may be involved in nest defence or supplementary feeding (Royama 1966) of the female.

When the cumulative energy invested in different sized broods is calculated for the full cycle the point at which males and females invest the same amount of energy occurs at a brood size of 3.28 (Fig. 4.5). Considering the possible errors inherent in the derivation of these figures a balanced investment at a brood size of 3.28 is very similar to the 3.71 calculated for the nestling (D_2O^{18} measured) period, and both figures are approximately equidistant from the actual mean first brood size of 3.52.

Thus once again it can be concluded that the mean first brood size of House Martins corresponds to that at which on average the energy invested by each parent is equal.

Viewed in this way, an immediate conclusion might be that the mean brood size in House Martins has somehow evolved in response to the energy expended by the adults. If this is so then it could be

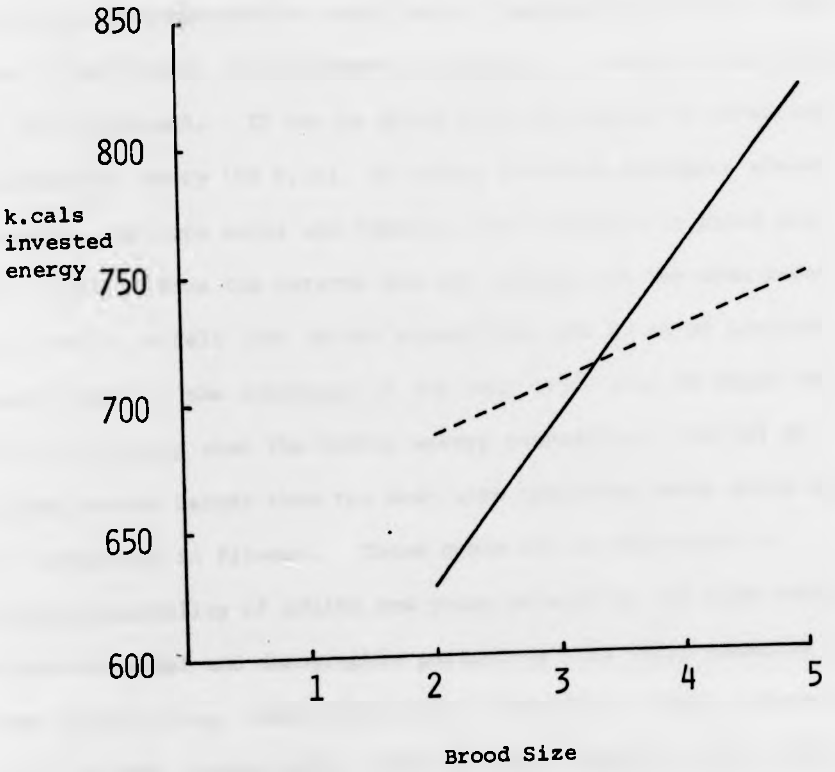

FIG. 4.5 Total energy invested in the reproductive cycle by male and female House Martins when producing broods of different size.

——— = male

----- = female

hypothesised, as stated earlier, that the efficiency of energetic investment in reproduction would be at a maximum at the mean brood size. Efficiency of investment is measured in terms of the return per unit invested. It can be shown that the number of offspring produced for every 100 k.cal. of energy invested increases almost linearly, for both males and females, with increase in brood size (Fig. 4.6). Thus the returns are not greatest at the mean brood size and it is felt that energy expenditure per se is of limited significance in the evolution of the mean brood size in House Martins. But it is likely that the higher energy expenditure involved in raising broods larger than the mean size introduce costs which lead to a reduction in fitness. These costs may be reflected in increased mortality of adults and young related to the wide variety of environmental and demographic parameters more fully examined in other studies (e.g. Lack 1954, 1966; Cody 1966; Gadgil & Bossert 1970; Charnov & Krebs 1974; Perrins 1965; Perrins & Moss 1975). Likewise a reduction in fitness results from rearing a brood smaller than the mean size since fewer young are produced.

However the question can still be posed, why is energetic investment by the parents equal at the mean brood size? It is likely that this occurs as a result of the type of mating system found in the House Martin. Mating systems have evolved in essentially three different ways (Lack 1968; Orians 1969):-

(a) Polygynous systems where the female bears most of the cost of reproduction, e.g. in Ploceidae, Icteridae.

(b) Polyandrous systems where the male bears most of the cost of reproduction, e.g. in species of Rostratulidae, Tinamidea.

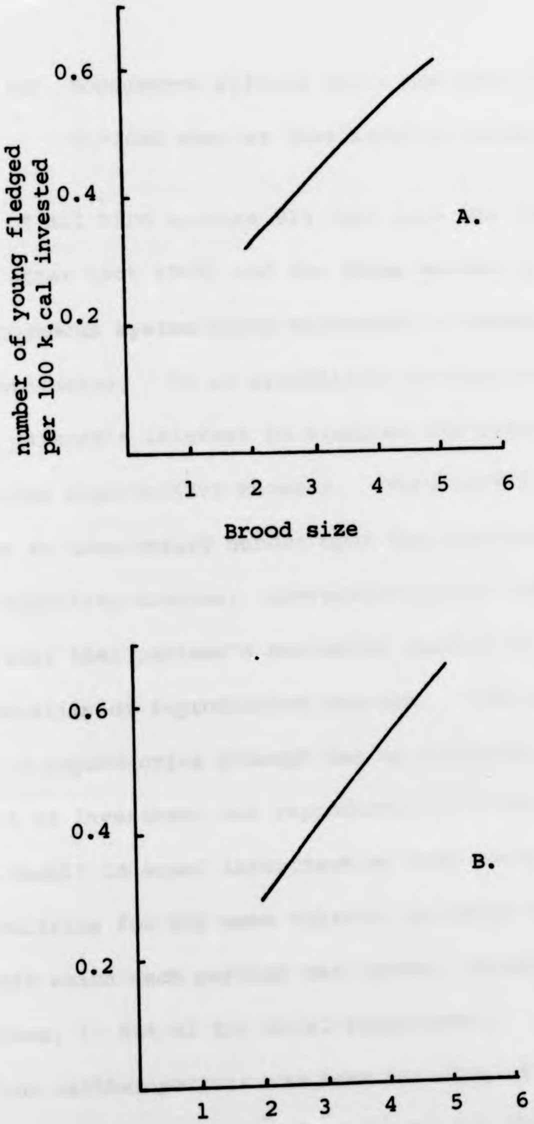

FIG. 4.6 The number of young fledged for every 100 k.cal. of energy invested by adult House Martins in broods of different size;
A. Males B. Females

(c) Monogamous systems where the cost of reproduction is divided more or less equally between the sexes.

Of all bird species 91% fall into the last category (Orians 1971 after Lack 1968) and the House Martin is no exception, having a monogamous system where successful reproduction requires the efforts of both sexes. In an essentially co-operative system it is within each partner's interest to minimise its investment whilst still ensuring reproductive success. Very high levels of investment will place an unnecessary burden upon that partner and presumably increase its mortality chances; conversely whilst under-investment will decrease that partner's mortality chances it also decreases the probability of reproductive success. Thus an individual embarking upon a reproductive attempt has to establish a balance between the level of investment and reproductive success. This in itself will not result in equal investment by both partners unless each of them is striving for the same balance, in which case the minimum amount of effort which each partner can invest, whilst ensuring reproductive success, is 50% of the total requirement. In a truly co-operative system neither partner can bear too much of the cost without endangering either himself or the brood, thus it is within the other's interests not to over-burden its partner since if that partner dies the success of the reproductive attempt will be jeopardised.

However the reproduction process cannot function in a way whereby each partner is investing at the same rate at any instant in time (Fig. 4.4), different levels of investment are apparent at almost every stage. Thus some form of reciprocal altruism (Trivers 1971; Dawkins 1976) must have evolved where one partner invests at a higher rate at any one time in return for the other partner investing more later. Such an arrangement not only allows one partner to minimise its own mortality chances whilst ensuring success of the brood, but also minimises that of its mate, which also increases the probability of reproductive success.

Despite this it is still possible that one partner will attempt to invest less than necessary and depend on the other to make up the deficit. Such a reduction in investment is akin to desertion; it has been stated (Trivers 1972; Dawkins 1976; Dawkins & Carlisle 1976) that in any co-operative breeding system it should only pay a partner to desert if the partner which remains can successfully complete the reproductive attempt. It has been shown, both in the House Martin and other species, that if the male bird does not fulfil his prescribed role the effect is to reduce reproductive success (Section 4.3.3; Purchon 1952; Nisbet 1973). Furthermore it would appear from the experimental broods of this study that females do not respond to a drastic change in reproductive demand and thus do not make up for any lack of effort on the part of the male (Section 3.6). Why this is so is not clear, but it may be a mechanism to prevent male desertion which would ultimately lead to an increase in the female's risk of mortality. The effect of female desertion was not observed in the present study but in most situations male desertion seems more likely than female. Again it is not clear why this should be so even though other authors have discussed it in detail (Trivers 1972; Dawkins & Carlisle 1976). It is possible to propose from the present study the chain of events following female desertion: the male would be unable to provide sufficient food for the young, which in turn would lose weight and become weak, this would probably weaken the begging response with the result that the male would lose the stimulus needed to maintain his feeding rate. This would be a self-perpetuating process leading to the eventual death of at least some if not all of the brood.

It is possible that some small deviation from a 50/50 division of investment can occur whilst still ensuring reproductive success, however such a deviation is likely to go in the direction of either the males or females, resulting in the average effect of a 50/50 division as estimated in the present study.

It must be emphasised that the relationship shown in Fig. 4.5 is a generalised one using averaged data from a range of birds. It should not be interpreted as indicating that, in those broods smaller or greater than the mean, parental investment is unequal partly because size and experience may play a role in the reproductive strategy of those birds, rearing broods smaller or larger than average. Thus it is quite possible that any particular pair of birds put equal amounts of energy into raising their brood irrespective of its size.

Trivers (1972) discusses sexual selection in the context of parental investment and states that where male and female parental investment is of a similar level it could be expected that the female choice of a male would be no more discriminating than the male choice. This is perhaps borne out in the House Martin by the fact that there is no sexual dimorphism in the plumage of the birds, suggesting that the male does not need to have elaborate structures to secure the appropriate female. In fact male House Martins select a nest site and then attempt to attract a female to it (Lind 1960), this way it can be imagined that some element of choice rests with both partners. It is necessary that this balance in partner selection should exist in the House Martin; it has been shown that the male bird responds to the mass of young in the nest, thus the female bird needs to ensure that the male she chooses will react in the correct manner to her investment in eggs and incubation. The effect of a male who does not respond correctly is to jeopardise much of the reproductive success (see Section 4.3.3, Purchon 1952; Nisbet 1973). Likewise a male bird with a large capacity for response needs to mate with a female capable of producing a clutch of sufficient size in order to realise his reproductive potential. Using data collected by D.M. Bryant from the same study colony, in addition to that gathered during this study, the body weight of parent birds was compared to the size of clutch they laid. Body weight was taken at a point as soon as possible after the 10th day after laying, in order to eliminate variations in the weight, linked with egg-laying, of the females (Bryant 1975b). Clutch size was significantly correlated with both male (Fig. 4.7) and female (Fig. 4.8) body weights, suggesting that at some stage during courtship there is indeed a selective process which ensures that the large male and large female birds come together, whereupon the large female lays a large clutch of eggs. Although the power requirements of the males mated to large females will be higher than smaller males, and also their relative capacity to increase their energy expenditure will be lower (Hill 1950; Pennycuick 1972), their absolute food gathering capacity will probably be higher since larger birds fly faster than smaller ones (Pennycuick 1972) and therefore cover a greater amount of air-space per unit time. Thus the larger males are more likely to be able to meet the demands of the large clutch laid by their mates. The greater costs incurred in this process could well be offset by age and experience (Section 4.3.3; Kluyver

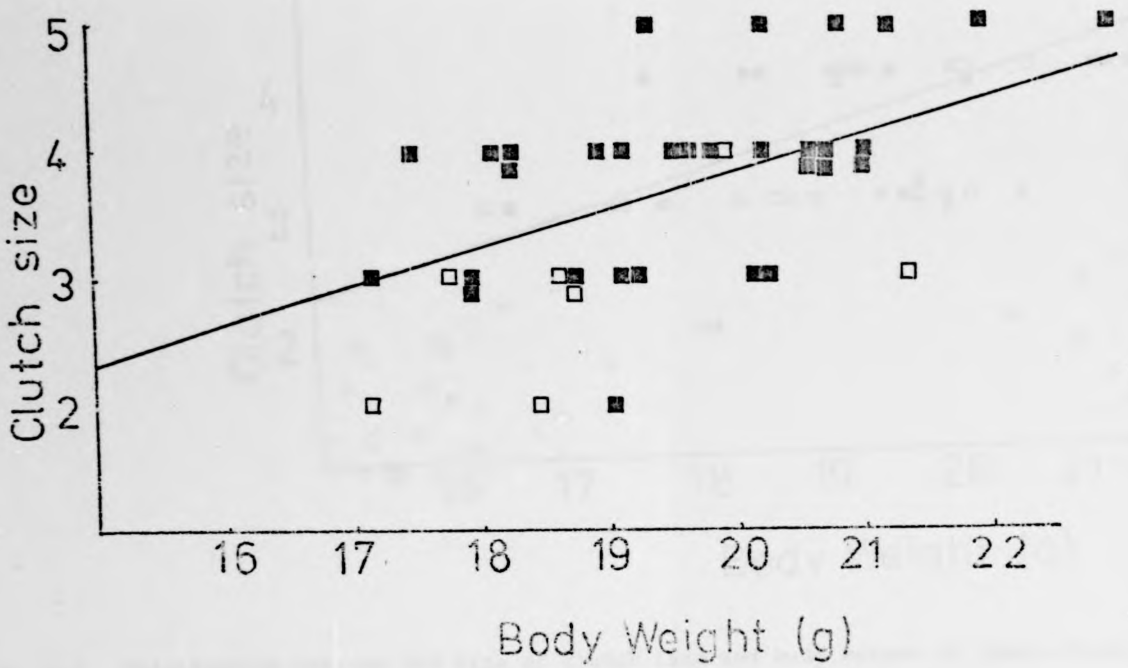

FIG. 4.7 Relationship between the size of clutch laid by the female and the body weight of the male for pairs of House Martins during the breeding season; line drawn to the equation $y = 0.29x - 2.14$; $r = 0.52$ ($p < 0.001$);

■ = first broods; ☐ = second broods

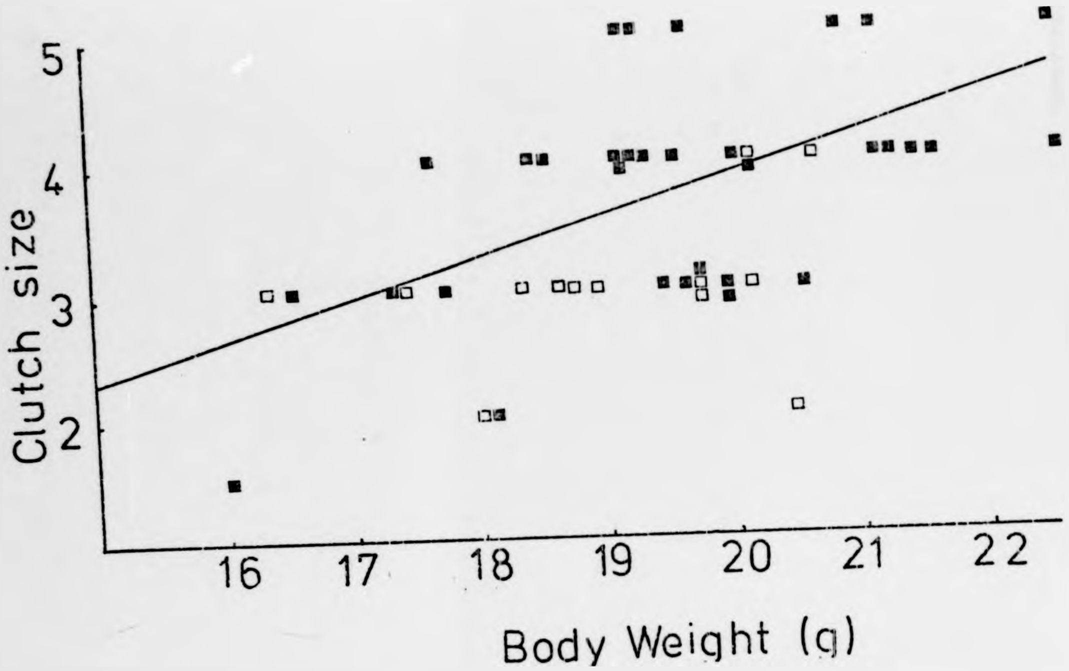

FIG. 4.8 Relationship between the size of clutch laid and body weight of female House Martins; line drawn to the regression equation $y = 0.29x - 2.08$; $r = 0.49$ ($p < 0.001$)

■ = first broods; □ = second broods

1961; Perrins 1965, 1974) but this requires confirmation by growth, parental age and experience studies, in relation to reproductive performance.

5. SUMMARY AND CONCLUSIONS

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i. The average daily metabolic rate (ADMR) of House Martins (Delichon urbica) was measured during the breeding season using the D_2O^{18} technique. Measurements were made on male and female birds rearing both first and second broods of different sizes.

ii. The ADMR of male birds was most closely correlated with the weight of the brood they were feeding, and was higher during second brood rearing than during first.

iii. The ADMR of female birds varied with the power required to fly and was higher during second brood rearing than during first.

iv. Environmental changes seemed to play a negligible role in determining the ADMR of either sex.

v. Measurements of the rate at which parent birds fed broods of different size showed a similar pattern to that of energy expenditure within first and second broods, but did not show the increase from first to second broods found in the energetics. It is likely that within first and second broods ADMR is a function of the work done in feeding a brood of nestlings.

iv. Results from experimentally enlarged broods indicated the importance of the role of the male bird in the fledging success of the brood, and also the lack of flexibility of response of the female to changes in reproductive demand.

vii. The proximate factors bringing about the increase in energy expended during second brood rearing by both sexes could not be identified with certainty, but were likely to be linked to changes in the quality and distribution of the aerial food supply; weather changes and depletion of energy reserves may also have been involved. The ultimate factor was probably increased fitness as a result of increased reproductive effort at a time of decreased residual reproductive value.

viii. From detailed calculations of the amount of energy invested by each parent in first broods it was found that they invested equal amounts of energy in the mean brood size; this was likely to be a result of the type of mating system found in the House Martin and the attempt by each parent to minimise the cost of reproduction whilst ensuring its success.

ix. Estimates of the cost of flight made during the study put the cost for Swallows (H. rustica) at 0.059 $k.cal.g^{-1}.h^{-1}$ and for House Martins in the range 0.038 - 0.057 $k.cal.g^{-1}.h^{-1}$. Comparison with other species showed that flight costs in these two hirundines were only 38% and 28% respectively of those of non-hirundines of similar weight. The greater efficiency was attributed to morphological and behavioural adaptations.

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APPENDIX I

Alternative methods of estimating free-living energy metabolism

1. Measurement of Heart Rate

Heart rate has been used as an index of energy metabolism in humans for many years,both at rest and at different levels of physical activity. The basic physiological relationship between heart rate and energy metabolism (measured as oxygen consumption) is:-

$$V\,O_2 = H.R. \times S.V. \times A\text{-}V\,O_2 \text{ difference}$$

where

$V\,O_2$ = volume of O_2 consumed ($ml\ O_2\ min^{-1}$)

H.R. = heart rate ($beats\ min^{-1}$)

S.V. = stoke volume ($ml\ blood\ beat^{-1}$)

$A\text{-}V\,O_2$ = difference in oxygen concentration in arterial and venous blood.

Validation studies on other organisms at rest have shown heart rate to be a useful measure of energy metabolism. Good correlations at different ambient temperatures have been obtained for birds and mammals (Clark 1927; Drent & Stonehouse 1971; Bartholomew & Hudson 1962). In humans heart rate is generally closely linked with metabolic rate at different levels of activity up to nearly maximal work. However at very high levels of activity heart rate reaches a plateau whilst oxygen consumption continues to increase.

Hart (in Gessaman 1973) found a good linear correlation between VO_2 and heart rate in Mallard (Anas platyrhynchos) running on a treadmill. However measurement of VO_2 and heart rate in flight showed that the relationship changed from linear to curvilinear and that heart rate became a less sensitive index. Tucker (1968, 1970) found that metabolism depended upon flight speed and angle in the Budgerigar (Melopsittacus undulatus) and Laughing Gull (Larus atricilla). In contrast to this Gessaman (1973) found the heart rate of a Kestrel (Falco sparverius) to be nearly constant at 720 beats min^{-1} irrespective of flight speed, between 16 and 25 mph. In addition Berger, Hart and Roy (1970) found that heart rate during flight was less variable than at rest and more closely correlated with body weight than energy metabolism. Thus it seems likely that changes in the ateriovenous blood oxygen concentration, rather than heart rate itself, accommodate the increased requirement for Oxygen and Carbon Dioxide transport at high levels of activity because stroke volume changes only slightly at maximum oxygen consumption whilst the arterio-venous oxygen concentration is very variable (Risher 1965).

Compounding these physiological difficulties are technical problems associated with transmitting electro-cardiograms from a free-living animal. Small commercial e.c.g. transmitters are now available; however weight is an especially difficult problem in avian studies. Modern electronics mean that battery size is the limiting weight factor and both range and life-span are reduced as battery size is reduced. The smallest transmitter commercially available in Britain is manufactured by Devices Instruments Ltd., and with battery, weighs 2.5g, with an effective range of 50 yards and life of 15 hours. Gessaman (1973) states that ideally a transmitter should not weigh more than 3% of the animal's body weight, with a maximum of 10%. With a transmitter of 2.5g this would limit the technique preferably to birds heavier than 83g, with an absolute minimum of 25g, which would mean excluding many small passerines.

Thus it would appear that heart rate measurements are a less than satisfactory measure of metabolism for avian studies. Gessaman suggests that they would be suitable for mammals where periods of rest are large and strenuous activity limited, and movements less likely to be hampered by the transmitter.

Notwithstanding those limitations heart rate measurements are reasonably inexpensive, and as technology advances transmitter size will be reduced. A detailed study of the exact relationship between heart rate and energy metabolsim during strenuous exercise would provide this technique with a stronger theoretical basis than it has at present.

2. Measurement of Respiratory Rate

The relationship between energy metabolism and respiratory rate is expressed in the following equation:-

$$VO_2 = f \times V_T \times (F_{IO_2} - F_{EO_2})$$

where VO_2 = oxygen consumption (ml. min^{-1})

f = respiratory rate (breaths min^{-1})

V_T = tidal volume (mls. expired $breath^{-1}$)

F_{IO_2} = fraction of O_2 in inspired air

F_{EO_2} = fraction of O_2 in expired air

However since the respiratory tract is utilised as a cooling mechanism in many organisms, changes in f in the above equation depend very much on the thermal relationships of the organism in question. In general at temperatures above the thermoneutral zone of homeotherms, respiratory rates does not correlate well with energy metabolism. Below the thermoneutral zone it is correlated in those animals which increase their oxygen consumption and respiratory rate inversely with temperature.

However existing studies on birds have shown respiratory rate to be too variable from one flight to the next to be of any use as an accurate metabolism measure. It is possible that ventilation may be a better index, but ventilation measurements have never been telemetered from a free-living bird.

3. Radiochemical Techniques

Odum (1961) proposed that if radio-active isotopes could be found that have a biological half-life, or excretion rate, related to energy metabolism these could be used to measure energy metabolism in a free-living animal.

Although initial work was promising further investigations showed the situation to be very complex. Problems seem to centre on the discovery of an isotope which has a sound biochemical basis as a metabolic tracer because many isotopes are preferentially retained or simply not related to energy metabolism at all. Even when a suitable tracer has been found, problems still exist with this technique as regards leglisation covering the use of radio-active substances in the field.

A rather interesting radio-chemical technique involves the measurement of the HCO_3^- pool by continuous infusion of $NaH\,C^{14}O_3$. However this requires the animal to carry the infusion apparatus continually and thus is inappropriate in the current context (see Gessaman 1973).

APPENDIX II

Description of Variables Affecting the ADMR of Free-Living Birds, Estimated Using D_2O^{18} Technique

1. Procedural Differences

Bias can be introduced into an experiment by small variations in the handling and processing of experimental material. In field experiments the problem of standardisation of procedures is often greater than in the more controlled environment of a laboratory. Although every effort was made in this study to process each bird in exactly the same way, some variation in procedure was inevitable. An attempt was made to identify these areas where variation could have occurred and what effects they had, if any.

The catching, injecting and blood sampling procedures have been described in the methodology section. Variation in the stress induced in catching and handling the birds was an unknown quantity in operating the D_2O^{18} technique. Since each bird received the same number of injections, blood samples etc., it can only be assumed that the stress induced in each case was the same. The amount of fluid injected into each bird was determined by weighing the bird and was a constant proportion of total weight, thus the level the concentration of isotope attained in the body water was effectively constant. It is not considered that any small errors of weighing and injection, which would have resulted in different isotopic concentrations between birds, could have influenced the results. The number of blood samples taken was likewise constant and is thus unlikely to have had any significant effect.

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The length of time that each experimental bird was free ranged from 21 to 52 hours. Thus difference in time may have induced variation into the results in two ways. Firstly since most other D_2O^{18} studies have employed constant time periods (Δt) the effect of varying the length of this parameter has not been investigated. Secondly since Δt varied so much each measurement did not incorporate the same amount of rest and activity, which in itself may have had a significant effect.

Finally although it was intended to begin each experiment at the same time each day, this was not always possible. Thus there was variation of the point in the daily cycle of the bird that each experiment began, and this effect was examined.

Since these procedural variations should have affected both sexes to the same extent they were considered together in the analysis.

2. Environmental Variables

Since all the measurements, of necessity, were made on separate days the environmental conditions prevailing on each day may have affected the ADMR of the experimental birds; such possible effects may be:-

i Weather. Factors such as temperature, rainfall, and wind speed have either a direct effect on the bird by altering the existence energy requirements or an indirect effect via the food supply (Bryant 1973) by affecting the energy required for foraging according to food availability.

ii Day length. The longer days of midsummer allowed greater time for free flight and foraging which could have affected the total amount of energy expended in one day.

iii Food supply. Variations in the quantity and quality of available food may have made foraging more energy expensive on days of low food availability.

3. <u>Reproductive Commitment Variables</u>

Using the D_2O^{18} technique, Utter (1971) measured a difference in the daily energy expenditure of breeding and non-breeding Mockingbirds (<u>Mimus polyglottos</u>) and Purple Martins (<u>Progne subis</u>); he found a higher level of energy expenditure in breeding birds. From these results it may be inferred that differences in reproductive commitment may be reflected in differences in ADMR. Such differences in reproductive commitment may be associated with:

i Sex. Differences in the role played in reproduction by each sex have been identified in a wide number of species (Purchon 1948; Royama 1966; Lack 1968; Nisbet 1975). It is therefore probable that differences in the reproductive role may have resulted in differences in ADMR.

ii Brood Mass. Larger sized broods place a greater energy demand upon the parents for their maintenance and growth. However this demand does not necessarily increase linearly with increase in brood size. In many passerine species the feeding rate per nestling has been shown to be lower in large broods, this has been attributed to the limited foraging ability of the parents and it was assumed that larger broods were undernourished (Lack 1954). However Royama (1966b) suggested that the lower feeding rate of large broods may be due to the thermoregulatory advantages of these broods. This takes the form of reduced heat loss due to a smaller surface : volume ratio and hence leads to a lower energy demand. Mertens (1969) showed that the heat production of broods of nestling Great Tits increased in proportion to the two-thirds power of the weight, the same relationship as the surface : volume ratio of a regular solid.

Thus in considering the effect of brood mass upon the energy demands of the parents it is more appropriate to consider brood mass as the two-thirds power of the weight ($\omega^{0.66}$), usually termed the metabolic weight (Kleiber 1964), as this usefully corrects for thermoregulatory differences.

iii Brood Number i.e. first or second brood. Conditions suitable for breeding prevail long enough for House Martins to raise two broods per year. All but a small percentage (13% Bryant 1975) of birds attempt to raise a second brood and it is generally smaller than the first brood raised by the same bird. As a rule those birds which begin breeding earliest in the Season raised the largest first broods and correspondingly raise the earliest and largest second broods. Since there is undoubtedly a cost associated with reproduction which has been recorded for a wide range of organisms (reviewed by Cody 1971; Ricklefs 1974; Stearns 1976) those birds rearing two broods may suffer increased costs. Since ADMR measurements were made on birds raising both first and second broods the data were analysed for differences which may have related to either of the broods.

4. Variation in Physical Attributes

In any population of organisms a normal distribution of sizes occurs. If any of these size differences are associated with locomotor organs they may result in differences in cost of locomotion. In birds weight and wing-length are two of the major factors determining the power required for flight (Pennycuick 1968; 1969; Tucker 1972).

Since House Martins spend the majority of their active day in flight any differences in power requirement for flight may significantly alter the final ADMR attained. Although all the birds were weighed not all had wing-lengths taken. For those birds for which both parameters were available power requirements for flight could be calculated according to the equation of Pennycuick (1972):-

$$\mathrm{Pmin} = 2.64 \times \frac{W^{1.5} \times [(6.2 \times 10^{-4})\ W^{0.66}]^{0.25}}{p^{0.5} \times (0.25\,\pi b^{2})^{0.75}}$$

where Pmin = minimum power required for flight (watts)

W = weight in Newtons

b = wing-span (metres)

p = density of air ($1.22\ \mathrm{kg.m^{-2}}$)

By comparing the theoretical power requirements for flight with measured ADMR the effect of differences in size of experimental birds could be investigated.

APPENDIX III

1. Field data gathered at the time of measuring the ADMR of Male House Martins

1a) Environmental Variables

Ref No.	Nest Box	ADMR cm^3. CO_2. g^{-1}. h^{-1}.	Max.T °C	Min.T °C	Rain-fall (mm)	Wind Speed Beaufort	Log Food Abund.	Daylength. (Hours)
First Broods								
1	A	4.15	16.50	11.10	00.0	09.0	3.2799	16.40
2	H1	6,27	19.55	12.55	00.0	02.5	3.0485	16.15
3	L	5.64	22.75	09.25	00.0	01.0	3.4357	16.64
4	E	6.05	22.00	09.50	00.0	19.0	2.9921	16.55
5	H	5.95	15.55	07.50	02.6	11.0	2.8583	16.63
6	L	6.74	21.00	11.60	02.8	00.0	3.4683	16.55
B	C1	9.08	25.60	13.95	02.3	03.5	3.4726	16.55
C	H3	5.09	19.2	14.95	00.0	03.5	3.0996	15.85
Second Broods								
9	C1C	6.31	19.95	09.00	00.0	18.5	3.4017	14.32
10	V	9.20	17.05	10.35	03.3	03.5	3.1761	13.23
11	D	9.32	16.3	09.40	03.6	01.0	3.0853	13.00

1b) Reproductive Variables

Ref No.	Date of Injection	ADMR cm^3 CO$_2$ g^{-1}.h^{-1}	Brood size No. of nestlings	Age (Days)	Brood Weight (g)	Brood wt.$^{-66}$ (g)	Δt hours
First Broods							
1	8.7.75	4.15	3	4	22.63	08.06	21.5
2	16.7.75	6.27	3	5	54.9	14.06	37.05
3	20.6.75	5.64	3	4	33.6	10.17	71.02
4	1.7.75	6.05	4	4	36.8	10.80	49.2
5	14.6.75	5.95	5	4	46.4	12.59	45.58
6	3.7.75	6.74	3	16	69.55	16.44	34.34
B	28.6.76	9.08	7	14	147.2	26.97	47.42
C	20.7.76	5.09	7	12	128.7	24.67	41.25
Second Broods							
9	20.8.75	6.31	2	5	22.3	7.76	39.17
10	6.9.75	9.20	3	16	56.7	14.36	37.0
11	9.9.75	9.32	4	17	70.15	16.54	50.0

2. Field data gathered at the time of measurement of ADMR of female House Martins using D_2O^{18} technique.

2a) Environmental Variables

Ref No.	Nest Box	ADMR cm^3 CO$_2$ g^{-1}h^{-1}	Max.T °C	Min.T °C	Rain (mm)	Wind Speed Beaufort	Log Food Abundance	Daylight Hours
	First Broods							
12	K	8.65	17.65	11.70	10.4	14.5	3.4202	15.85
13	A	9.60	16.50	11.10	00.0	09.0	3.2799	16.40
14	H1	4.98	19.80	12.55	00.0	02.5	3.0485	16.15
15	L	7.59	22.75	07.15	00.0	01.0	3.2227	16.64
16	E	7.44	22.00	09.50	00.0	19.0	2.9927	16.55
17	H3	8.94	19.7	11.20	01.4	01.0	3.3927	16.55
18	H	5.21	15.55	07.50	02.6	11.0	2.8583	16.63
A	C1	5.74	27.35	07.00	01.4	03.5	3.6928	15.14
20	H1	5.98	21.45	14.45	01.4	02.0	3.7543	15.52
21	L	5.31	21.00	11.20	01.4	01.0	3.3927	16.55
B	C1	6.71	25.60	13.95	02.3	03.5	3.4726	16.55
C	H3	7.33	19.20	14.95	00.0	03.5	3.0996	15.85
	Second Broods							
24	C1C	8.76	19.95	09.00	00.0	18.5	3.4017	14.32
25	H	9.85	20.75	09.30	00.0	04.5	3.1421	13.89
26	V	8.06	17.05	10.35	03.0	03.5	3.1761	13.23
27	C1C	9.12	18.50	09.35	00.0	01.0	3.0645	13.45

2b) Reproductive Variables

Ref	Date	Brood Size No. of nestl.	Age (days)	Brood wt. (g)	Brood wt.$^{.66}$ (g)	ADMR	Δt hours
First Broods							
12	22.7.75	1	15	23.08	7.93	8.65	37.59
13	8.7.75	3	4	23.63	8.06	9.6	22.08
14	16.7.75	3	5	54.9	14.06	4.98	33.08
15	20.6.75	3	4	33.6	10.17	7.59	52.25
16	1.7.75	4	4	36.8	10.8	7.44	43.5
17	3.7.75	5	19	105.2	21.6	8.94	49.75
18	14.6.75	5	4	46.4	12.59	5.21	45.92
A	8.8.75	6	15	120.1	23.58	5.74	48.84
20	28.7.75	3	17	66.9	16.03	5.98	37.41
21	3.7.75	3	16	69.55	16.44	5.31	46.83
B	28.6.76	7	14	147.2	26.97	6.71	47.09
C	20.7.76	7	12	128.7	24.67	7.33	40.83
Second Broods							
24	20.8.75	2	5	[illegible].3	7.76	8.76	39.0
25	24.8.75	2	14	[illegible]6.25	12.56	9.85	38.16
26	6.9.75	3	16	56.7	14.36	8.06	37.58
27	2.9.75	2	18	45.0	12.33	9.12	36.75

APPENDIX IV

Calculations of Daily Energy Expenditure During Different Stages of the Reproductive Cycle

1) Egg Formation

The energy cost of enlargement of gonadal material and the production of sperm by the male is considered negligible (King 1973; Rickefs 1974) and can be omitted. However the energy devoted to egg formation by the female must be accounted for.

Ovarian maturation in adult Sand Martins (Riparia riparia) takes four days (Peterson 1955), the egg passes down the oviduct on the fifth day and is laid on the morning of the sixth, this situation was assumed to pertain in the House Martin (Bryant 1972). The daily deposition of egg material for concurrently developing eggs was calculated by Bryant (1972) for the House Martin and using these figures the extra cost per day to the female of forming different numbers of eggs was calculated. To this was added a value for existence metabolism calculated by using a seven hour rest/seventeen hour active diurnal behaviour pattern (pers. obs.) and the measured values for flight costs and SMR described earlier. In this way the total daily energy expenditure by females forming different sized clutches was calculated.

2) Incubation

The cost of incubation in birds has been a subject of much controversy in recent years. In reviewing the literature, much of which identifies a positive cost of incubation, King (1973) said that since a resting bird loses heat as a matter of course, it still remains an open question whether a bird must significantly increase its energy metabolism in order to incubate eggs. Contrary to this view in discussing King's paper, Kendeigh (1973) presented a substantial case for an increased cost to the bird; Ricklefs (1974) also subscribes to this view. In the present study it is considered that there is a true metabolic increase in the parent bird whilst incubating eggs. The heat required for incubation has to come from the parent, and adult breeding House Martins have a well-developed brood patch to facilitate this (Bryant 1975b); thus the adult birds must suffer increased heat loss, since losses from other areas of the body are not reduced. Using similar logic Kendeigh (19~~6~~73) formulated an equation to calculate the amount of heat required to maintain a clutch of eggs in a nest, at constant temperature:

$$\text{k. cals. day}^{-1} = n.w.h.b.(t_e - t_{na}).i.(1 - ca)/1000$$

where n = number of eggs
w = mean weight of eggs (g)
h = specific heat of eggs (cal. g^{-1})
b = rate of cooling (°C h^{-1} Δ $temp^{-1}$)
t_e = egg temp. (°C)
t_{na} = nest air temp (°C)
i = incubation interval (hrs)
c = proportion of egg surface covered by bird
a = proportion of time bird is on nest.

Kendeigh's equation does not take into account any heat provided by the developing embryo, and indeed he discounts this. However studies on a nidifugous species (Drent 1970) have shown that the embryo can supply 75% of its own heat requirement on the last day of incubation. However the same situation does not apply to species l

with attricial young where the hatchlings are essentially poikilothermic and with very low heat output (Ricklefs & Hainsworth 1968; O'Connor 1975). For this reason the heat increment of embryonic metabolism was disregarded in the calculations. Incubation in the House Martin is divided approximately 66% female and 34% male (Bryant 1975), and as previously a 7h/17h diurnal activity pattern was used. The total cost to each bird was then calculated as follows:-

i Total hourly heat requirement of eggs was calculated from Kendeigh's equation (above) using egg and nest temperature measured during the period of study at the same colony by S. Guy (pers. comm.)

ii The female was then assumed to contribute 11.22 hours of the daytime heat requirements (66% of 17 hours) and the male 5.78 hours (34% of 17 hours). To this was added the cost of the same number of hours at SMR (i.e. at rest). The cost of the remaining daylight hours spent in flight was then added to the previous totals to compute total day time energy expenditure by each bird. This calculation assumes i) all time off the nest is spent in flight, ii) that there was never more than one bird on the nest at a time during the day.

iii To calculate the seven hours night time energy expenditure for each bird the heat requirement of the eggs for this period was divided equally between the birds since they both roost in the nest (pers. obs.). To this was added the cost of seven hours at SMR.

iv By adding the calculated day and night time energy expenditures together total daily energy expenditure to incubate broods of different size could be estimated.

3. First Four Nestling Days

Broods of six young are brooded for 100% of the day for the first two days and 90% for the next two days, whilst broods of three young arebrooded for 100% of the day for ? days! (Lind 1960). In the absence of more detailed data it was assumed that the range of brood sizes considered (2-5) were brooded by the parents for 100% of the day and that 66% of this was carried out by the female. There is good evidence (Ricklefs & Hainsworth 1968; O'Connor 1975; Bryant & Hails 1975) to assume that for the first four days the newly hatched young are essentially poikilothermic with very low heat output of their own. In order to try and estimate the energy cost to the parents of brooding the growing mass of nestlings the clutch weight method outlined by Ricklefs (1974) was used. Here the energy required per gram for the adults to maintain their body temperature at the mean nest temperature was calculated from the equation (Lasiewski et al 1967):-

$$\text{cal g}^{-1}.\text{h}^{-1}\,°\text{C}^{-1} = 4.0 \times w^{-0.508}$$

where $°C$ = temperature gradient between nest and body temperatures

w = weight of bird in grams

This figure was then multiplied by the metabolic brood weight of the young for each of the first four days, temperature gradients used were a nest temperature of 26°C and chick body temperature of 36°C (S. Guy, pers. comm.).

In this way the cost was estimated as the cost to the parent of maintaining a given extra mass of body tissue at a given temperature. The figures derived in this way were added to the time budget estimates for the remainder of the day as described for the incubation period.

4) 5th - 28th Nestling Day

The energy expended by the adults during the remainder of the nestling period was derived by summating the daily measurements of the D_2O^{18} data (Fig. 3.4) for different brood weights.