

- ~~E~~ ERRATA

- 179 Line 3. For Fig. 10 read Fig. 8.10.
- 182 Line 17. Insert, Egg laid June 9th subsequently
deserted.
- 183 Fig. 8.10 For Total aerial insect abundance ~~and~~
Hypothetical laying distribution
- 183 Fig. 8.11. For see text read probable δ s.
- 186 Add. July - 2.76×10^{-3} ; August - 4.27×10^{-3}
and September 3.80×10^{-3} Kcals/item.
- 195 Line 17. For during read after.
- 216 Line 10. For Wedwards read Edwards.
- 218 Line 19. For increasingly dependent on read
increasingly dependent, as brood size
enlarges, on.
- 228 & 230 Line 22 and 1. For feeding themselves). process
of natural read feeding themselves).
The possible resulting mortality could
reduce the representation of adults in the
population that are disposed to lay these
large clutch sizes, through the process of
natural.
- 247 Line 8. For Hirundinas read Hirundines.
- 253 Line 18. For requirements with read requirements
(R) with.

THE BREEDING BIOLOGY OF THE HOUSE MARTIN ~~(DELICHON~~
~~URBICA~~ (L) IN RELATION TO AERIAL INSECT ABUNDANCE.

Thesis submitted for the degree of Doctor of Philosophy in
the University of London.

by

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London.

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ABSTRACT

The breeding biology of the House Martin Delichon urbica (L) is described, with particular reference to the influence of variation in the abundance of aerial insects. The selection of food items from the available resources is explained in terms of a predation strategy which demonstrates that the Martin consistently maximises the efficiency of food collection. The timing of the breeding season and breeding success are respectively shown to be closely associated with the development of the aerial phase of several insect populations and with food abundance. A hypothesis is presented, with some supporting evidence, which describes the potential selective forces acting on broods both smaller and larger than the most frequent natural brood sizes which would possibly inflict a disproportionately large mortality on these extreme brood sizes and also on the adults involved in rearing them. This is particularly relevant to those species where artificially enlarged broods or the largest naturally occurring broods are more productive than the most frequent brood sizes, as is the case in this study. Differences in food and feeding station are described which ensure a degree of ecological isolation between aerial feeding birds in Britain.

ACKNOWLEDGEMENTS

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Dr G.Murdie advised on statistical matters and Mr E.E.Green helped in a number of ways in the field.

SECTION 1.

INTRODUCTION

The study of the regulation of animal numbers has received much attention in recent years, stimulated in part by the detrimental effects of certain animal populations on Man's interests. Until about ten years ago much effort was expended in demonstrating that one of three basic theories of the regulation of populations was valid, to the exclusion of the other two. These theories are most closely associated with Nicholson (1933, 1954), Andrewartha & Birch (1954) and Wynne Edwards (1962). Nicholson emphasised the importance of density dependant (Smith 1935) processes in population regulation, while Andrewartha and Birch proposed that in the natural state density independent factors are invariably responsible for the determination of animal numbers around their observed levels. Wynne Edwards proposed that populations are maintained about an optimal level through behavioural mechanisms which prevent overexploitation and the consequent depletion of food resources. The relative merits of these three approaches, and of the work of others associated

with them, have been reviewed by Clark et al (1967), Lack (1966), Richards and Southwood (1968), Huffaker and Messenger (1964) & Solomon (1970). Partly as a result of these discussions emphasis has now shifted from the emphatic proposal of a single explanatory theory, and towards an approach that examines the mechanisms of population regulation, with an acceptance that such mechanisms may not only vary between different classes of animals but also within species when they occupy different habitats of different parts of that species geographical range. Now therefore, illumination of population processes is sought, rather than the all embracing theory. This approach is exemplified by the work of Varley & Gradwell (1960, 1965) who developed a method (key factor analysis) of exploring the action of factors important in determining population numbers. The analysis of the processes of population regulation has been carried further by Holling (1963, 1968) through the approach of component analysis. Concurrent with these developments have been the proposals of Pimental (1961, 1965) and Chitty (1960, 1965) which provide alternative explanations of the mechanisms of population changes. However they are conceded not to be applicable to all animal systems.

With this emphasis on processes I turn to the specific study of bird populations which have often played a crucial role in the development of the theories outlined above (Lack 1954, 1966 and Wynne Edwards 1962). However, as if to emphasise the lack of information about certain events, both Lack (1954) and Wynne Edwards (1962) make use of the same example, that of Jespersen (1924, 1929), in support of their viewpoints on population regulation. The purpose of the present work was to reduce the possibility of such alternative explanations being proposed for the same phenomenon, through a close study of a bird, the House Martin (Delichon urbica), and its environment. Particular emphasis was laid on the pattern and causes of mortality throughout the breeding season, the timing of the breeding season, the determination of clutch size, food and food selection and ecological isolating mechanisms found in the aerial feeding birds normally breeding in Britain.

Seven processes are listed by Richards and Southwood (1968) as being potentially important in modifying (insect) populations and all of these were considered to be influential to a certain degree in the House Martin. However much of the work in this thesis is centred on the influence of the

food supply on population processes, and the House Martin is a particularly suitable subject for such a study because it breeds colonially (and data of statistical significance can therefore be collected in a comparatively short time, in contrast for example to a dispersed population as studied by Southern (1970) where data collection was a time consuming process). Also, its food supply can be monitored accurately by means of aerial suction sampling methods.

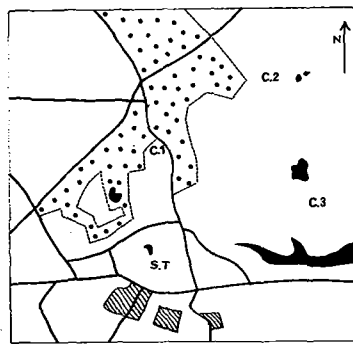
SECTION 2.

MATERIALS AND METHODS

The breeding House Martin (Delichon urbica L.) was studied at three colonies in Windsor Great Park, Berkshire from 1968 to 1970. The vegetation of the surrounding areas was similar in each case, composed of mixed arable and grazing farmland with extensive hedgerow timber and stands of mixed woodland in which Oak (Quercus sp) is dominant. Also in the study area were a number of open waters and some housing. The main features of the area are shown in Figure 2.1.

Nestboxes were placed under the eaves at each colony in sites occupied in previous years by natural nests. Ten nests additional to the previous year's number were provided. The boxes were of commercial origin and were adapted so that they could be easily removed for inspection. The distribution of boxes and natural nests at each of the colonies is illustrated in Figure 2.2.

Colonisation of the nestboxes and natural nests from the previous year, and the building of new nests occurred concurrently. The bias inherent in the results because certain birds did not have to build their own nests is



- C.1 SUNNINGHILL PARK FARM COLONY.
 C.2 KENNELS COLONY.
 C.3 CUMBERLAND LODGE COLONY.
 S.T. SUCTION TRAP.
 OPEN WATER.
 FOREST.
 URBAN AREAS.
 ROADS.

FIG. 2.1. Map showing the main features of the study area and the sites of three colonies and the suction trap.

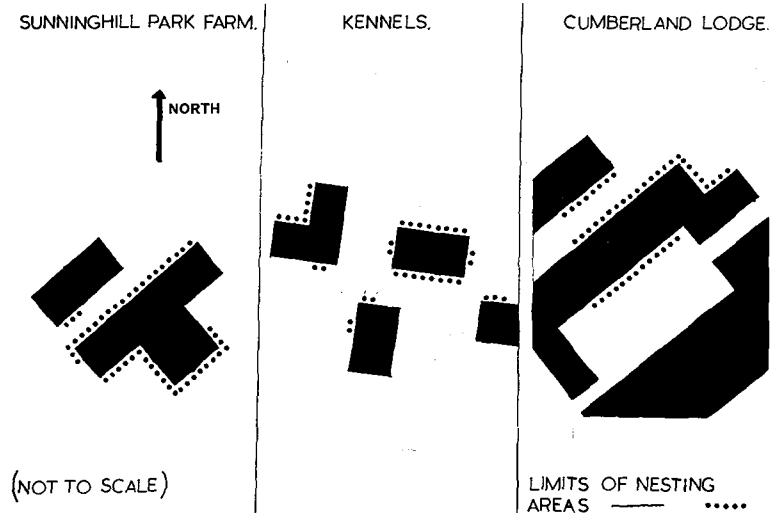


FIG. 2.2. Map showing distribution of nesting areas at each of the study colonies.

considered negligible. Many natural nests at other sites were in good repair and were occupied with only minimal maintenance, a process requiring a similar allocation of labour as the occupation of a nestbox. Lind (1960) suggested that the small clutches characteristic of the latter part of the laying season occurred because of exhaustion from nest-building activities, however I will present later an alternative suggestion.

The nestboxes were inspected daily throughout the breeding season at two main sites and at less regular intervals at Cumberland Lodge. Eggs and young were weighed at each visit at 9. a.m. All weighings were made with Pesola Spring Balances of 5 and 30 gram range, with the specimen in a cellulose acetate container. The balances were checked at monthly intervals against standard weights.

Faecal samples were collected for a study of food selection in the House Martin. It proved possible, though time consuming, to count the cuticular remains of insects, and assess their frequency of occurrence^e throughout a 24 hour period. A discussion of the inherent errors are postponed to chapter 4 on food selection.

The faeces were collected by placing a tray beneath the nestbox which caught all the pellets ejected from the nest by the developing young. The tray was cleared at daily intervals at 10 a.m. Removal of faeces by the adults was observed only on a single occasion and probably only occurred in the first four days of nestling life, before the nestlings acquired the ability to defaecate out of the nest opening, Faecal samples from young of less than six days were not used in the present study.

The aerial insect food supply was monitored using an Aerofoil Insect Suction Trap (Fig. 2.3) (Johnson 1950a and Taylor 1962) at 40 feet above ground level and 260 feet (220 + 40 ft) above sea level. The trap was sited about two miles from the nearest colony and was surrounded by the same vegetational components of mixed woodland and farmland etc as the study colonies. The trap drew air into the 10 inch aperture at the rate of 9.6×10^4 cu ft/hr. The catch was removed at 9 a.m. each day throughout the year and stored in alcohol and glycerine for examination at a later date. The insect catch period was thus effectively in phase with the House Martin inspection period.



FIG. 2.3. The suction trap

The 24 hour catch was sorted into families and each insect was allocated to one of 4 size categories: length = 0.3 mm, 3.1 - 6 mm, 6.1 - 9 mm and 9.1+ mm. From these data the aerial insect abundance could be presented daily in a number of forms. The form chosen will be indicated in the appropriate section, however the most useful formulations were the total calorific value of the catch and the total numbers of insects caught. Using these units rather than mean aerial density reduces the importance of daylength as a variable when estimating the food available to the feeding birds. This is convenient in many cases but means that no data ^{are} ~~is~~ available at the present time on whether the greater food abundance of mid summer is a function of constant density available over a longer daylength or whether mean aerial density is changing as a more complex function of season and daylength. A correlation coefficient of $r = 0.76$ for a plot of total insects caught (Log scale) from May to October, on daylength suggests that 58% of the variance in flying insects trapped per day is associated with a seasonal change in daylength.

The insect sampling method will minimise errors caused

by different flight periods and abundance within these periods. For example how useful to the feeding Martin is a species at low density flying for much of the day, compared with a species at a high density flying for a short period each day? The suction trap sampling at a constant maximum rate will simulate a maximum potential predation rate by the Martin. The total catch of that species as a percentage of the total catch will thus be a measure of its relative aerial abundance and availability to a predator on that day. This is important in the study of food selection in relation to estimated relative abundance in the air. The advantage of a full 24 hour sample period, or at least a full daylight sample is emphasised by the following points. The flight periodicities of different insects will mean that different species will be available at different times of day (Lewis & Taylor 1965). The mean height of flight will change throughout the day and circumstances may cause a sample taken in any one hour to completely miss an insect abundant earlier or later in the day, or will grossly underestimate total abundance because most insects are above or below the sample height (Johnson 1969). However a continuous sample from a fixed height will record both upward and downward transport of insects each

day and minimise such potential errors.

The meteorological data was collected at the Field Station. No physical barriers exist between the meteorological recording site and the colonies, that are likely to invalidate extrapolation of climatic data to each of the sites (Watt 1968).

Other apparatus used in conjunction with particular studies is described in the appropriate section.

SECTION 3.

GENERAL BIOLOGY OF THE HOUSE MARTIN AND THE AERIAL INSECT FOOD SUPPLY

Biology of the House Martin

This chapter describes the physical features and biology of adult and nestling House Martins. A summary of the breeding cycle is presented and relevant information from the literature is detailed.

The Adult Adult Martins were trapped, weighed and measured throughout the breeding season of each year. They were caught in mist nets in the vicinity of the colony and captured on the nest at dusk or during incubation. Only a single desertion resulted from the use of the latter method and this occurred in unusual circumstances. A total of 96 birds were examined, together with a similar number of controls.

Mean Weight of Sample - 19.4 gms (± 1.3 S.D.)

Mean Wing Length - 106.5 mm (± 2.1 S.D.)

The frequency distribution of the weights and winglengths are shown in figs 3.1 & 3.2. A distinct bimodality is illustrated in fig 3.1. This was assumed to be a sexual difference and the distributions were separated to give the following means (Fig 3.3) Examination of the cloacal region

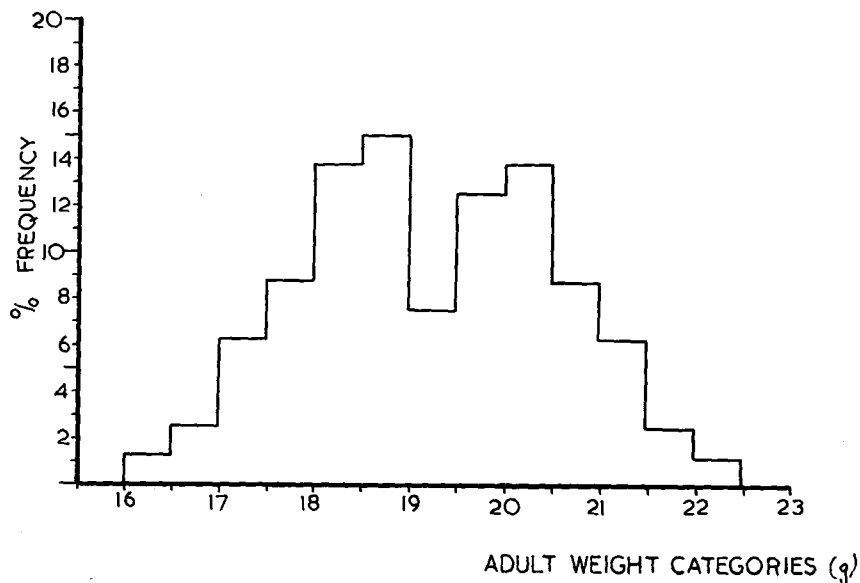


FIG. 3.1. The frequency distribution of adult House Martin weights.

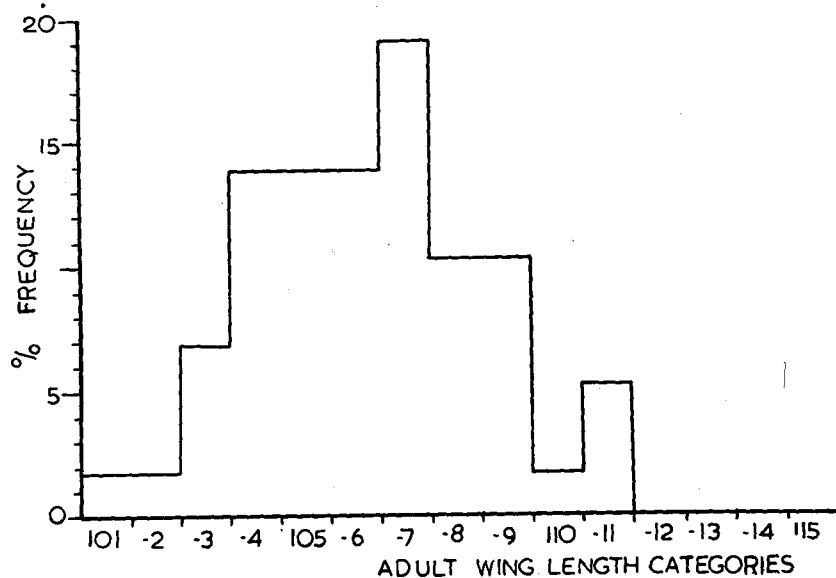


FIG. 3.2. The frequency distribution of adult House Martin wing lengths.

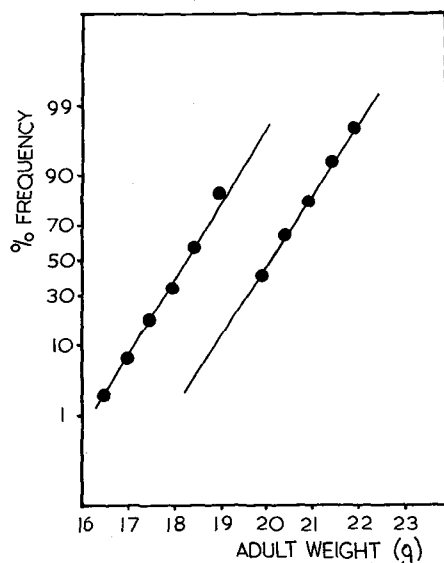


FIG. 3.3. The frequency distribution of adult House Martin weights separated on probability paper to illustrate the bimodality of the data. The implications of this are discussed in the text.

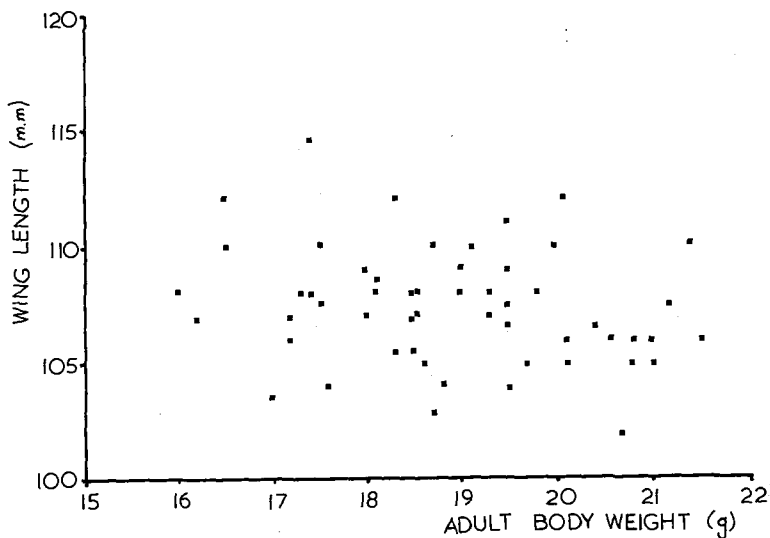


FIG. 3.4. The relationship between adult body weight and wing length in the House Martin.

in the laying period indicated that the female birds were the heavier, and all those birds assigned to each sex on cloacal characteristics fell within the predicted range.

Adult Males (and others) 18.0 gms $\pm$ 0.9 gms

Adult Females 19.9 gms $\pm$ 0.9 gms

However the use of weights as a criterion for sexing House Martins is invalidated because of the overlap region and the dynamic nature of weight change with ovarian condition (Petersen 1955). Petersen indicated in the Sand Martin (R. riparia) that both sexes will be of similar weight after incubation but that the females are heavier in the egg formation and incubation periods. The sampling method is therefore likely to select laying and incubating females from the population and it seems probable that the two modes of the frequency distribution represent incubating females and others, including males and post incubation females.

Wing length showed no corresponding bimodality though longer wings were generally associated with lighter birds (Fig 3.4) ($b = -0.44$, $r = 0.25$ $p < 0.05$). This could have resulted from abrasion of the females flight feathers during incubation, as the females are involved in incubation to a greater extent than the males (Lind 1960).

The weight and wing length differences between the sexes during and preceeding incubation are of unknown significance in relation to flight speed and feeding potential. Pennycuik (1968) demonstrates an increase in optimum flight speed ($V \propto W^{\frac{1}{6}}$) with an increase in body weight. The relationship is linear after transformation over the whole range of bird weights. The optimum flight speed of each of the sexes is therefore likely to differ thus theoretically increasing prey capture potential. This may be significant firstly in enhancing powers of food collection by the females to facilitate formation of the egg or secondly to ecologically isolate the sexes at a critical phase of the breeding cycle. However whether the weight differences at this time are effected for this purpose or are merely a by product of the egg formation process is not known. Sexual differences in structure have been shown to influence prey spectra in Carrion Crows Corvus corone (Holyoak 1970) and the Woodpecker, Melanerpes striatus (Selander 1966).

Adult plumage showed no characters that were consistent with sex or age constants judged from size and behaviour criteria. However the secondaries of birds of the year

retained their white tips for periods in excess of two months.

No birds were trapped in moult and this evidently occurs on the wintering grounds in Africa as in the Swallow (H. rustica) (Snow, 1967).

The Egg

The mean weight of first brood eggs for 1969 was 1.73 gms $\pm$ 0.18 and for second brood eggs 1.67 gms $\pm$ 0.16 gms. The size was mean length = 20.26 $\pm$ 1.1 mm. and mean width = 13.64 $\pm$ 0.5 mm. Egg colour is a translucent white at laying, becoming increasingly opaque as incubation proceeds. A single clutch of the form bearing red brown spots was recorded. Also many bore the defaecations of blood sucking insects, but on these the markings were darker in colour. Egg weight declines throughout incubation. Details are presented in section six.

The Incubation Period

The incubation period of the House Martin in Britain is recorded by Witherby et al (1938) as 14 days. Lind (1960)

referring to a Scandinavian population, records 15.5 ± 0.18 days, while periods of 12 to 14 days, 14 to 15 days and 14 days are recorded respectively by Hoffman (1927), Niethammer (1937) and Voipio (1952) for various European sites. The present study recorded a value of 14.6 ± 1.15 days for all broods from 1968 and 1969, where the incubation period was that defined by Moreau (1946).

Individual eggs had a variable incubation time according to their weight at laying. The relationship is illustrated in Fig 3.5 and refers to eggs from all clutch sizes from the breeding season of 1969. There is a significant correlation where $r = 0.20$ ($p = < 0.05$). The relationship is described by the equation $y = 12.11 + 1.37 x$ where x is the egg weight in grams.

The incubation period did not differ significantly between first and second broods. The values for each season and brood are presented in Table 3.1.

Lind (1960) examined the incubation period in relation to intensity of incubation (i.e. percentage of total time eggs were incubated) which he found varied in relation to external temperature. He proposed that food shortage

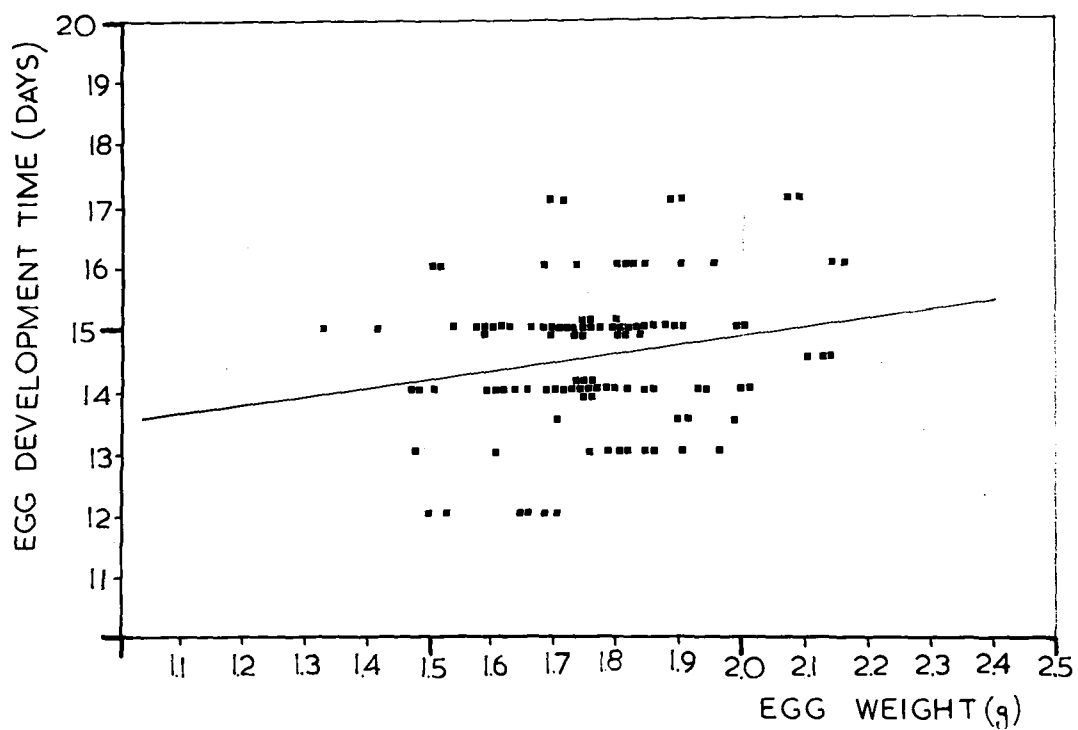


FIG. 3.5. Egg weight at laying in relation to the length of the subsequent incubation period for the whole clutch.

associated with low temperatures increased the necessary foraging time for the adults which therefore left the clutch unincubated while they collected food. It is proposed to examine this in relation to aerial food abundance at a later date.

The Nestling Period

The nestling period of the House Martin has been recorded by Witherby et al (1938) as 19 to 22 days in Britain, by Niethammer (1937) as 25 to 26 days in central Europe and as a minimum of 24 days by Lind (1960) in Scandanavia. Following the terminology of Moreau (1946) I recorded a mean nestling period of 30.6 ± 2.3 days for 1968 and 1969. This differs considerably from Witherby's estimates and can possibly be explained by differences in method. Witherby did not define the nestling period and it is possible that the figure they give, refers to the period from the last chick to hatch to the first to fly. Errors could therefore be introduced because of a mean duration of hatching of 2.4 days (Lind 1960) and the poorly defined fledging date, where the young display an increasing independence, but where the flights on the first day of fledging may be only of a few minutes duration and hence passed unrecorded. The nestlings I examined were not

capable of sustained flight until the winglength was on average 80 to 85 mm (a nestling age of 22 to 24 days). They were not voluntarily seen to leave the nest (observations were made from a concealed position) until a minimum recorded figure of 88 mm (nestling age 26 days). Usually this figure was 90 to 95 mm and indicated the approximate age and size at which full flight ability had just been realised. This corresponds to an age of 25 to 29 days depending on brood size. My figure refers to a value derived from the sampling visits, either at 09.00 or at 19.30, when all the young were found to be absent or left the nest voluntarily before examination was made. However it does in fact refer more specifically to the nestling period of the last bird to hatch and the last bird to fledge (as this is destined to be the runt of the brood with the slowest development rate). Moreau's method therefore tends to elevate the figure beyond a more realistic mean figure, but this is unlikely to be less than 26 days in any event.

The length of the nestling period was found to vary significantly with brood size (Fig 3.6) and can be described by the equation $y = 29.19 + 0.404x$ with $r = 0.25$ ($p = < .05$). However this relationship is at least in part a function of

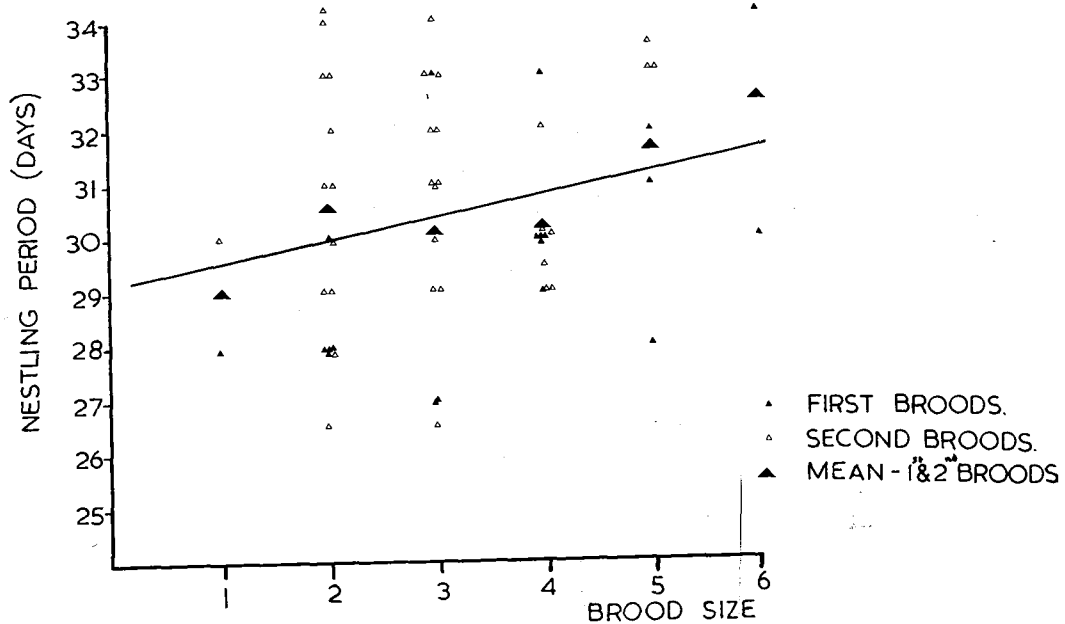


FIG. 3.6. The length of the nestling period (where this is the time from hatching of the last egg to fledging of the last nestling) in relation to brood size.

employing Moreau's definition. Thus the hatching time is longer in larger broods and therefore the size differences soon after hatching are greater, in effect predisposing the last nestling to hatch to have an extended nestling period. The values used were derived from the 1968 and 1969 breeding seasons.

The nestling period did not differ significantly between first and second broods in spite of a variation in mean clutch size. The mean values for the nestling periods for 1968 and 1969 are presented in Table 3.2.

Nestling Growth

The form of the nestling growth curve has been found to differ between species. Nestling growth may be approximately sigmoid in form as in the majority of species investigated, or it may reach an asymptote during nestling development and then decline until fledging. This phenomenon of weight recession occurs in the Sphenisciformes, Procellariiformes, Pelecaniformes, Apodiformes and in some Passeriformes notably the Hirundinidae and has been discussed by Edson (1930), Lack (1968) and Ricklefs (1968). The growth curve may also vary to a certain extent within species according to the

particular environment i.e. Weather, Habitat and Brood Size variation.

The mean growth curve of nestling House Martins is shown in Fig 3.7. It resembles that of the Swift Apus apus and the Manx Shearwater Puffinus puffinus. Lack (1951 & 1968) and Harris(1966) suggest that the form of the curve is due to the deposition and subsequent utilization of fat. In the House Martin it is due to an increase and subsequent decline in the percentage water content of the nestling tissues. A similar situation was demonstrated by Ricklefs (1968) for Hirundo rustica. I examined this in the House Martin by analysing four nestlings for water content. The wet weight showed the usual asymptotic form, while the dry weights showed a linear increase with age suggesting that if variation in water content could be eliminated, growth would approximate to linearity (though would probably be slightly sigmoid) (Fig. 3.8)

Ricklefs found that protein and lipid content varied little in the second half of the nestling period, though a possible increase in lipid is apparent from his figures. The change in water content is likely to be ultimately a function of the change in the composition of the body, because body

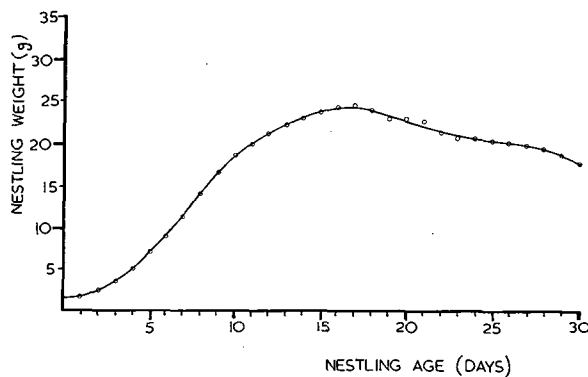


FIG. 3.7. The mean growth curve for body weight in the House Martin.

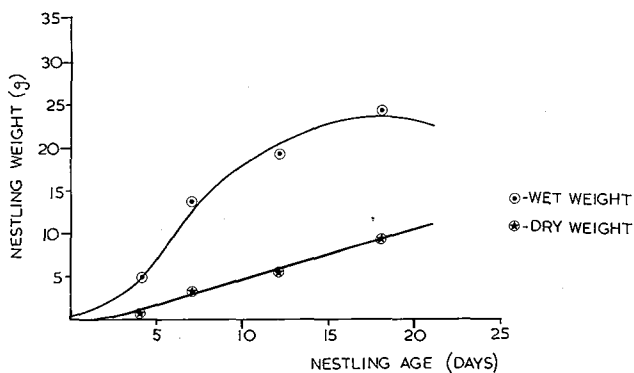


FIG. 3.8. The relationship between both wet weight and dry weight of nestlings and nestling age.

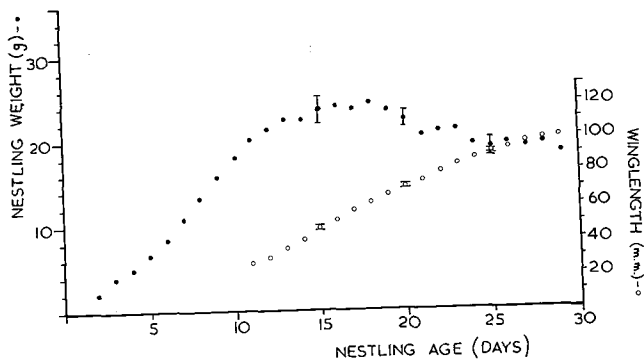


FIG. 3.9. The mean growth curve for body weight and wing length for second broods of two nestlings.

water is naturally associated more with some tissues than others. Therefore as muscle contains 75% water, and fat only 6 to 20% water, the % water content will vary inversely with % fat content. Possibly the rise in fat at the end of the nestling period causes a concurrent drop in % water. However I have no evidence for this view in the House Martin and Ricklefs' figures for the Swallow are inconclusive. The most important contributant to the weight recession is the decline in water content of the integument (skin and feathers) for which Ricklefs (1967 and 1968) presents figures. The integument undergoes little change in bulk at the time of the weight recession while it is declining in the water content. Thus in the period immediately before the wet weight asymptote the water content of the integument is 256% of the dry weight, but only 115% 3 days after the asymptote. The gross weight difference over the 4 day period is on average 1.45 gms, which makes a considerable contribution to the total weight change observed in the second half of the nestling period. The reasons why such a weight recession does not occur in all birds is discussed by Ricklefs (1968).

The growth of the primary feathers serves as a useful

index of nestling age and growth rate (Lack, 1951). The mean growth form of one brood size is shown in Fig 3.9. It can be seen that wing length growth approaches linearity though it is in fact slightly sigmoid. The growth forms for different brood sizes indicating both weight changes and wing length increase are presented in Fig. 3.9 and Table 3.3. The latter records the variation about each of the selected ages on the graph. The coefficient of Variation (C), which is independent of the units considered allows comparison to be made between the variation in weights and wing lengths at given ages. It can be seen that C tends to be generally higher for weight increase than for wing length increase, but the differences were only significantly different in the first broods (where $F = 4.7$ (Variance Ratio) $p = < 0.05$) and not in the 2nd broods. However a more valid comparison involves comparing the coefficients of variation from the same period of growth (i.e. days 15, 20 and 25 of nestling growth, rather than 5 to 25 for weight increases and 15 to 25 for wing length increases). Then no significant differences in variation were found for either the first or the second broods. Another comparison involves examining the principal periods of weight increase and wing length

Table 3.3

Mean Nestling Weights and their variation for selected days through development.

Mean weight - M.Wt.
Standard deviation - S.D.
Coefficient of variation - C

Brood	Size	Day-5			10			15			20			25			Mean
		M.Wt	S.D.	C	M.Wt	S.D.	C	M.Wt	S.D.	C	M.Wt	S.D.	C	M.Wt	S.D.	C	
1st BROODS	1	NO DATA															
	2	8.1(2.1)	-	26.0	19.2(2.7)	-	14.0	24.5(1.1)	-	4.5	23.8(1.0)	-	4.2	20.0(1.0)	-	5.0	13.4
	3	6.1(0.7)	-	11.5	19.8(1.3)	-	6.6	21.6(1.8)	-	8.3	21.2(1.5)	-	7.1	19.1(0.7)	-	3.7	7.4
	4	6.7(1.2)	-	17.4	17.4(3.9)	-	22.4	23.4(1.3)	-	5.5	22.7(1.2)	-	5.3	18.4(1.4)	-	7.6	11.6
	5	8.0(1.5)	-	18.7	18.6(2.0)	-	10.7	21.5(1.5)	-	7.0	22.0(1.7)	-	7.7	16.8(2.0)	-	11.9	11.2
	6	6.8(1.4)	-	20.6	13.4(2.7)	-	2.0	16.7(1.6)	-	9.6	23.2(1.6)	-	6.9	18.7(1.7)	-	9.0	9.6
2nd BROODS	1	8.1	-	-	19.0	-	-	24.0	-	-	21.5	-	-	19.3	-	-	-
	2	6.9(1.2)	-	17.4	17.9(2.1)	-	11.7	23.5(3.6)	-	15.3	22.2(1.3)	-	5.8	18.9(1.3)	-	6.9	11.4
	3	8.9(1.2)	-	13.5	17.4(1.5)	-	8.6	23.1(1.2)	-	5.2	21.9(1.8)	-	8.2	18.7(0.9)	-	4.8	8.06
	4	5.9(1.1)	-	18.6	18.3(1.1)	-	6.0	22.4(1.0)	-	4.5	22.9(1.8)	-	7.9	19.8(1.7)	-	8.6	9.1
	5	-			15.6(2.7)	-	17.3	21.4(2.5)	-	11.7	21.2(1.3)	-	6.1	19.4(1.3)	-	6.7	10.45

Table 3.3 (cont.)

Mean Nestling Wing Lengths for selected days
throughout development

Brood Size	Wing Length on Day 15			Wing Length on Day 20			Wing Length on Day 25			Mean C
	S.D.	C		S.D.	C		S.D.	C		
1										
2	50.9(2.6)	-	5.1	72.6(5.5)	-	7.6	91.1(4.7)	-	5.2	5.9
3	50.7(2.7)	-	5.3	74.4(3.2)	-	4.3	94.5(2.7)	-	2.8	4.1
4	47.1(3.4)	-	7.2	70.2(4.1)	-	5.8	90.0(4.1)	-	4.5	5.8
5	48.8(3.9)	-	8.0	70.3(5.5)	-	7.8	86.8(7.5)	-	8.6	8.1
6	44.5(4.7)	-	10.6	64.7(5.6)	-	8.6	86.9(4.9)	-	5.6	8.3
1	50.0(2.8)	-	5.6	73.5(0.7)	-	9.5	92.5(0.7)	-	7.6	7.6
2	48.5(4.6)	-	9.5	71.8(3.6)	-	5.0	90.5(3.4)	-	3.7	6.1
3	50.1(4.3)	-	8.6	73.9(3.3)	-	4.5	93.0(3.0)	-	3.2	5.4
4	48.4(3.6)	-	7.4	63.8(3.5)	-	5.5	84.3(4.1)	-	4.9	5.9
5	47.7(5.4)	-	11.3	69.7(8.8)	-	12.6	90.0(7.6)	-	8.4	10.8

growth. (where this is day 5 to 15 for weight increases and day 15 to 25 for wing growth). There is here a highly significant difference in the variation of weight increase and wing growth where $F = 9.1$ for 1st broods ($p = <.001$) and $F = 8.6$ for 2nd broods ($p = <.001$). It can therefore be concluded that variation in weight increase is significantly greater than the overall variation in wing growth when their periods of most intense increase are considered. Therefore the most sensitive index of growth rates will be provided by weight changes in the first half of the nestling period. I later make the assumption that ^{the} variation is in some way a product of the environment. It was also calculated that the variation in weight was not significantly greater than the variation in wing growth in the second half of the nestling period. This contrasts with the data of Lack (1968) and Harris (1966) who propose that in the Swift and the Manx Shearwater selection has favoured minimisation of variation in wing growth, often at the expense of body growth or accumulated fat reserves so that flight capability is not impaired at a later date because of the consequent stunted feather growth. The difference could possibly be due to a more extreme variation in environmental conditions (and hence food

availability) that the Swift and Shearwater experience.

The distribution of feathers on nestlings of different ages is shown in fig 3.10. Seel (1966) demonstrated the importance of a complete feather cover, before nestlings were able to maintain deep body temperature when removed from the nest. It follows therefore that the role of the parent in brooding the young will progressively decline throughout the nestling period until complete feather cover is achieved. Feather cover at hatching covers 13% of the uppersurface in the House Martin, remaining at this level until about the eighth day. Feathers then rapidly develop until cover is effectively complete by the sixteenth day. (Fig 3.11) Lind (1960) records percentage brooding in broods of 3 and 6 young. Generally less than 100% brooding began on the seventh day in broods of six but persisted until the 15th day in broods of three. In summary therefore the potential relative contribution of any factors to heat conservation or production will be at a maximum at hatching when the surface/volume ratio is at a maximum and then decrease slowly until the seventh day, thereafter decreasing rapidly until 80% feather cover is present on about the thirteenth day. Such factors include the greater Mutual insulation in larger brood sizes

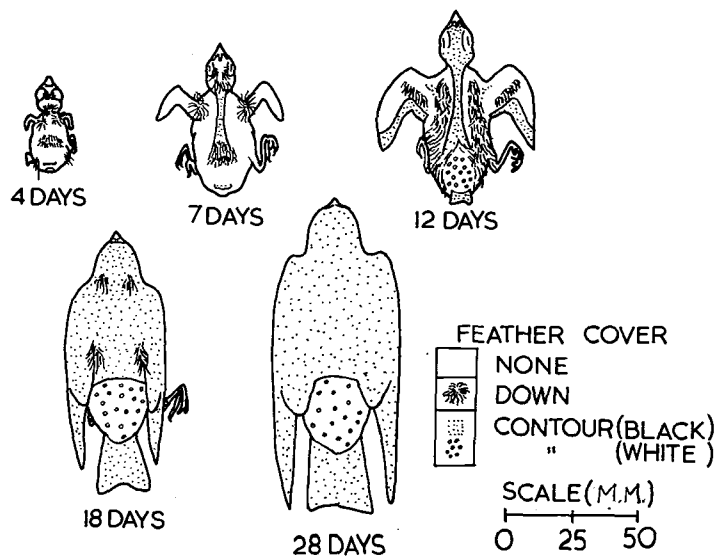


FIG. 3.10. The distribution of feather cover on the dorsal surface of House Martin nestlings at five ages. Bare skin, down and contour feathers are distinguished.

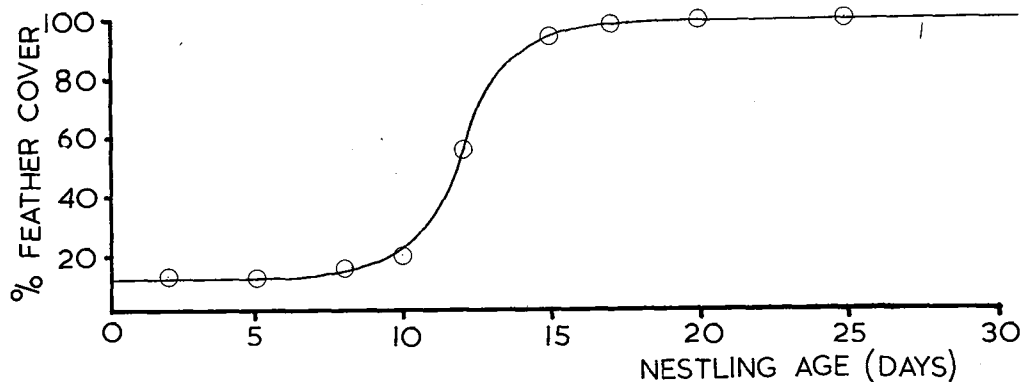


FIG. 3.11. The development of feather cover (including down and contour feathers) on the exposed dorsal nestling surface, as a function of nestling age.

brooding, nest lining and structure, and quality and quantity of food delivered to the nestlings.

An analysis of the precise factors causing this variation in growth rates and their differences between different brood sizes in first and second clutches are investigated in section six.

The factors that contribute to the variation in the quality of the nestlings at the end of the nestling period (in terms of gross weight and wing length) are described in section seven.

Distribution and Habitat

The Hirundinidae are represented in Europe by five species, of which three breed throughout Britain, the Swallow Hirundo rustica, the Sand Martin R. riparia and the House Martin. They may be found in all areas of the country though evidently less commonly on the north west coast and islands of Scotland (Parslow, 1969). Their habitat requirements have been described by Witherby et al (1938). However it is useful to make the distinction between association of a species with a certain habitat for feeding purposes and because its exacting nest site requirements make it inevitable. The Sand Martin.

is notably considered to be a bird associated with water and indeed sandy river banks must have provided most of the suitable nest sites throughout the bird's evolution. However since man has extensively extracted sand and gravel for his industrial needs, suitable nest sites have been provided many miles from water. That these sites have been utilised successfully by large colonies of the birds suggests that their feeding ecology is not inevitably associated with water, but rather that they were ^{er}formally restricted to such sites by specific nest site requirements.

The House Martin is a bird of open country, and woodland edge with perhaps the most favourable habitats being provided by arable or scrub land, with a high proportion of their insect fauna migratory (Southwood, 1962) interspersed with belts or clumps of trees. However colonies are found in sites ranging from ~~city centres~~ to sea cliffs. The nest may be built under the eaves of houses or on cliffs. Details of the mechanics of nest construction are given by Lind (1960).

Migration

The family is generally migratory, summering in the Pala^aerctic and wintering in the case of the House Martin in central Africa, extending to S. Africa (Voous 1960). The

species has no ringing recoveries outside Europe and is little known in its winter quarters. This is in contrast to the Sand Martin and Swallow which have been extensively ringed and recovered at both extremes of their range. This suggests that the House Martin is widely dispersed in its winter quarters and probably feeds in small groups or singly, as opposed to the massed concentrations of the Sand Martin.

The Breeding Season

House Martins arrive in Britain in mid April and are often abundant around the colonies by the turn of the month. However previously absent pairs may occupy nests as late as early July. This probably involves late arriving first year birds or birds that have endeavoured and failed to establish themselves elsewhere. The latter situation is apparently not precipitated by the loss of the clutch though it may follow nest destruction by householders or occupation by House Sparrows. The birds usually commence building in the last week of April, while laying will extend from the second week of May. Two broods are usually reared, though in certain conditions up to 50% of the pairs fail to attempt a second brood. Witherby et al (1938) records an occasional

third brood, though none were recorded in the present study. Relayings or a change of nest occupants could lead to errors even in the most closely watched colony, however the season is theoretically long enough for three broods to be reared by the earliest starting pairs. Breeding activity is usually terminated in mid September though several birds may still be rearing young into October or rarely early November. Breeding has been recorded in South Africa on several occasions during the Northern Hemisphere winter, though whether the same birds travel north and breed again is not known (Moreau, 1966).

Feeding Behaviour

All members of the Family feed entirely aerially. Feeding is commonly communal within the species, especially on migration or when the species breeds colonially (Lack, 1968) as is the case with the House Martin. Also mixed species flocks occur, particularly in association with large or localised aggregations of insects. Of the British nesting species, feeding may take place from ground level to several hundred feet. Exceptionally when utilising insect aggregations built up as a result of atmospheric instability or the passage

of weather fronts House Martins may be observed feeding with Swifts (A. apus) at 500 to 1,000 feet. However personal observations do not include Swallows and Sand Martins in these occurrences and I can find no references in the literature to them doing so. Feeding may be concentrated over water or alongside shelter belts of trees and a discussion of the precipitating factors will follow in a later chapter. House Martins have been recorded being attracted to a garden fire by Paull (1968) presumably on the insects aggregated by the convection currents. Also there are many records of Hirundines which have been recorded feeding from the ground (Lee & Rolls, 1967). However these records must be treated with caution as all my observations on this habit have shown that the birds were collecting grit.

In the present study feeding birds could be observed at all times in close proximity to the colony, though it is likely that certain conditions encouraged a proportion of the colony to feed up to several miles away, for example over a lake or on emerging ants.

Predators and Parasites

Hobbies (Falco subbuteo) were probably a significant

predator in the study area, though the evidence is circumstantial. Over the three years four broods progressively lost weight, while still being fed by at least one adult bird. Hobbies were regularly observed in the vicinity and it was therefore tentatively assumed that one of the pair had been taken, and the remaining bird was unable to adequately feed the brood. Both Kestrel (Falco tinnunculus) and Sparrowhawk (Accipiter nisus) were observed in the area and the former is recorded as taking House Martins. The greatest threat to breeding Martins is probably ejection by House Sparrows (Passer domesticus) though in this study the nestboxes used, prevented disturbance by these birds. Ejection of Martins, probably by Sparrows was recorded in only one case each, from nests with eggs and with young and both these in the poor season of 1968 when either or both may have been previously deserted. Some House Martins are involved in building more than one nest at the beginning of the season and it may be these nests that are taken over by the Sparrows. Many alternative sites were available for Sparrows in the vicinity of the colonies, and therefore nest parasitism may be more severe in other areas where the sparrow population is high and nest sites are scarce. I

suggest that such a habitat might be a new housing estate. A cat was known to have taken at least one adult Martin at Cumberland Lodge in 1968.

The adults and nestlings were heavily infested with the Hippoboscids, Stenopteryx hirundinis, and on two occasions Ornithomya sp was found on an adult martin. The nestlings and the adults when in or in contact with a nest were exposed to a multitude of external arthropod parasites. In addition to the Hippoboscids, the Martin bug Oeciacus hirundinis (Jen) was often recorded in large numbers, while Mallophaga, Siphonaptera, Mites and a single Tick were also found. The assessment of the energy loss from the nestlings to the parasites is a considerable task, and it was therefore decided simply to minimise infestations by clearing the nest lining over winter and removing pupae and diapausing adult parasites from the vicinity of the nest. Thus the continuity of the population of most of the parasites was destroyed. Although infestations invariably became re-established, a similar initial situation pertained to each breeding pair. That House Martins readily reoccupy nests from the previous season and therefore inherit its parasite load suggests the parasites are well adapted to tap the

available nutrients without causing mortality in their hosts. No instances of abnormal growth rates were recorded in association with unusually high infestations of Hippoboscids or Cimicids, however a full study might reveal a contributory effect in cases of nestling starvation brought about for other reasons.

TABLE 3.4

Colony Statistics 1968 to 1970

The total number of pairs at each colony and other relevant information is tabulated below. Most of the study data is extracted from the nestbox sample and if this is not the case it is indicated in the appropriate section.

		1968	1969	1970
Number of Pairs at each colony (Nestboxes plus natural nests)	Kennels Colony	14	15	17
	Home Farm Colony	Not known	28	28
	Cumberland Lodge Colony	18	15	Not known
Total Number of Pairs in nestboxes examined daily		19	25	29
Additional pairs in boxes examined less regularly		2	5	0
Total pairs examined each year in mud nests		12	6	13
Total pairs examined each year		33	36	42

FLYING INSECTS - Characteristics of the food supply

The present section describes material from the literature that pertains to the study of feeding ecology in the Hirundinidae and Apodidae. A summary of the factors important in determining the measured abundance are detailed and discussed.

Factors affecting aerial insect abundance

The number of insects in the air at any time and hence the catch on any day will depend partly on the net product of factors favouring upward transport and those favouring downward transport (Johnson, 1969). Also the size of the alate population in the area of origin and the percentage of that population in a physiological state conducive to flight will determine the catch potential in optimum conditions. These might be called "population factors", while weather induced flight responses or "activity factors" will determine the percentage of that population that takes to the air at any time. Johnson (1969) discussed the caution that should be exercised in using these terms but their descriptive clarity makes them useful in the present context. Activity factors include the effects of prevailing weather and light

intensity while preceeding weather may influence both the state and size of the population and the percentage available for flight.

Population Factors

Calnaido (1965) demonstrated that 46% of the variance in numbers of Oscinella frit flying above an oat crop was due to variations in the rate of new adults taking off. Williams (1961) analysed the effects of minimum temperature and rainfall on insect activity and abundance, in the three months prior to the period of investigation and found that it accounted for 25% in spring and 69% in summer of the total variance in daily insect catch. These results illustrate the considerable effect that changes in ground populations can have in determining the number of insects in the air.

Activity Factors.

The influence of prevailing weather on flight activity and hence aerial abundance is induced principally by windspeed, rainfall and temperature changes. The considerable effort expended in the past on analysis of flying insect populations and associated weather conditions has yielded results of some

accuracy for predictive purposes (Williams, 1961 & 1962) even though it has masked the causal processes involved (Taylor, 1963). Taylor (1963 & 1970) describes a process of flight thresholds in Aphids on the basis of changes in temperature and light intensity, where low temperature and light intensity inhibit~~s~~ take off. Thus an increasing temperature can be expected to activate the overlapping thresholds of many species as it rises. Hence plotting percentage flight occurrence^e against temperature, yields a linear relationship for mixed species complexes (Johnson, 1969). Also total catch in a suction trap in summer may thus yield a linear relationship when plotted against mean daily temperature, but variance is high. Strong wind may inhibit take off (Hans & Thorsteinson, 1961) or alternatively light winds may encourage it (Digby, 1958).

However although such affects may both reduce insect numbers in the open air and slightly affect the efficiency of the trap it will also encourage aggregations behind shelter belts of trees and therefore the total aerial abundance in such situations could change little.

Cloudiness and consequent reduction in light intensity may inhibit take off (Taylor, 1957; Pajunen, 1962), however

Aphids often migrate in dull weather and light rain (Tilden, 1962).

Green (1962) demonstrated the effect of rain on the flight of the moth Rhyacionia buoliana and clearly illustrated the effect of very heavy rain on flying insects. A plot of total daily catch against mean daily rainfall (mm per 24 hrs) (Fig 3.12) again reveals a relationship, however all significance disappears when those three days with 6+hrs of rain are excluded. It may therefore be concluded that rain is insignificant in determining flying insect numbers, except associated with very high rainfall. However it may alter the availability of the prey to the feeding House Martin. Heavy dew may prevent take off by temporarily incapacitating settled insects. (Nielsen & Nielsen, 1950).

Both atmospheric pressure and electrical activity may affect activity in insects (Edwards, 1960a 1961a). However caution must be exercised in the extrapolation of these results to field conditions, particularly as the relationship between experimental activity and flight activity is unclear.

In summary Hurst's (1964) analysis of the weather conditions suitable for mass flights of migratory Thysonoptera

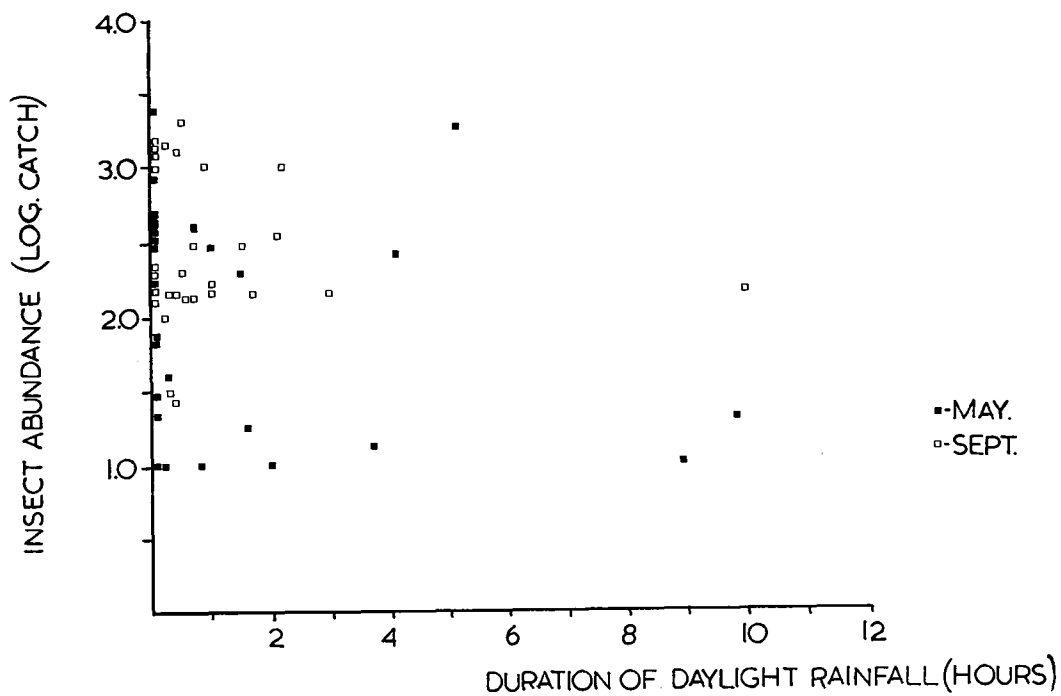


FIG. 3.12. Aerial insect abundance in May and September, 1968, in relation to the duration of rainfall.

in Southern England may be cautiously extrapolated to many of the small insects preyed upon by aerial feeding birds, as a guide to conditions in which the smaller aerial insects are generally abundant. Hurst enumerated the following conditions:-

- a. No rain or drizzle during the day.
- b. Day maximum temperature at least 20°C .
- c. Day maximum temperature not exceeding 29°C .
- d. Day maximum temperature above that of previous day.
- e. No convection above 5,000 feet, but with atmospheric instability below that height.
- f. A dew point within the range $5^{\circ}\text{C} - 15^{\circ}\text{C}$.
- g. At least one hour of sunshine during the day.

Flight Periodicity

The flight periodicities of insects taken in suction traps in Southern England are given by Lewis and Taylor (1965). The very extensive data emphasise the dynamic nature of the components of the aerial populations and illustrate the phenomenon of activity peaks occurring in all hours of the day. The principal proximate factor in determining the time of flight is changes in light intensity. Flight periodicities

are important in determining when and if species or families are available to the diurnal aerial feeders. Also the different duration of periodicities will determine the time each diurnal species is available for predation. However only limited data is available for diel flux in total insect numbers or biomass, a definitive statement probably being inappropriate as habitat will influence the relative abundances of families associated with different light intensities. Therefore for example a habitat with a preponderance of swarming species i.e. Chironomidae and Trichoceridae would exhibit maximum biomass in the evening whereas in another habitat the day flying Aphids and Bibionidae might be dominant giving rise to a biomass maximum around midday.

Mean Height of Insect Flight

Johnson (1969) states that in general insect density diminishes regularly with increasing height and as a working approximation the logarithm of the density against the logarithm of height is regarded as linear over a wide range. A number of factors operate to invalidate this empirical relationship for example atmospheric instability and mass

flights of single species. Calnaido (1965) showed that increased rain, wind, atmospheric stability and numbers taking off, reduced the mean height of flight. Maximum temperature and variations in sunshine however were unimportant.

Factors influencing availability of flying insects to the feeding House Martin.

It is important in this study of resource exploitation to isolate other factors that might increase the availability of aerial insects to the feeding birds, while the measured catch remained constant. In effect to determine the causes of error in accepting the estimated sample as a true sample of the available food. That the House Martin does not feed at random and that small flying insects only approximate to a random distribution in a horizontal plane (Lewis & Taylor, 1967) emphasises the need for such matters to be considered. It is particularly important as these factors often give rise to conditions in which aerial feeders are able to optimise feeding efficiency, for they concentrate insects in relation to density in the open air. These factors include effects associated with Shelter, Atmospheric instability and Mass flights.

Aggregations of most obvious significance to feeding Hirundines and Swifts are the combined effects of wind and shelter. Lewis (1965c) illustrates profiles of relative insect density to the lee of a perforated fence and records ⁱⁿ aerial densities/certain taxa ranging from 2x to 27x that in surrounding open areas. These figures refer to Aphids and Syrphids respectively. The zone of maximum density moved further to leeward with increasing windspeed. Aggregations were higher the more dense the windbreak, and also increased with the angle of incidence of wind to the shelter, being at a maximum at 90° . Accumulation may also occur above the height of the shelter. This generally involved the more mobile insects, the smaller insects behaved like inert particles and occurred well below the height of the fence. By extrapolation these results may be applied to shelter belts of trees, buildings etc and illustrates the potential importance of shelter in the feeding ecology of aerial feeding birds.

66 Atmospheric ~~instability~~ is characterised by extensive convection activity. This may be associated with hot clear weather or with the passage of weather fronts. Overcast conditions involve atmospheric stability and low convection

activity. Insect flight in such conditions is generally at low altitudes. Convection activity will redistribute insects by carrying those already airborne further aloft. That this situation does provide an easily exploited food source is suggested by the aggregations of feeding birds in such situations. Convergent air systems associated with thunderstorms cause air to rise and it has been estimated that effectively inert insects associated with such air movements might be concentrated by two times in twenty minutes (Rainey, 1963). Other illustrations of the phenomenon of upward transport of insects though without suggestion of unusually dense aggregations are given by Rainey (1951) for locusts, Horsfall (1954) for mosquitoes and Hodson and Cook (1960) for the Harlequin bug (Murgantia histrionica). As a weather front moves across country insects will accumulate before it (Horsfall, 1954) and be carried for many miles. These processes acting together could remove concentrations from the lower atmosphere and concentrate them in the upper atmosphere. It may therefore be particularly pertinent for aerial feeders to exploit such a supply as the air downdraughts associated with the passing of the front will carry insects

to the ground leaving the open air comparatively devoid of insects. This will therefore be of greatest importance in the open air feeders the Swift and House Martin. The greatest atmospheric mobility is associated with cold fronts. These are of importance to the Swift and House Martin and compare closely with sea breeze fronts described by Simpson (1969). Such situations provide the most spectacular aggregations visible from the ground with often hundreds of Swifts and House Martins preceeding the dark cumulus clouds at a height of 500 to 1,000 feet.

Local insect emergences are at times of great significance and may pass completely unrecorded by a single sampling site. Swifts, Hirundines, Gulls and Starlings can frequently be seen from late June onwards exploiting Ant (Formicoidea) emergences.

It is of possible significance in connection with Swift roosting behaviour to elaborate on insect flight after dark. Berry and Taylor (1968) recorded aphid densities at 1,000 feet over Southern England (01.00 - 04.00 hours) which reached a maximum density of $2.66/10^6 \text{ ft}^3$ compared with a mean daylight density of $13.13/10^6 \text{ ft}^3$. However these night densities exceeded the day densities on 33% of the days investigated

They indicated a causal relationship between these high densities and mean night temperatures of $19.5^{\circ}\text{C}+$. The insect fauna at 1,000 ft at night might therefore present a resource of greater food value than that obtainable on 33% of the days in the breeding season, and this might be particularly suitable if one of the agencies that aggregate insects in the air operated. For example the passage of a cold front across the country at night after a very hot day would certainly result in considerable accumulations of insects before the approaching storm. However the question of whether a Swift is able to exploit such a resource remains unanswered. The opportunity to feed in the extended twilight of mid summer may by itself justify roosting in the air in close proximity to a food supply to facilitate relocating it quickly and efficiently next morning. The Nightjar (Caprimulgus europaeus) feeds partly after dark in Britain and bears the same well developed rectal bristles of the Swift, which have always been considered to aid food capture in nocturnally feeding birds.

In conclusion it can be stated that these vagaries of climate and food supply provide the opportunity for aerial

feeding birds to maximise their food collection efficiency. Field observations confirm that they have behaviourally adapted to each situation and rarely feed in a random (or near random) manner. The mechanisms by which degrees of ecological isolation between species are maintained are expanded in a later section. (Section 11).

SECTION 4

FOOD AND FOOD SELECTION IN THE HOUSE MARTIN

The Aerial Food Supply

The distribution and abundance of insects at different heights in the air is described by Hardy and Milne (1938). Johnson (1969) has collated much of the information on the subject, utilising the studies of Taylor (1960, 1963) Glick (1939), Williams (1951, 1961, 1962) and Lewis (1965a 1965b) and Lewis and Taylor (1964).

The present author employed a single sampling site at 40 feet above ground level (220 feet above sea level) to obtain an index of aerial abundance for each day of the breeding season. The total suction trap catch ($= \log_{10} N+1$; where N = total insects taken per day) for each day of the months February to October 1968 and 1969 is shown in Fig 4.1. It illustrates the low catch throughout the winter and the rapid increase in April and May which coincides with the arrival of many migratory birds in Britain, and the onset of breeding in many species. Numerically, peak aerial populations may be recorded by mid May (as in 1968) with stabilisation within more restricted limits by early June. A decline in abundance is detectable by September, though in ~~October~~ 1968 a mean daily catch in excess of Log 2.0 persisted until early November.

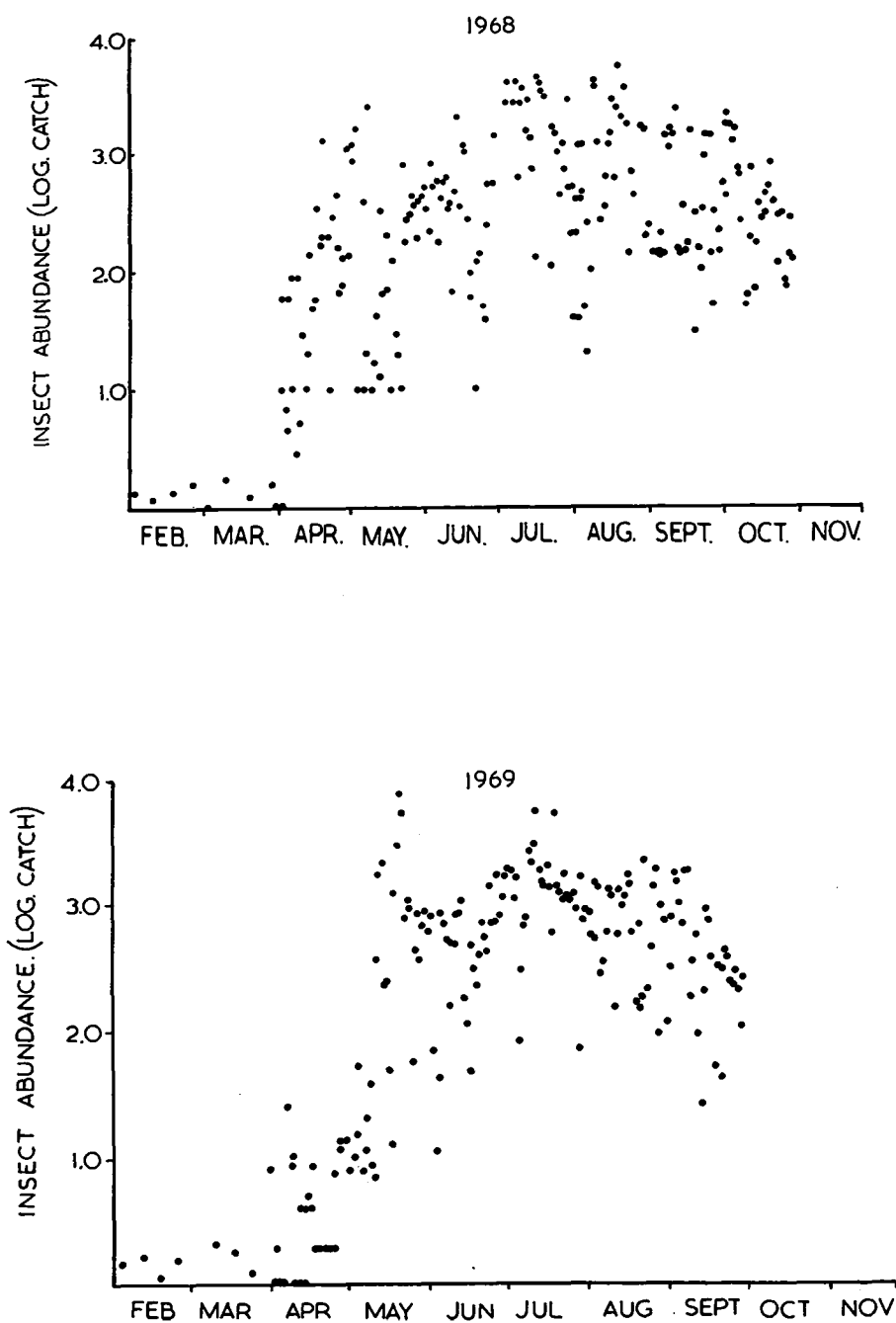


FIG. 4.1. Aerial insect abundance for each day of the 1968 and 1969 breeding seasons. Insect abundance is the total catch for each 24 hour period plotted on a logarithmic scale.

Mean daily catches for each month of 1968 and 1969, and incorporating data from the first few months of 1970, are presented in Table 4.1. It is intended that this approximates to the average expected daily aerial abundance for each month of the year.

Although total numbers flying may be a useful index of abundance it is potentially subject to a number of errors. The mean size of component insects may be different in different months, or the calorific value of a single species may change with season. Therefore while total numbers remained constant the biomass or calorific value of the catch could vary widely. An alternative index of abundance was therefore the total calorific value of the daily catch. This was calculated as follows, by an indirect method because the catch had to be preserved. All insects with a flight periodicity peak after astronomical twilight were excluded (on the basis of data in Lewis and Taylor, 1964), although the percentage representation of these families in practice made such a correction insignificant at the present site. Also excluded were the day flying Thysanoptera which are minute and were unrecorded in the Martin's diet and insects too large to be taken by Martins, for example Neuroptera and Coleoptera usually exceeding 1cm in length.

Table 4.1

The mean daily suction trap catches for the months of February to October in the years 1968 and 1969.

Date	Mean Catch (N = Number of Insects/Day)	Mean Catch (& S.D.) ($\text{LOG}_{10} N+1$)
February	1.40	0.145 $\pm$ 0.06
March	1.36	0.135 $\pm$ 0.10
April	14.10	1.15 $\pm$ 0.57
May	148.00	2.17 $\pm$ 0.86
June	309.00	2.49 $\pm$ 0.51
July	1175.00	3.07 $\pm$ 0.42
August	525.00	2.72 $\pm$ 0.51
September	295.00	2.47 $\pm$ 0.48
October	302.00	2.48 $\pm$ 0.45

These were never recorded in the faecal samples. All other insects recorded in the diet and trapped were included. This involved small day flying insects, potentially available, but very rarely exploited (i.e. Cecidomyidae).

To calculate the calorific value of the catch the following method was employed. Insects trapped aurally at a second site were sorted down to family for each month of the study period, and further into size categories according to wing length. Total calorific values for each size category within each taxa was estimated for each month of 1969, using a micro bomb calorimeter of low thermal capacity and built after the design of Phillipson (1964). A calorific value could then be assigned to each insect, once family and wing length had been determined. Data for representation of different families and sizes within the suction trap sample, were then used to calculate the total calorific value of the daily catch. It was found that variation within families through the season made an insignificant contribution to total change in food value, such effects being marked by changes in mean size of the constituent insects. The percentage numerical representation of families and broad size groupings are presented in Table 4.2 using data for both 1968 and 1969. It

can be seen that the dominant family in terms of numerical representation, ~~is~~ the Aphididoidea followed by the Bibionidae. The relative representation of each of these taxonomic groupings as a food resource, (i.e. by calorific value) is presented in Table 4.3. The Bibionidae and Aphididae are again dominant, although the precise percentage contribution differs.

Correlation of the total number of insects in a daily catch with the total calorific value of that catch (with a double logarithmic transformation) gave $r = 0.89$ ($p = < 0.001$) and $b = 1.06$. It can therefore be stated that 80% of the variation in the food value of the daily catch is associated with changes in the number of insects flying. (Data; May to July, 1968) .

The Food of the House Martin

A number of studies have recorded the food of aerial feeding birds. Lack and Owen (1953) present data for the Swift Apus apus and ^{R.F.} Johnson (1969) examined the Purple Martin Progne subis. Gunten and Schwarzenbach (1962) studied certain aspects of the feeding biology of the House Martin Delichon urbica, while recently Hesperheide (1971) has drawn upon the data collected by Beal (1912, 1918), in a study of food size preference of certain families of birds including Swallows

Table 4.2

Percentage representation of taxonomic groups of insects in the suction trap for each month of 1968 and 1969.

	May	June	July	Aug.	Sept.	Mean %
Coleoptera (1)	6.8	0.6	2.9	2.1	0.0	2.5
Formicoidea	0.0	0.0	0.1	3.8	0.0	0.8
Parasitica (1)	6.0	4.7	6.3	7.4	4.6	5.8
Parasitica (2)	0.0	0.5	0.3	0.0	0.0	0.2
Homoptera		1.9		0.1		0.4
Heteroptera	3.2	0.1	0.7	0.1		0.8
Psyllidae			0.3	0.4	1.8	0.5
Aphididae	12.9	49.0	50.0	13.3	14.8	28.0
Neuroptera			0.1	3.1	6.7	2.0
Tipulidae	2.3			0.1	2.4	1.0
Bibionidae	32.0	3.8		29.2	34.5	19.9
Mycetophilidae	23.2	12.4	6.3	9.6	12.5	12.8
Chironomidae (1)	9.0	11.4	1.3	4.1	3.5	5.9
Chironomidae (2)		0.2	4.9	10.9	1.5	3.5
Stratiomyidae						
Longchopteridae						
Syrphidae		0.01	0.3	0.47		0.2
Empididae	0.5	4.1	10.8	1.8		3.4
Phoridae						
Scatopsidae	4.5	7.8	10.8		2.5	5.1
Dolichopodidae			0.3			0.0
Cyclorrhapha (1)	0.8	4.8	3.2	11.6	4.3	4.9
Cyclorrhapha (2)		5.7	0.5	1.2	2.3	1.9

Categories 1 0 - 3 mm
 2 3 - 6 mm
 3 6 - 9 mm
 4 9 + mm

All families below 0.1% representation are excluded (except Syrphidae).

Table 4.3

Percentage Representation of taxonomic groups in suction trap by calorific values.

	Size Category	May	June	July	Aug.	Sept.	Mean %
Coleoptera	1	5.1	0.5	2.8	1.3		1.9
Coleoptera	2			0.5	12.2		2.5
Parasitica	1	5.0	4.3	6.9	5.3	3.5	5.0
Parasitica	2		0.9	0.7			0.3
Homoptera			4.0		0.2		0.1
Heteroptera		7.8	0.3	1.8	0.2		2.0
Psyllidae				0.1	0.2	0.7	0.2
Aphididae		10.7	44.5	54.5	9.5	11.3	26.1
Neuroptera				0.3	6.8	15.7	4.6
Tipulidae		3.4			0.2	3.3	1.4
Bibionidae		48.1	6.2		37.0	47.5	27.8
Mycetophilidae		12.2	7.1	4.3	4.3	6.0	6.8
Chironomidae	1	4.7	5.5	0.8	1.5	1.4	2.8
Chironomidae	2		0.3	6.7	9.8	1.4	3.6
Stratiomyidae							
Longchopteridae							
Syrphidae			0.1	1.1	1.2		0.5
Empididae		0.3	2.7	23.2	1.0		5.4
Phoridae							
Scatopsidae		2.0	3.8	6.3		1.0	2.6
Dolichopodidae				0.2			0.0
Cyclorrhaphan	1	0.5	3.2	2.5	6.0	2.4	2.9
Cyclorrhaphan	2		16.7	1.7	2.8	5.7	5.4

(Hirundinidae) and Flycatchers (Tyrannidae). This study and that of Johnson notably make comparisons between prey species and those available in the environment.

The assessment of prey taken in these studies has been by stomach analysis or by collection of food boli brought to the developing young. Therefore a food sample taken at a particular time of day will be a reflection on the food availability only at that time of day. The flight periodicity of many insect species ensures that they will be available for only a restricted period during each day and may therefore not be represented in such a sample. The present study therefore employed the following technique to obtain a food sample that was representative of the entire feeding period on each day. The potential accuracy of the method encouraged me to take the study beyond the specific confines of the feeding House Martin, to the study of predators and their prey in general and plankton feeding predators in particular.

Faecal samples were collected from adult and nestling House Martins in all months of the study period. For the purpose of the current study all samples were composed of a 24 hour accumulation of faeces from below at least four nestboxes for each day. These were thoroughly mixed and a

further subsample taken from the resulting material which represented at least 5% of the total (by volume). The early May samples were less satisfactory as they are almost entirely from adults. Therefore, as adults may defaecate away from the nest, samples from certain times of day could be absent. The June to October samples were predominantly from nestlings of more than 7 days old because qualitative food differences were not recorded after the fifth day (see Royama, 1970). The faecal samples were examined for insect wings, which were identified and sorted into a number of readily identifiable taxa and counted and measured. In most cases wings could easily be categorised into family but specific identification was rarely made. The reasonable assumption was made, that the taxa represented in the faeces would have an adequately similar specific composition to those in the suction traps. This was confirmed for certain families, i.e. Bibionidae, where only one species was found in abundance in both the suction trap and the faeces. The percentage representation numerically, and in terms of food value, of each family is presented in tables 4.4 and 4.5 respectively. The calorific value of prey items was calculated from data relating winglength to calorific value referred to in the previous section.

Table 4.4

Percentage representation of taxonomic groups in faecal samples from House Martin nestlings (and adults)

	May	June	July	Aug.	Sept.	Mean %
Coleoptera (1)	2.8	4.3	8.6	7.3	1.8	5.0
Coleoptera (2)		0.1				0
Formicoidea		10.9	2.6		0.1	2.7
Parasitica (1)	6.5	8.8	10.7	9.4	9.4	9.0
Parasitica (2)		1.7	2.9	2.6	1.0	1.6
Homoptera (1)			0.8	0.4		0.2
Homoptera (2)	0.1					0
Psyllidae	0.8		0.2	0.1		0.2
Aphididae	45.8	21.8	12.9	4.5	4.2	17.8
Heteroptera (1)		0.1	0.2	0.1		0.1
Heteroptera (2)		0.5		0.1		0.1
Chrysopidae : Neuroptera			3.9			0.8
Hemerobiidae: Neuroptera	2.5	1.6		0.8		1.0
Psychodidae	0.4					0.1
Tipulidae	0.1			0.1		0
Culicidae	0.8					0.1
Anisopodidae						0
Bibionidae	4.0	5.9	5.8	46.6	37.9	20.0
Mycetophilidae	7.5	1.3	1.7	0.8	1.0	2.5
Chironomidae (1)	8.3					1.7
Chironomidae (2)		2.2		1.2		0.7
Stratiomyidae	0.1	4.0	6.5	0.1		2.1
Dolichopodidae						0
Longchopteridae	2.2		0.5	0.4	4.4	1.5
Phoridae	0.6		0.1	0.1	0.2	0.2
Empididae	1.0		1.6	0.4	2.1	1.0
Scatopsidae				0.8	0.7	0.3
Syrphidae		2.4		2.2	0.5	1.0
Brachycera	1.3	0.2	0.2			0.3
Cyclorrhapha (1)	8.6	29.4	37.2	13.7	31.1	24.0
Cyclorrhapha (2)	1.5	3.7	6.5	3.9	4.5	2.8

TABLE 4.5

Percentage representation by calorific value of taxonomic groups in faecal samples from House Martin nestlings.

	May	June	July	Aug.	Sept.	Mean %
Coleoptera (1)	2.8	2.4	7.6	4.8	1.3	3.8
Coleoptera (2)		0.1				0.0
Formicoidea		24.8	9.2		0.3	6.9
Parasitica (1)	6.5	5.0	9.4	6.2	6.9	6.8
Parasitica (2)		13.5	2.3	2.4	1.0	3.8
Homoptera (1)			1.8	0.7		0.5
Homoptera (2)		0.2				0
Psyllidae	0.4		0.1	0.0		0.1
Aphididae	50.4	13.6	12.5	3.3	3.4	16.6
Heteroptera (1)		0.2	0.5	0.2		0.2
Heteroptera (2)				0.2		0
Chrysopidae : Neuroptera			11.2			2.2
Hemerobiidae: Neuroptera	6.5	2.4		1.2		2.0
Psychodidae	0.2					0
Tipulidae	0.2			0.1		0.1
Culicidae	1.6					0.3
Anisopodidae						
Bibionidae	7.2	7.2	10.8	55.6	49.8	26.1
Mycetophilidae	0.5	0.5	1.0	0.4	0.5	0.6
Chironomidae (1)	5.0					1.0
Chironomidae (2)		1.7		1.1		0.6
Stratiomyidae	0.04	1.3	3.4	0.04		1.0
Dolichopodidae						
Longchopteridae	2.2		0.5	0.3	3.2	1.2
Phoridae	0.4		0.3	0.0	0.1	0.1
Empididae	0.8		1.1	0.2	1.2	0.7
Scatopsidae				0.3	0.3	0.1
Syrphidae		5.4		5.8	1.5	2.5
Brachycera	2.6	0.3	0.3			0.6
Cyclorrhapha (1)	6.9	13.4	26.3	7.3	18.1	14.4
Cyclorrhapha (2)	5.7	8.0	1.7	9.8	12.5	7.5

Hartley (1948) discusses possible sources of error when using faecal samples as a qualitative measure of prey consumption. However concerning differing digestⁱabilities and destructⁱabilities in the present study, note that many of the wings of very small insects (i.e. Aphids) were invariably intact in the faeces. The wings of the larger insects were more often broken, however their numbers could be efficiently estimated by counting only small sections of the wing (i.e. the Pterostigma in certain Parasitic Hymenoptera). Occasional samples were extensively mascerated, probably during processing, and these were discarded. It is likely that by confining counts to wings the problem of differing rates of digestion was eliminated, wings passing through the gut at approximately a constant rate, while tissues associated more closely with heavily sclerotised parts with different digestⁱabilities might be retained longer.

Specific identifications were made of a number of House Martin prey and these are listed in the Appendix.

Examination of Table 4.5 reveals the relative monthly contribution of different insect families and the principal taxonomic groups contributing to 50% of the food ingested is shown in Table 4.6

TABLE 4.6

1.	May.	Aphidoidea
2.	June.	Hymenoptera : Formicoidea. Cyclorhaphan Diptera Aphidoidea & Hymenoptera (Parasitica)
3.	July.	Cyclorhaphan Diptera Aphidoidea Bibionidae
4.	August.	Bibionidae
5.	September.	Bibionidae

These families are in effect the 'key' food resources for each month. The unexpectedly prominent position of Ants in the June food sample needs explanation. Ants rarely appear in the suction trap until July, which suggests that if they fly, they do so in proximity to vegetation. In practice they are heavily selected on certain days and entirely absent on other days. It appears that the Martins are exploiting an irregular resource in proximity to vegetation. It is therefore proposed that the alternate resource of Cyclorhaphan Diptera is more important because of its dependability. In the same manner as the dominant families in other months are dependable and are regularly represented in the faecal samples.

Food Selection in the House Martin

Many animals exhibit food preferences. The selection of food from the available resources on the basis of such preferences serves to increase the efficiency of food collection.

Tinbergen (1960), Ivlev (1961) and Royama (1970) have investigated food preferences in relation to the variation in abundance and quality of available food, while Richter (1942) and Murdoch (1969) have studied certain behavioural responses to changes in the quality of the available food, and their effects on the diet. Thomson (1965) has demonstrated variation in food preferences within a single species and Paine (1963) has investigated the role of toxic substances in potential food resources.

The studies of Johnson (1967) on the Purple Martin Progne subis and Hesperheide (1971) on a variety of aerial feeding birds (Hirundinidae, Tyrannidae) compare the prey in the stomach with the prey potentially available in the environment. They are concerned respectively with the utilisation of a food resource for breeding, and the differences between food preferences of various sympatric aerial feeding birds. Johnson indicates a close correlation between the representation of the number of families within orders of

insects (i.e. diversity) in the air and in the stomachs of Purple Martins ($r = +0.95$ $p < 0.01$). Elliot (1970) records a close correlation between the occurrence of invertebrates in drift samples of freshwater plankton and the stomach contents of Trout Salmo trutta (ranging from $r_s = 1.00$ $p = < 0.01$ to $r_s = 0.31$ $p = N.S$). However Royama (1970) reports very low correlation between the relative abundance of invertebrates in the foliage of Oaks (Quercus petraea(~~Mattuschka~~)Liebl.) and the representation of these in the diet of nestling Great Tits (Parus major). This suggests that differences are to be expected between predation strategies adopted for exploiting a planktonic resource and those existing in the more complex arena of terrestrial systems. However this evidently does not always follow for planktonic food supplies, as illustrated by Brooks and Dodson (1965), who indicate a heavy selective predation by the clupeoid (Alosa pseudohaergus) on the larger prey items of a lake's zooplankton, eventually resulting in their elimination.

The present study compares the quality of prey taken by a predator, the House Martin Delichon urbica, with that available in the environment. (Where this is the effective environment as defined by Clark et al (1967)). It proposes to establish

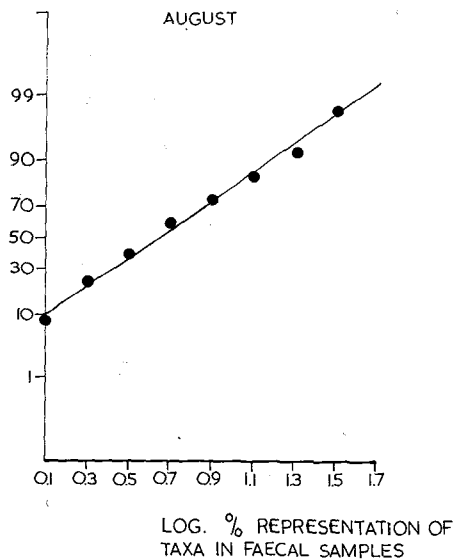
whether the House Martin feeds at random or if items are selected from the environment, and if so on what criteria and under what conditions does selection take place. It is suggested that the results of the present study apply to any predator exploiting a planktonic or 'planktonic-like' resource (i.e. the "so called" aer^o plankton, see Johnson(1969)for discussion).

Method

The selection activity of the feeding House Martin was determined by the following method. If the suction trap catch was an accurate sample of a randomly distributed aerial insect population, and ~~that~~ the Martins fed at random (at a constant rate throughout each day : dawn to dusk : at a height of approximately 40 feet), then percentage representation of insect families in both the suction trap and the faecal samples would be the same. In these ideal conditions the correlation coefficient between the two samples would be $r_{\text{selection}} = +1.0$. This situation will be interpreted as random feeding. Therefore if the Martin feeding strategy or aerial insect distribution departed from random, percentage representation of insect families in the two samples would become less well correlated. This will be interpreted as an increase in selection activity, if it can be shown that it does not significantly involve variation in aerial insect distribution. (N.B. Selection activity - as denoted by the correl-coefficient will be referred to as "r selection"). The coefficient of correlation could ultimately be depressed to $r = -1.0$ if the Martins fed on components of the aerial population in inverse proportion to their abundance.

The percentage representation of each insect group in the field data was first transformed logarithmically to obtain a bivariate normal distribution. Williams (1959, 1964) discussed the approach to log-normality of many species spectra and certain aspects of this in relation to the food of flying birds is discussed by Hesperheide (1971) (See Fig.4.2).

FIG. 4.2. The frequency distribution of the abundance of different taxa in faecal samples collected in August, 1969. The abundance of each taxa is expressed as a percentage of the total



taxa, and the data is plotted on Log. x Probability paper to illustrate the approach to log-normality.

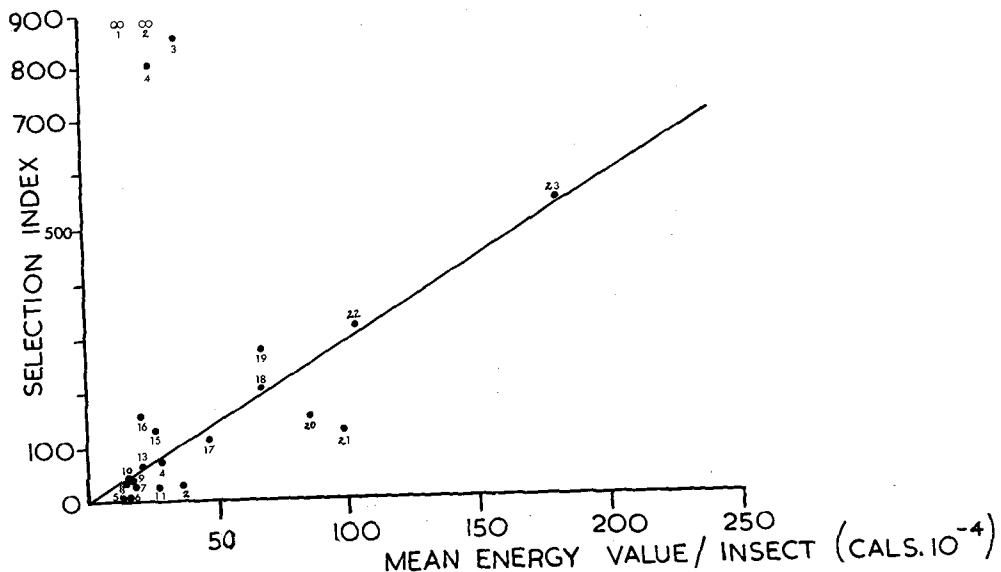


FIG. 4.3. The seasonal Selection Index for each taxonomic group represented in the diet of the House Martin, in relation to the mean seasonal calorific value of individuals within each taxa.

Table 4.7

Correlation coefficients for percentage representation of taxonomic groups (mostly insect families) for mean monthly figures, in the aerial suction trap and the faeces of House Martins.

	r	p
May	+0.47 $\pm$ 0.17	p = 0.05
June	+0.38 $\pm$ 0.19	N.S.
July	+0.33 $\pm$ 0.18	N.S.
August	+0.62 $\pm$ 0.13	p = 0.01
September	+0.45 $\pm$ 0.18	p = 0.05

Results

Correlation coefficients were derived for each month and are presented in Table 4.7, to demonstrate seasonal variation. The results indicate an approach to random feeding in August, when representation of families in the suction trap and the faecal samples approached equality, and to a lesser extent in May and September. Selection for particular families was most intense in June and July. However the processes causing such variation in r , cannot be resolved on the basis of these monthly means. Therefore seven to ten days were selected at random from each month of the breeding season (June to September 1969, with some data from 1968) and by the same method as above correlation coefficients were calculated for the samples from each day, and examined in relation to variation in the following: Table 4.8.

1. Wind speed x duration Index, 2. Rainfall (hours/day and m.m/day), 3. Hrs of sunshine, 4. Mean daylight temperature, 5. Relative humidity, 6. Daylength, 7. Aerial insect abundance, 8. Aerial insect diversity and 9. Energy requirements of nestlings of pairs concerned.

The three most significant associates of variation, Mean Temperature, Wind and Log. Insect Abundance together accounted for only 19% of the variation in $r_{\text{selection}}$ in a multiple

correlation analysis, and it is likely that this was influenced by a departure from a random distribution of the flying insect population (see Lewis (1969)), rather than by a change in the feeding strategy of the Martins. This low coefficient of determination indicates that the causes of variation in $r_{\text{selection}}$ must be found elsewhere.

It was considered that examination of the selection intensity on each taxonomic group individually, would elucidate the causal mechanisms involved in the variation of r . To investigate the selection intensity on each family the following method was used. If percentage representation in the faecal sample of any one family (equivalent to $\log_{10} N+1$ percentage representation) is equal to that in the suction trap then:-

$$\frac{\text{Log percentage representation in Faeces } (\log_{10} N+1) \times 100}{\text{Log percentage representation in Suction Trap } (\log_{10} N+1)} = 100$$

where N = percentage representation. (Transformations used for consistency and to impose linearity). Similar calculations were made for each family represented in the faeces and the suction trap for each day. An index was derived that indicated the degree to which Martin feeding or the aerial distribution of that insect group departed from random (where the Index = 100) to give the measured index. However it was

assumed that as the meteorological data were not significantly involved in this variation (i.e. $r = -0.016$ for Wind and Aphids), that this indicated a departure from random of the Martin's feeding strategy. The index was therefore termed the "Selection Index" (or S.I.) The association between the abundance, distribution and quality of insects in the air and factors in the physical environment has been well documented (see discussion in section 2 and Johnson, 1967). It is highly probable that if one or more weather factors was either the only or the principal influence on variation in S.I. some relationships would have been established between this and the selection index. This did not occur. A family that is inordinately represented in the faeces with respect to the suction sample will have a Selection Index >100 , while an index of <100 indicates either positive avoidance of that item or its unavailability. The causal nature of these indices is demonstrated in Fig 4.3. Here a Selection Index (Geometric Mean of all values June- Sept. $\times 100$ [Faeces]/G.M of all values Jun-Sept. [Suction Trap]) has been derived on a seasonal basis and plotted as a function of the mean calorific value of the items of that family. It can be seen that the S.I. behaves for the most part as a linear function of the mean calorific value.

($y = 10.1 + 0.302x$ $r = 0.91$ $p = <0.001$). However four taxa remain quite separated from the majority. It is proposed that these taxa were disproportionately sampled in relation to their aerial abundance. Lewis (1969) cites figures for the aerial abundance of 77 taxa in both the air and in the proximity of a low hedgerow in southern England. The low hedgerow is a habitat that physically fairly closely resembles the belts of trees with which Martins associate for feeding. Also figures are available for this habitat but not for tree belts. The relative abundance of the four relevant taxa are shown in table 4.9. It was found that of these four taxa, three were relatively more abundant in the proximity of hedgerows, in relation to the total insect abundance in that habitat. It is likely therefore, that as Martins often feed in close proximity to shelter belts, that the abundance of these taxa in the Martin's feeding zone was underestimated by my sampling method and the selection index was elevated in consequence. A more critical analysis of this problem awaits similar quantitative information for the aerial insect fauna in the proximity of tree belts. Thus generally the larger the item, within the limits of the Martin's prey size range, the higher will be the Selection Index, and therefore the greater

TABLE 4.9

The relative abundance of four insect taxa in two aerial habitats (data from Lewis, 1969).

Aerial Catch distant from Vegetation		Aerial Catch in close Proximity to a Hedgerow
Total Catch 146855 insects		2218 insects
<u>Percentage total catch</u>		
a.	Coleoptera 3%	10%
b.	Hymenoptera	
	incl. Tenthredinidae	
	Ichneumonidae 2.4%	6.8%
	Apidae	
c.	Longchopteridae $0.95 \times 10^{-4}\%$	$0.4 \times 10^{-2}\%$
d.	Stratiomyidae $0.68 \times 10^{-5}\%$	0.0%

the gross energetic reward on capture of that item. Presumably this implies a net energetic reward for this situation to have evolved. Interestingly the S.I. doubles for each doubling of the calorific value of the prey items, though this may be an artefact of the logarithmic transformation of the basic data. The data from this graph was used to compile an order of preference for each taxonomic group and to see which groups were generally selected i.e. $S.I. = 101 +$ (the "preferred prey") and which were avoided or unavailable i.e. $S.I. = < 99$ ("less preferred" prey). It was found that many of the families in the latter group contained a majority of crepuscular species with regard to their flight periodicity (Lewis & Taylor 1967), which would therefore not be available to the feeding Martin for their full flight period, though would be sampled, by the suction trap for the whole of this period. It is therefore expected that the S.I.s for these families would be below 100. (Table 4.10)

The variation in the selection index of each family in relation to environmental conditions will not be discussed here. The interrelations between seasonal changes in the taxonomic composition of the catch and the selection activity of the

Table 4.10

Relationship between the Selection Index and the mean calorific value of each family.

Key to points in Fig. 4.3.

1. Stratiomyidae
2. Longchopteridae
3. Parasitica: Hymenoptera (2)
4. Coleoptera (1)
5. Psychodidae
6. Chironomidae (1)
7. Mycetophilidae
8. Phoridae
9. Scatopsidae
10. Psyllidae
11. Tipulidae
12. Chironomidae (2)
13. Empididae
14. Aphididae
15. Parasitica: Hymenoptera (1)
16. Cyclorrhapha: Diptera (1)
17. Bibionidae
18. Hemeroboidea: Neuroptera (1)
19. Homoptera
20. Hemeroboidea: Neuroptera (2)
21. Cyclorrhapha: Diptera (2)
22. Formicoidea
23. Syrphidae

Martins has not been fully analysed, & also will not be further discussed here. It is suggested that the feeding Martins were attempting to maximise the rate of prey ingestion by exploiting the most profitable items available (see Royama, 1970).

A number of potential predator strategies were therefore hypothesised that attempted to interpret the variation in the daily correlation coefficient in terms of this strategy. By quantifying these hypotheses and comparing them with field results it was established which process was likely to be operating. The hypothetical predator strategies compare the size frequency distribution of the available prey with that taken by the House Martin. Three basic possibilities are presented for the available prey. They are either normally distributed with regard to the logarithm of percentage size frequency or the distribution is skewed to the larger or the smaller items. Two methods of exploitation are illustrated, where feeding is either at random or is constantly selecting for the largest items available (The frequency of prey families taken is assumed to approach a log normal distribution Hesperheide, 1971, Bryant unpublished). These hypotheses are

presented in Fig. 4. 4.

It can be seen that when feeding is at random $r_{\text{selection}} = +1.0$ in each case. However when the larger items are selected, a hierarchy of correlation coefficients is obtained with $r = -0.62$, when available prey is skewed to the smaller items, through $r = 0.12$ (available prey normally distributed), to $r = +0.9$ when prey is skewed to the large items. To summarise, a shift in the mode of the frequency distribution available of prey items, to the 'larger items' end of the scale, is associated with an increase in the correlation coefficient. In fact the situation when larger prey items are available approaches truly random feeding. It might be that in such a situation the energetic cost of feeding at random is insignificant, because the probability of encountering 'economic' prey is high. Also random feeding might involve fewer adjustments in speed and direction, which are energetically expensive, which would however be an integral part of a selective feeding strategy. The predation strategy can alternatively be expressed in the following way. If selection pressure is constantly directed towards the most profitable items, then when these items become relatively less abundant, the energetic advantage of exploiting incidentally encountered prey increases

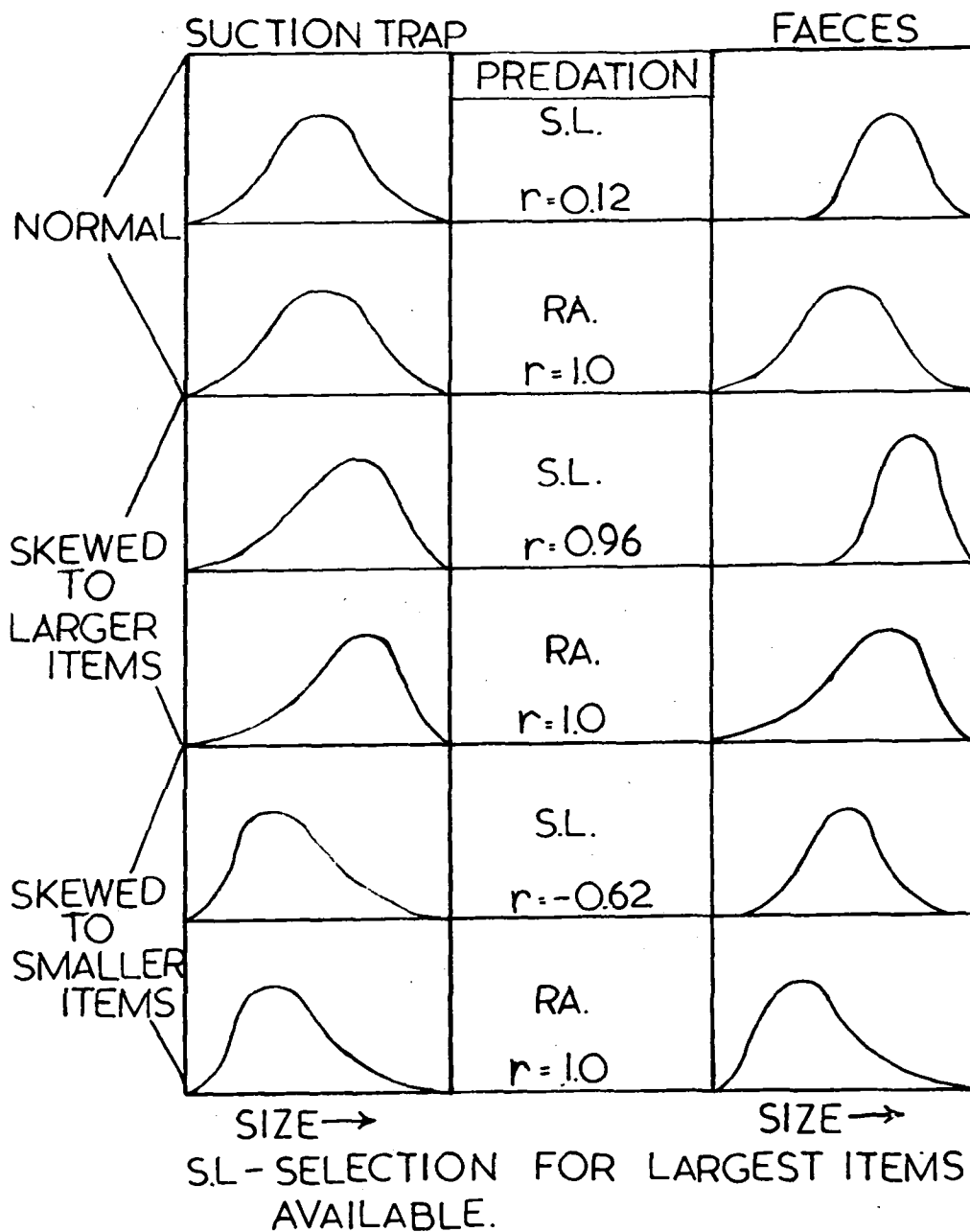


FIG. 4.4. The hypothetical size distribution of prey items in the diet in relation to that available in the air, as a function of two contrasting predator strategies. These strategies illustrate (1) a predator that feeds at random, ingesting items as they are encountered and (2) a predator that consistently selects the largest items available.

and so selection pressure on less favoured items will increase. In effect a switch to less preferred items (Murdoch, 1969) never occurs, but rather there is an expansion of the "area of acceptability" of prey items.

It is an implicit correlate of a shift in the mode of a frequency distribution, that the mean will vary sympathetically. Therefore if selection was directed towards the most profitable items (and this prey spectrum was relatively stable), then if the mean calorific value of available prey items is high, the means of the two spectra will be coincident and hence the correlation coefficient will be high. A reduction in the mean calorific value of available prey, causes a divergence of the means and a consequent depression of the correlation coefficient.

The hypothetical strategies suggest a causal function of prey size in the variation of $r_{\text{selection}}$. Therefore variation in $r_{\text{selection}}$ was examined in relation to the mean calorific value of the available prey for the field data. They were highly significantly correlated ($r = +0.81$ $p = <0.01$) and the coefficient of determination, $r^2 = 66\%$. An attempt to explain the residual variance in terms of other environmental variables involved a multiple correlation and regression analysis (Table 4.11) incorporating similar variables as in Table 4.8.

TABLE 4.11.

Multiple Correlation and Regression Analysis to investigate influence of environmental variables on daily selection intensity of feeding House Martins.

Variables (Environmental) a. Wind Index; b. Mean Calorific Value of Available Prey; c. Total Insect Abundance (Log); d. Temperature (Mean); e. Abundance of Insects whose S.I. exceeds 100.

Variables Used	($r^2 \times 100$)	Variance Ratio (Sig)	(Beta Wts) ²	B (Mult. Reg Coeffic't)	r p
1. a,b,c,d,e (n=27)	68%	p=<0.005	a. 0.03	-1.39	-0.08 N.S.
			b. 0.76	0.03	0.81 <0.01
			c. 0.00	3.43	0.28 N.S.
			d. 0.00	-0.81	0.17 N.S.
			e. 0.01	-2.81	0.56 <0.01
2. b only (n=27)	65.6%				0.81 <0.01

It accounted for only a further 2.5% of the variation. Therefore it is reasonable to propose that variation in $r_{\text{selection}}$ between the aerially sampled insects and the Martins diet is principally a function of variation of the mean size of the available prey, where this in effect involves an increase in the percentage representation of profitable families i.e. Syphids, Ants and Parasitic Hymenoptera etc. In this situation, the highly variable taxonomic composition of the available prey becomes coincident with the taxonomic composition of the relatively stable Martin prey spectrum, and a correlation coefficient calculated for such data would be high. Where the percentage representation of less favoured items increases the calculated correlation coefficient ($r_{\text{selection}}$) is depressed, indicating an increase in selection activity and an accompanying increase in the rate of rejection of items encountered, where these are unprofitable items of low calorific value.

The residual variation (34%) is probably a product of both the invalid assumption of a random distribution of the aerial insects on a vertical axis (Lewis, 1965, Johnson, 1957; Taylor 1960) and also the system of categorising species in taxonomic groups of family and size, rather than as species groups.

Discussion

Variation in the quality of the nestling Martin's diet is largely explicable in terms of concurrent changes in the characteristics of the available prey. The suggestion of Royama (1970) that the profitability of items to adult birds feeding independently and those feeding nestlings may be different, is likely to be less significant in the aerial feeding birds for the following reasons. Handling time for each prey item is not subject to such a wide variation as hypothesised for the Tit (Parus major) nor are items brought individually to the nest. Both these factors tend to increase the differences between the relative profitabilities of feedings nestlings and independent adults. Therefore it is considered that these conclusions apply to both the adults and the nestlings diet

Holling (1965 p.52) and Emlen (1966) both propose a reduction in feeding discrimination (and therefore decreased selection) as total available food becomes scarce. This would involve an increasing convergence to equality of the percentage representation of items in the diet and the air. However the present work found that variation in ($r_{\text{selection}}$) did not behave as a function of the total food available, where

for $r_{\text{selection}}$ and total catch (Log N+1) $r = +0.28(\text{N.S})$ and for total calorific value of catch and $r_{\text{selection}}$, $r = +0.29(\text{N.S})$. Therefore $r^2 = 0.081$, indicates that only 8% of the variation in $r_{\text{selection}}$ could be explained by variation in the total abundance of food. It is suggested therefore that the total food abundance is not significantly involved, but rather that the relative frequency of profitable items will dictate whether selection is intense or slack. However it is acknowledged that extreme food shortages were not encountered within the sample period, and in such a situation it might become profitable to exploit every item encountered. The critical level of food abundance at which this changeover might occur, is when the probability of obtaining a given quantity of energy in a given time is greater if every item is captured than if less favoured items are ignored and effort concentrated only on more profitable items.

SECTION 5

THE PATTERN AND CAUSES OF MORTALITY IN NESTING HOUSE MARTINS.

Several recent analyses of the pattern of mortality in bird populations have utilised Varley and Gradwell's modification (Varley and Gradwell, 1960, 1963 . b and 1965, Varley, 1963) of Morris' key factor analysis (Morris, 1959, 1963~~4~~). The analyses of Southwood, Blank and Cross (1967) on the Partridge (Perdix perdix), Southern (1970) on the Tawny Owl (Strix aluco) and Krebs (1970) on the Great Tit (Parus major) were based on extensive data and the significance of the results is hence high. Population data must be available for at least three annual cycles for satisfactory analysis, however the timing of this study prevented this criterion being met. Therefore as the principal period of interest was the breeding season, I adopted a modification of the method suitable for within season investigation. The mortalities within and outside the breeding season were thus treated quite separately. The latter topic will be discussed in section 10.

The Mortality Within the Breeding Season.

A precise knowledge of the breeding season mortality was confined to that occurring within the nests of breeding House Martins. It is probable that a number of adults died also during the breeding season but this could not be verified. This section is therefore confined to identifying the principal causes of variation in breeding mortality (K_B) in effect the factors causing variation in the productivity of Martins per pair in each season and between each colony. The key factor influencing total annual mortality is briefly discussed in a later section.

The potential causes of population change in the breeding season are then:-

1. Adult mortality during the breeding season.
2. "Mortality" due to variation in clutch size. Mortality here refers to a fall in natality from the potential maximum, due to variation in clutch size.
3. Mortality due to variation in the hatchability of the eggs
4. Mortality due to variation in nestling survival.
5. "Mortality" due to variation in the percentage of breeding pairs attempting second broods. Mortality here refers

to a fall in natality, due to variation in the percentages of pairs laying second clutches.

(Categories 2 - 4 apply to both the 1st and 2nd broods)

The significance of the results over the three breeding seasons has been increased by examining each of the main colonies as separate entities in two out of the three years. This was not possible for the first year of study because information is only available for the latter half of that season for both colonies. A total of 5 season/colony K_B s were therefore available for analysis. (where K_B refers to the within nest mortality alone and = Total breeding season mortality)

It should be noted that the total production of young from each colony in each year may be primarily influenced by the colony size at the beginning of each season, depending on the extent of the differences in colony size. The differences in the present study of the sample colony size, although not directly related to total colony size, were sufficient that the total number of young emerging from these nests was largely a function of that sample colony size. Using the method described by Southwood (1966) for single generation subjects, it was found that 82% of the variation in total flying young produced each year (P_R) could be explained by

variation in the natality in the sample colony (P_E), where P_E was completely uncorrelated with variation in clutch size (1st and 2nd) ($r = 0.09$) but almost significantly correlated with the number of pairs breeding $r = 0.79$ ($p = c. 0.1$).

Analysis of Breeding Season Mortality

The results of the breeding season census at two colonies in three seasons is shown in Appendix II. The total breeding season mortality (K_B) is the sum of the individual mortalities where these are:-

- k_1 = Mortality due to variation in 1st clutch size. Where this is expressed as the difference between the mean clutch size at the period of interest and the maximum observed mean clutch size over the whole period of study.
- k_2 - Mortality due to hatchability loss. This includes desertion of eggs, infertility, and eggs laid in untenanted nests.
- k_3 - Mortality of chicks (1st brood).
- k_4 - Mortality due to variation in the number of pairs laying second clutches. This is expressed as the difference between the % pairs laying at the period of interest and the maximum observed % over the whole study period.
- k_5 - Mortality due to variation in second clutch size

k_6 - Mortality due to hatchability loss of the second clutch.

k_7 - Mortality of chicks (2nd brood).

K_B - Total breeding season mortality, and it equals the total difference in the numbers potentially able to be reared by the observed number of pairs, and those actually reared in each season by those pairs.

A graphical analysis demonstrated no distinctive correlation between any of the mortalities and K_B . Even when these are grouped as total chick mortality etc. i.e.

$(k_1 + k_5)$, $(k_2 + k_6)$, $(k_3 + k_7)$.

The correlation coefficients were therefore calculated for the mortalities individually (k_1 , k_2 etc) and for the grouped mortalities ($k_1 + k_5$ etc.). In the first case it was found that the percentage of the pairs laying second clutches was the most significant correlate of K_B . Here $r = 0.96$ ($p = < 0.01$) For the grouped mortalities this was confirmed, where r naturally remained the same. However the correlation of some of the other mortalities was depressed when they were grouped, below the maximum of some of the individual mortalities. As for first brood chick survival $r = 0.67$ (N.S) $[k_3]$ while for

$(k_3 + k_7)$, $r = 0.54$. In other cases the r for the grouped mortalities exceeded that for either of the individual k 's.

The results are shown in Table 5.1 (See data in Appendix III.)

Table 5.1. Correlations between individual k 's & K_B

		r	P	Order of Importance.
I	k_1	0.46	N.S.	3
	k_2	0.37	N.S.	4
	k_3	0.67	N.S.	2
	k_4	0.96	<.01	1
	k_5	0.07	N.S.	7
	k_6	-0.19	N.S.	5
	k_7	0.13	N.S.	6
II	$k_1 + k_5$	0.61	N.S.	2
	$k_2 + k_6$	0.47	N.S.	4
	$k_3 + k_7$	0.54	N.S.	3
	k_4	0.96	<.01	1

Firstly it is evident that the percentage of pairs laying a second clutch is the most important influence on K_B .

Thereafter chick mortality (particularly 1st brood) and
are
variation in clutch size (1st brood)/of considerable influence.

All of the avian studies mentioned hitherto have been on single generation per annum species and comparisons cannot

therefore be made, regarding the relative importance of k_4 in different species. An important aspect of this work is to examine the mechanisms by which mortalities are incurred. I therefore examined each of these mortalities, whatever their influence on total K_B to illuminate the process involved.

Adult Mortality During the Breeding Season.

Because adult mortality was never positively recorded in the breeding season, the key factor (K_B) analysis was confined to the mortality suffered in the processes described below. It seems very probable however that some of the nestling mortality was ultimately a product of adult death rather than any other factor. This will be further discussed below.

A. The influences on variation in clutch size (k_1 and k_5)

The factors that might depress the mean clutch size below the maximum recorded may be categorised as follows.

- a. Internal Factors.
- b. External Factors.

The internal factors includes only the age of the laying female. While the external factors include all aspects of the environment, i.e. weather, habitat, population density,

season and food abundance.

a. Internal Factors.

Age.

The studies of von Haartman (1967), Kluyver (1951) and Coulson & White (1961) describe the influence of age on the mean clutch size in several species of birds. Klomp (1970) records a maximum difference between the mean clutch sizes of different aged birds as 1.15 eggs in the Starling (Sturnus vulgaris). However the figure for the majority of species is much less than this, whereas for the Swift (Apus apus) it is only 0.44 eggs(Weitnauer, 1947). It appears that in most species, the mean clutch size depends on factors apart from a change in the age structure of the population. Indeed the change in age structure needed to achieve even 50% of the total difference recorded in most species would involve such an absolute difference in successive years that it is inconceivable. However no data on the age structure of the House Martin population is available to illustrate this.

b. External Factors.

Weather.

There are no indications that the mean clutch size and

its year to year variation is influenced directly by the weather. The correlations between mean daily Temperature, Rainfall, Wind and Hours of Sunshine and clutch size were not significant . (The highest, $r = 0.58$, was for both May mean Temperature and the Laying Period Temperature). However as discussed below I consider that the weather could act by directly influencing the food supply which in turn might affect clutch size, as it is known that weather is correlated with the numbers of insects flying (Johnson, 1968). I conducted a multiple regression analysis involving several environmental parameters (Temperature, Rainfall, Relative Humidity, Hours of Sunshine, Daylength and Wind, against a Logarithmic Transformation of Total/Daily Insect Catch at 40 ft.). The coefficient of determination was 56% illustrating the degree to which aerial insect abundance is associated with weather factors. Wind, Rainfall and Temperature were all importantly associated with the size of insect catch, while all the factors investigated were significantly correlated below the 5% level, except daylength.

Habitat.

There are many recorded differences in mean clutch size

by populations inhabiting different habitats. The mean clutch size of some of the Paridae, the Pied Flycatcher and the Blackbird are different in different habitats (Kluyver, 1951; Lack 1955; Creutz 1955; Snow 1958). The colonies I studied underwent no gross habitat changes while under observation (i.e. modification by man - drainage, woodland felling) and are all surrounded by similar vegetation (see introduction). This factor is therefore not considered important in the yearly variation in clutch sizes.

Population Density

There is evidence in several passerine species to suggest that the mean clutch size declines as population density rises (Kluyver, 1951; Perrins, 1965). It is not however an effect that is found in all species (Blank and Ash, 1960; Berndt and Winkel, 1967). Examination of 1st and 2nd clutch sizes separately gave no indication of consistent variation with population density (i.e. Colony size). However when first and second clutches are plotted together as a function of the log. total numbers of Martins in the colony at the time the 1st and 2nd clutches are laid (Adults and nestlings) a negative correlation is observed ($r = -0.63$, $p = < .05$). If

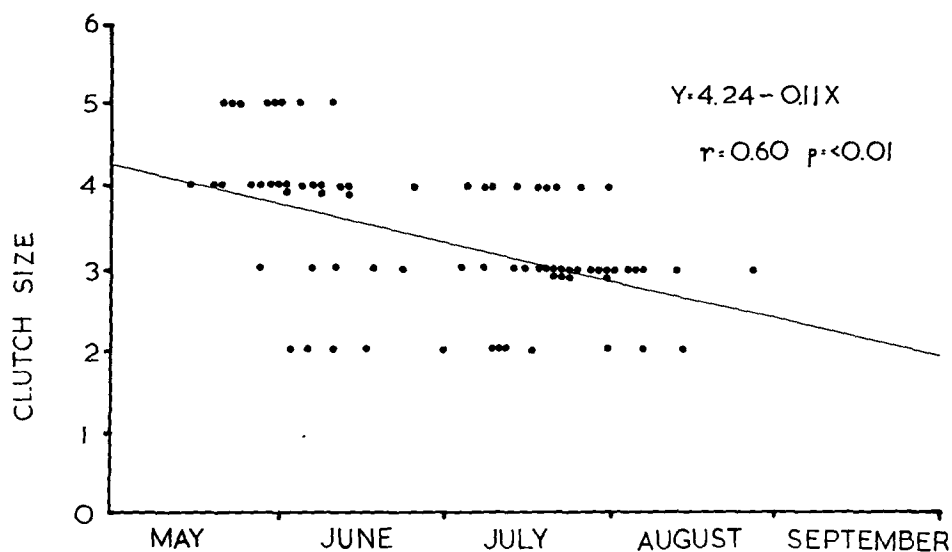
this correlation is causal rather than correlative it implies that as the density of birds within the colony increases, within each breeding season, competition for food also increases and hence the total food available to each member of the colony decreases. However this in turn implies that both the first and the second clutch size would be negatively correlated with the population size at the onset of breeding and at the end of the rearing of the first brood respectively. There is no evidence that this is so, and hence the relationship is not thought to be indicative of a modification in clutch size simply as a response to population density, but rather that the second clutch size is modified in relation to certain ultimate factors discussed in a later section and this gives rise to a spurious correlation.

Season

In the great majority of species a seasonal decline in clutch size has been reported (Klomp, 1970). A few predatory birds have a clutch size which increases during the course of the breeding season (Lack, 1947). It is possible that the variation in mean annual clutch size is only

a reflection of the time of year in which the clutches are laid. A seasonal decline in the clutch size in the House Martin was identified and is described by the following equation. $y = 4.24 - 0.114 x$ and $r = 0.60$ ($p = <.01$)(Fig 5.1) (where x is the n th week from the first week in May in the breeding seasons of 1968 and 1969 and the clutch size is considered in terms of weekly means). A similar relationship can be demonstrated within the first clutch alone ($b = -0.23$ and $r = 0.65$ $p = <.05$) but not within the second clutch ($b = -0.12$ and $r = 0.56$ N.S.). I calculated the expected mean clutch sizes for each of the study years on the basis of the mean date of laying, and the expected differences in mean clutch size can then be calculated. The maximum observed difference in mean laying date was 12 days $\approx 2n$ (weeks). Therefore on the basis of the equation for the first clutch alone the calculated maximum difference in clutch size was 0.46 eggs. The recorded difference was considerably in excess of this and therefore much of the variation must be accounted for by other factors.

Nevertheless it is of interest to interpret the cause of this seasonal decline. Possibly the age structure of the population involved in laying, changes as the season



The seasonal decline in clutch size in the House Martin. Data from 1968 and 1969 is included.

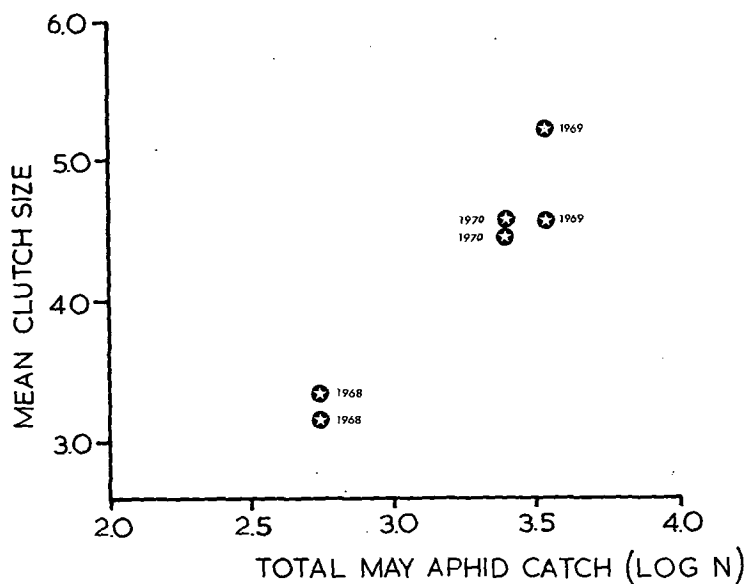


FIG. 5.2. The mean first clutch size at the main study colonies in the three years, 1968-1970, in relation to the total Aphid

advances. It is known that the younger birds of several species (see above) lay smaller clutches, and the order of magnitude of the decline is such that this could be occurring. However many species of birds even within age classes exhibit such a decline (vonHaartman, 1967 ; " Coulson & White, 1961) and so other factors are involved. It is obviously not related directly to the amount of food available as this increases throughout the period of decline, and so the clutch size is presumably modified in relation to the suitability of the season in which the young will be raised. The adjustment comes under the influence of ultimate rather than proximate factors. This will therefore be discussed in the section on the influence of food abundance on clutch and brood size. The influence of the food supply on the timing of the season, which will influence the mean date of laying in each year and hence to a certain extent, the mean clutch size, will also be discussed in a later section. (Section 8)

Food Abundance.

An additional figure for the mean clutch size was derived for the purpose of this analysis. A sample of six nests observed elsewhere in the spring of 1968 had a mean clutch

size of 3.17 eggs. The incorporation of this figure into the analysis increased the significance of the results. Clutch size was then examined in relation to a range of environmental parameters including mean daily Aphid abundance in May for 1968 to 1970. / (Fig.5.2) Many species are known to adjust their clutch size according to the abundance of food (Klomp, 1970). Therefore because House Martins are known to feed largely on Aphids during this month (see section, 4) it is not surprising that the correlation for Aphids and clutch size is significant ($r = 0.93$ $p = <.01$) and further, exceeds that for Mean Total Insect Abundance ($r = 0.76$ N.S.). This correlation is not to suggest that the effect of changes in Aphid abundance on mean clutch size is direct, and confined in its implication simply to a difference in mean clutch size. For example, if a correlation existed between aphid abundance at this time and one month later, when the nestlings were being fed, there would be a clear advantage in being able to predict the likely state of the food supply one month after egg laying and to optimise the clutch size accordingly, to rear as many young as possible. I therefore examined the correlation between aphid abundance over 5 day periods in May and one month later in June. (Thirty days is the mean interval between egg laying

and the period of maximum energy requirements of the nestlings while in the nest). There was a significant correlation where $r = 0.47$ ($p = < 0.05$), when all the data was examined together. However it is possible to obtain a spurious result arising simply as a function of population increase. More properly results from the same 5 day period (or 10 day) in the three years should be examined in isolation. The results of such an analysis are shown in table 5.2. It can be seen that with such a low number of samples correlation is insignificant ($r=0.72$ ($p=n.s$) to 0.99 $p = < .05$) in many cases. However there is invariably a positive correlation of a fairly high degree. However aphids are not the principal food, of nestling Martins in June, instead a wide range of food is taken. Therefore total insect abundance in June was examined, in relation to aphid abundance, temperature (unless otherwise stated Temperature - refers to the mean monthly temperature) and total insect abundance one month previously i.e. for May. It was found that of the factors significantly correlated with clutch size, Aphid Abundance was most closely correlated with the total insect abundance in June ($p = < .02$). Therefore if the Martin does adjust its clutch size according

Table 5.2

Correlations between May Insect abundance for several insect families, and their abundance one month later in June.

No. Site and Insect Taxa Involved		r	b	a	n
1	Rothamstead, Aphid Catches (all species) for May and June 1964 to 1970.	+0.36 N.S.	0.20	1.72	7
2	Silwood. Aphids 1968 to 1970. (5 day periods) May 1-5	No result because no aphids in 1st week of May.			
	6-10	+0.998	0.47	1.38	3
	11-15	+0.724	0.331	1.73	3
	16-20	+0.865	0.285	1.41	3
	21-25	+0.741	0.586	0.61	3
3	Silwood. Aphids 1968 to 1970. (10 day periods) May 1-10/June 1-10 May 11-20/June 11-20	+0.857 +0.784	5.16 0.297	1.48 1.58	3 3
4	Silwood. Aphids in May and Total Catch in June (5 day periods) May 6-10 11-15 16-20 21-25	+0.635 +0.604 +0.177 +0.904	1.54 0.45 0.04 0.68	2.58 2.52 2.51 1.47	3 3 3 3
5	Diptera (Data from Williams, 1961)	+0.645	0.79	0.85	4
6	Simulium sp. (Data from Williams, 1961).	+0.823	0.45	0.29	4
7	Diptera (Oscinella frit) Data from Southwood (unpublished) (Suction Trap catches)	+0.874	0.81	0.49	5

to prevailing conditions in May, the most accurate variable to be employed to "predict" June food abundance is the Aphid Abundance prior to laying. Correlation between aphid abundance over the whole of May and in June was not significant (yet $r = 0.88$). It has been suggested previously concerning several passerine and non-passerine species that such an adjustment in clutch size takes place in response to environmental conditions. Referring to the Alpine Swift (Apus melba) Lack and Arn (1947) found that a large clutch size was correlated with a low nestling mortality and therefore deduced that the birds responded to some spring correlate of favourable summer breeding conditions. Also the Short Eared Owl (Asio flammeus) is known to lay larger clutches when voles are particularly abundant (Adair, 1892, 1893) evidently "in anticipation" of there being abundant food for feeding their young (Lack, 1966). In exceptionally poor food situations the clutch size may be reduced to nil in certain species - i.e. breeding does not take place (Southern, 1970, Moreau, 1944). Because rearing young in such conditions would not be possible. I therefore propose that the House Martin responds to a proximate indicator of food abundance at the time of maximum requirements. The most likely proximate factor appears to be Aphid Abundance, though it should be

noted that both May Temperature and Total May Insects are significantly correlated with June Insect Abundance and might therefore also be implicated.

The range of variation in mean second clutch size was small and hence k_6 was also small. Ranging from 2.78 in 1970 to 3.10 in 1968, a difference of only 0.32 eggs. Furthermore this range was also effectively spanned within a single season (1970), when the Kennel site had a mean second clutch of 2.78 eggs while the farm site had a mean size of 3.09 eggs which was effectively equal to the largest mean second clutch recorded. The mortality contributed by this variation was the lowest recorded and was uncorrelated with K_B ($r = 0.07$). The second clutch size however was significantly correlated (negatively) with first clutch size ($r = -0.89$ $p = < .05$) suggesting a possible effect of population density, though this is not substantiated by examination of population densities in relation to second clutch size (see above).

B. The Influence of Variation in Hatchability (k_2 and k_6)

The key factor (K_B) analysis indicated that variation in hatchability was uncorrelated with variation in total mortality. However the total extent of the mortality attributable to poor hatchability from all the seasons and colonies was greater than ~~for~~^{many} other cause of mortality. It is therefore of interest to investigate the causes of such low hatchabilities. A subdivision of the total eggs not hatching into their gross causes are shown in Table 5.3.

Table 5.3. The causes of failure of eggs to hatch.

Total Eggs failing 1968 & 1969 (N) = 62.

Percentage eggs failing because:-

1.	Desertion	30.6%
2.	Infertility	48.4%
3.	Laying in untenanted nest	21.0%
4.	Predation	0%
	First Broods alone	Second Broods alone
	% (n)	% (n)
1.	39% 17	11% 2
2.	37% 16	78% 14
3.	25% 11	11% 2
4.	0% 0	0% 0

The principal cause of failing to hatch was (category 2) Infertility. This refers to those eggs failing to hatch within otherwise successful nests. In all probability this was due to them not being fertilized, because they were not exposed to different environmental conditions (only one out of 18 eggs, in 1969 was the first laid egg in the clutch and therefore potentially susceptible to different conditions to the other eggs) and showed no signs of damage. Of five eggs checked specifically in 1968 none showed signs of embryo development. This infertility was apparently of relatively greater importance in second broods.

Desertion of whole clutches was recorded for five clutches and accounted for the second most important cause of egg failure. Eggs were also frequently laid in unattended nests. This may have been simply error or possibly the product of unrecorded behavioural activity, acting along group selection lines (see Wynne Edwards, 1962) that reflects an action by the Martin, which results in^a reduction in clutch size after egg development had been initiated. The home nest of these pairs was usually identifiable because it was often adjacent, and the laying sequence would be interrupted for a day, or would begin the following day if the first egg was laid in the

" wrong" (adjacent) nest. If this was a mechanism for clutch size reduction (given the impossibility of egg resorption once the ovarian follicles had been stimulated by gonadotrophic hormones) it would seem to be unnecessary for laying to take place in another nest because that or another egg could have equally been ejected from the home nest. It may be that an egg particularly poor in quality, and thus unlikely to produce a viable fledging is disposed of in this way. However a students 't' test demonstrated no significant difference between the weight of a group of normal eggs and this group of 'abandoned' eggs (at laying) which indicates that there is no significant difference in quality. Predation on eggs was not recorded in the study though on several occasions single eggs or whole clutches disappeared between inspection intervals. It is thought that this was caused by egg chilling or damage and subsequent ejection of these eggs by the adults. Indeed such eggs were usually found below the nest exit. They were recorded as deserted or infertile as considered appropriate. There was no indication that the extent of egg hatchability was influenced by environmental conditions including food abundance (k_2 and May Aphids, $r = 0.04$). It is possible that infertility and the laying in a wrong nest is a function of age

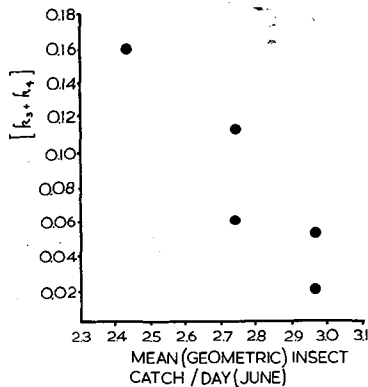
and experience of the laying bird but this is not known. However there is some indication that desertion of clutches may occur after the eggs have been chilled. If food is very scarce the adults collect food independently and the eggs remain unbrooded. If the eggs became sufficiently chilled the embryo is killed and the eggs are deserted. Of the total of five clutches deserted it was considered that two were caused by my interference, another was of unknown cause and the other two were associated with unusually low food abundance and temperature for two consecutive days during laying. It is known that the eggs were not brooded during this period and were therefore probably chilled sufficiently to terminate development. They were subsequently incubated for several days before desertion.

C. The Influence of Variation in Nestling Mortality (k_3, k_7)

The mortality caused by the death of 1st brood nestlings was the second most important correlate of total breeding season mortality. However 2nd brood nestling mortality was almost negligible and uncorrelated with K_B . Also, as no information was available for various environmental parameters during the autumn of 1970 no further examination was made of the second brood chick mortality. The first brood mortality k_3 was examined in relation to the prevailing conditions, where this was food and weather parameters for June in each year.

k_3 was correlated with various food abundance indices (only significant at $p = < 0.10$), though not with June Temperature. The highest correlation involved Mean Insect Catch/Day (Logarithmic Transformation) (Fig 5.3) where $r = 0.82$ ($p = < .10$). This broad approach conceals much of the detail of nestling mortality and this is therefore discussed in more detail. In 1968 and 1969 a total of 26 nestlings were found dead in the nest. i.e. 11.2% of the total young hatching in closely observed nests. The distribution of this mortality with respect to nestling age is shown in fig 5.4 and includes information from both 1st and 2nd broods. However the pattern is essentially similar when this is broken down into 1st and

FIG. 5.5. The combined "mortality" due to variation in the number of pairs attempting second broods (k_4) and the mortality due to nestling death



before fledging (k_3), in relation to aerial insect abundance in June, over the period 1968 to 1970.

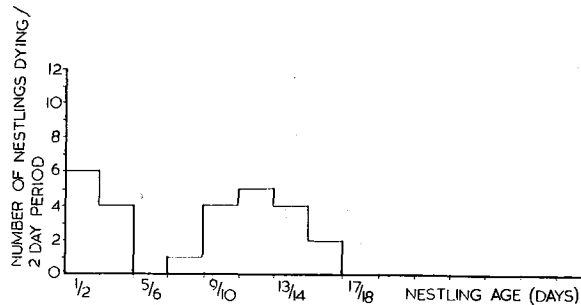


FIG. 5.4. The distribution of nestling mortality throughout the nestling period in the House Martin.

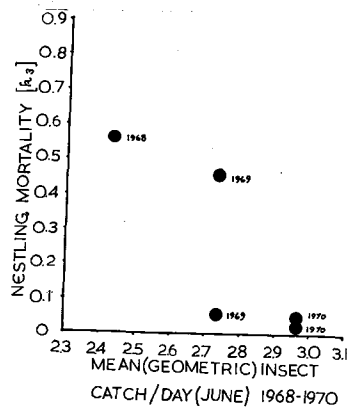


FIG. 5.3. The mortality of nestling House Martins in the first broods (1968 to 1970) in relation to the aerial abundance of insects in June.

2nd broods separately. There appear to be two critical periods for nestling survival. Firstly soon after hatching and secondly around the 11th and 12th nestling days. The first occurs at a time when feather cover is at a minimum and yet the surface/volume ratio is at a maximum for the individual nestlings. Thus although food requirements are limited at this stage, the nestlings are subject to exposure as for example when food is short and the parents fail to brood the newly hatched chicks. This was thought to account for 50% of the nestling deaths at this time. The remaining 50% involved brood "runts" which as a result of hatching last were consequently smaller than other nestlings within the brood and were eliminated by brood competition for food and the consequent starvation. The bulk of the total nestling mortality (61%) occurred from the 7th to the 16th nestling day. The median days of the distribution (Day 11 and 12) were about those at which the nestling energy requirements (see Section 9) reached a maximum and yet the insulative feather cover was only partially complete. It would seem rational therefore that if brood reduction was going to occur as a result of food shortage it would occur at this time. Of the total mortality at this time, in 50% of the nests it involved a single nestling which

died probably as a result of this process. The other 50% of the broods involved the death of whole broods of 4, 3 and 2 of 2 nestlings. It therefore seems possible that disease was involved here though no overt signs were apparent. A more likely explanation is that one of the adults was taken by a predator which left only a single parent and possibly first brood young also attending the nest. It was observed that the birds were being fed even while they were losing weight prior to death. It is therefore interesting to speculate that the adults are particularly prone to predation at this time because of the extent of their involvement in brood rearing. Their susceptibility may be exaggerated when food is short. At such a time they are collecting food and therefore exposed to avian predators for much of each day.

The principal cause of nestling mortality appears to be food shortage, which reflects on the nutrition of the nestling in the variety of ways outlined above. The relative importance of food abundance and other environmental parameters on nestling mortality in nidicolous as opposed to nidifugous species will be discussed below.

D. Influence of Variation in the Percentage of Pairs Laying
Second Clutches (k_4)

Much of the variation in total breeding season "mortality" (strictly speaking a variation in natality) is due to differences in the percentage of pairs in each season/colony that attempt to rear a second brood. It is therefore important to establish what factors influence the variation in this percentage. If a pair is attempting to maximise the production of young within each season as proposed by Lack (1966) it is anomalous that the opportunity to rear a second clutch is foregone, unless the probability of survival of the young so raised is low, or that it leads to a detrimental effect on the adults concerned. If the initial premise is valid, it should be a matter of identifying that factor that makes the probability of successfully rearing young low. And this will be the factor, or correlated with the factor, that, makes survival probability of second broods low, unless adult overwinter mortality is more important. It appeared that nestling survival within the first broods was primarily a function of food abundance and it would be profitable to examine the variation in the number of pairs laying second clutches in relation to food abundance. However

data is not available for the autumn of 1970 and so this was not possible. An analysis was conducted however in which the lateness of the season ((a) mean laying date of first broods and (b) percentage of pairs laying in June) was examined in relation to k_4 . No significant correlation was apparent ($r = 0.56$ N.S. for % pairs laying in June). Also k_4 was not dependent on the density of birds at the time of laying of the second broods (where this is the log. of:- (the number of adults in the colony + number of young being fed within the nest + fledged young)). A final suggestion is that the percentage of first year birds in the colony varies from year to year and some of these probably only rear a single brood in each season as well as laying a reduced clutch size. The percentage of such inexperienced birds present will be reflected in the percentage rearing second broods. However it must be noted that variation in food abundance may well contribute additionally. Indeed if either k_4 or the % of pairs laying second clutches is plotted against June food abundance for each of the colony/seasons, $r = +0.89$ ($p = <0.05$). There therefore is the possibility that June food abundance is related to the autumn food abundance, and the correlation might then be considered causal. However for the present no

further evidence on this point is available as I am unable to explain how June food abundance could affect the percentage of pairs rearing second broods if the correlation is directly causal.

The influence of adverse weather conditions acting directly on the birds, rather than through the food supply, has not yet been systematically analysed. However in no year was adverse weather sufficiently sustained to materially upset the second clutch laying distribution and it seems unlikely therefore that it could postpone laying to such an extent that it was not profitable to lay at all.

Discussion of Breeding Season Mortality.

It is evident that one source of "mortality" is outstandingly important in determining the mean production of young per pair/season in nesting House Martins. This is (k_4) the percentage of pairs rearing second broods. Nestling mortality in the first broods is of secondary importance regarding the whole colony though if a pair does rear a second brood it will be of primary importance. It was demonstrated that both (k_3) and (k_4) were significantly correlated with Log Insect Abundance in June and when the two mortalities are

combined ($k_3 + k_4$) the significance is higher, where $r = 0.90$ (and $p = < 0.05$) (Fig 5.5). Although the precise mechanism is incompletely known it is evident that an abundance of flying insect food is the most important correlate or cause of a productive martin breeding season. It is of interest in this context to compare the various influences on the productivity of the season with those obtained by Southwood and Cross (1968) for the Partridge. On the one hand a nidifugous species and on the other a nidicolous species, and differences could be expected in the relative influence of different environmental factors. A multiple regression analysis was therefore conducted using the same environmental parameters as Southwood and Cross in relation to the young:old ratio in autumn. The results of this analysis and those of Southwood and Cross are presented in Table 5.4

Table 5.4.

		$r^2 \times 100$	F	P	B Wts Food Abundance (June)	Mean June °C	
Bryant	1. k_3	67.0 %	2.0	N.S.	0.81	0.015	House Martin
	2. Y/O	58.0 %	1.4	N.S.	0.91	-0.310	" "
Southwood & Cross	Y/O	90.9 %	25.1	<.01	0.88	0.122	Partridge

It can be seen that the total variance explained is much less in the House Martin indicating that the total environmental influence is less, and by implication that some aspect of the birds' biology is more important (i.e. possibly age structure of the population). The B Weights for insect abundance are similar (B Weights = 0.91 for the House Martin and 0.88 for the Partridge). The influence of temperature illustrates the protective function of the nidicolous nesting habit. In the enclosed environment of the House Martin nest, temperature appears to be inversely related to breeding success B Weight = -0.31 . However the breeding success of Partridges depends directly to a certain degree, on temperature influences (B Weight = 0.12) as would be expected where the nidifugous species is fully exposed to the weather, except when being brooded. However the data for the House Martin is as yet not adequate for satisfactory analysis. This discussion will be taken further in the section on factors influencing brood size.

It is notable that of the four principal categories of mortality $(k_1 + k_5)$, $(k_2 + k_6)$, $(k_3 + k_7)$ and (k_4) , the three most closely correlated with K_B have been demonstrated to be

significantly correlated with variation in food abundance. It is further notable that none of these factors (k's) is influenced by population density and therefore cannot be considered regulatory. The regulatory mortality presumably occurs overwinter or at least outside the breeding season. However variation in food abundance is an important disturbing factor and can significantly affect the variation in breeding success of nesting House Martins.

SECTION 6.

ENVIRONMENTAL DETERMINANTS OF GROWTH RATES IN NESTLING HOUSE MARTINS (DELICHON URBICA).

It is well recognised that the amount of food and its quality are important factors determining rates of growth of animals. Thus a shortage of dietary energy or a dietary deficiency of a specific nutrient may cause depression of growth rates (Lister, Cowen and McCance, 1966). I examined the effects of energy shortage in the growth of nestling Martins, though I consider that nutrient shortages (for example calcium) are also important in limiting certain aspects of growth. It is possible that other environmental factors may affect nestling growth directly or that they may disturb the availability of energy (in the form of aerial insects) while the apparent abundance, estimated by the suction sampling apparatus, remains constant. It is therefore important to either assess the effect of these factors on growth rates or to eliminate them, in a study where the primary interest is on the limitations imposed by energy shortages. It is possible in many animals to investigate such interactions in the laboratory by suitable manipulation of the conditions. However extrapolation to the field situation is open to error principally because of the difficulty of simulating the

variability of the natural situation. I therefore examined the growth rates of whole broods in relation to concurrent environmental conditions and assessed the influence of variation in food abundance and quality, temperature, rainfall, wind and daylength. In the knowledge that food is likely to be the principal determinant of growth rates, the analysis therefore also investigated the validity of the sampling technique.

Method

The growth rate of nestling House Martins is a changing function of age. Weight increase is approximately sigmoid up to the asymptotic weight, which thereafter declines until fledging. If growth rates were to be compared between different aged nestlings within the same brood and between different brood sizes, in relation to environmental variables it was necessary to eliminate differences due to age and brood size. The method adopted was the application of Probit analysis to the sigmoid phase of nestling growth. The method may be made essentially graphic by the use of probability paper (x equal divisions), though I achieved greater accuracy by the direct consultation of the transformations in Fisher and Yates (1938). The precise methodology is explained in the

section on comparative growth rates of different brood sizes. Briefly however, by extracting the difference between successive points on the probability plot, in effect the gradient of the line between two such points over a one day period, a value for the growth rate could be derived. For ease of interpretation these values were then expressed as percentages of the mean value for each brood size.

An example of the normal growth curve for a single brood and the corresponding probability plot is shown in fig. 6.1 .

The principal purpose of this approach was to eliminate variation due to the change in growth rate with age & brood size. There was no significant difference in the mean transformed growth rates of broods from 4 days to 10 days (see over).

The differences in the total wet weight, and calorific value, of the whole brood increments due to differences in brood size were standardised by expressing the increments as a function of the asymptotic weight for that particular brood size. The variation in potential growth due to differences in individual nestling increments over the daily periods, was restricted by confining comparative rates to a range of nestling increments from 2.0 to 2.4 gms/nestling/day. This involved confining the period of interest for each brood to within

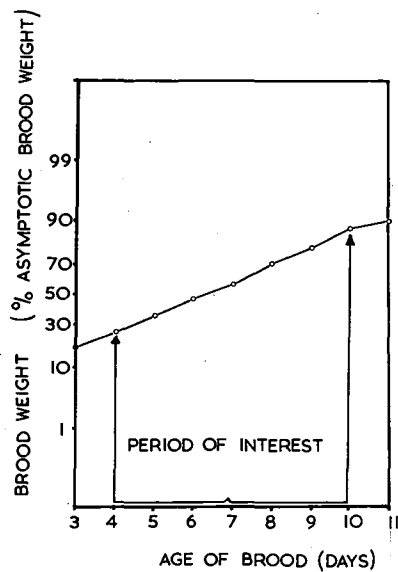
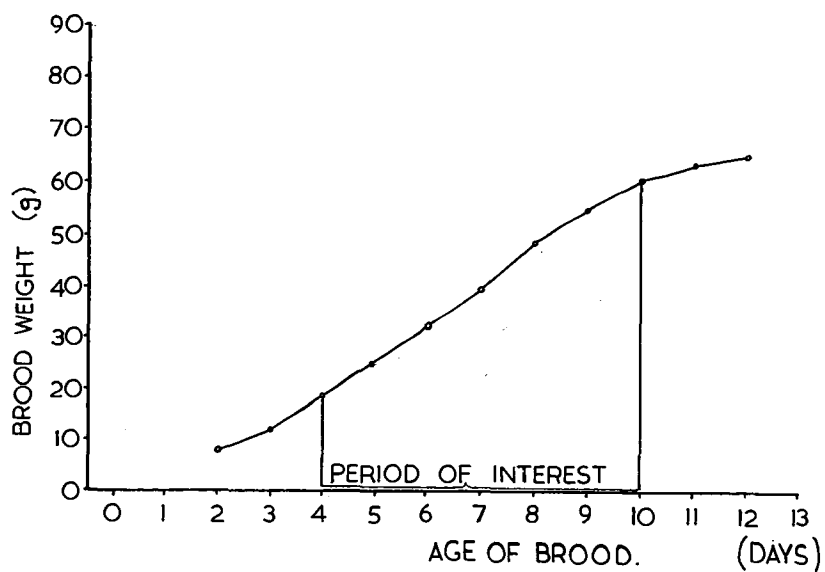


FIG. 6.1. A growth curve of a brood of three nestling House Martins from day 4 to day 10 plotted on (a) a linear scale and (b) on probability paper. See text for explanation.

3 days of the median growth point. Ricklefs' (1967) work on the Barn Swallow (H. rustica) suggests that the proportional representation of biochemical constituents is constant during this period of growth and therefore the calorific value of the increment per nestling per unit weight will be constant.

For the analysis these daily growth indices were examined in a multiple regression analysis in relation to concurrent environmental factors for all brood sizes together, though the 1st and 2nd broods were kept separate. This indicated the cause of variation in growth rates. However it was also of interest to assess the relative importance of the different factors in different brood sizes. It seemed probable for example, that the direct effect of temperature would affect the smaller broods relatively more intensely than food shortage, when compared with the larger broods because of the reduced thermal efficiency of such small broods. Therefore a similar analysis was carried out for each brood size. The environmental factors were examined in isolation to see if their effect on growth was non linear. It was found that nestling growth behaved as a linear function of the logarithm of the insect catch and the data was transformed. The

other parameters were most significantly correlated with growth, in isolation, simply as arithmetic functions and were therefore employed in the analysis in this form.

Results

The results for the first broods are presented in Table 6.1. Only Insect Abundance was significantly correlated with growth rate ($r = 0.51$ $p. = <.001$). The $(B)^2$ weightings amplify the results for the linear correlation coefficients and also assign the greatest influence on growth rates to insect abundance. The magnitude of the $(B)^2$ Weighting considerably exceeds that for temperature and wind. The coefficient of determination (r^2) indicates that 42% of the variation in growth rates can be accounted for by the variables supplied, leaving a considerable residual variation. That this residual variation is a product of the methodology is suggested by the results when all brood sizes are examined separately. This is discussed below.

In the second broods (Table 6.1) insect abundance is only of minor importance in influencing growth rates. The $(B)^2$ Weightings for Rainfall and Daylength exceed that for insect abundance by several orders of magnitude. This is

Table 6.1

Multiple Regression Analysis to examine the influence of named environmental parameters on nestling growth rates.

$$1\text{st BROODS } Y = 22.0 + 86.4X_1 - 7.2X_2 - 0.4X_3 - 0.5X_4 + 3.7X_5 + 0.1X_6$$

$$2\text{nd BROODS } Y = -60.7 + 10.7X_1 - 0.8X_2 - 0.4X_3 - 1.0X_4 + 0.7X_5 - 0.5X_6$$

F(Variance Ratio) and Significance		β Wts.							
		1	2	3	4	5	6		
1	6.90 (p = 0.001)	1.0	-0.4	-0.2	-0.0	0.4	0.0		
		$(\beta)^2$ Wts.							
		1	2	3	4	5	6		
		1.1	0.2	0.0	0.0	0.2	0.0		
		β Wts.							
		1	2	3	4	5	6		
2	4.74 (p = 0.001)	0.1	-0.1	-0.4	0.3	0.1	-0.1		
		$(\beta)^2$ Wts.							
		1	2	3	4	5	6		
		0.0	0.0	0.1	0.1	0.0	0.0		
Correlation Coefficients (r) & Significance								$r^2 \times 100$	(N)
		1	2	3	4	5	6		
1	0.51 0.001	0.24 N.S.	0.15 N.S.	0.18 N.S.	0.11 N.S.	0.06 N.S.		42%	65
		1	2	3	4	5	6		
2	0.25 0.05	0.05 N.S.	-0.52 0.001	0.44 0.001	-0.35 0.01	-0.02 N.S.		33%	65
X_1	Insect Abundance - Log Insect Catch								
X_2	Mean Temperature ($^{\circ}\text{C}$)								
X_3	Rainfall - Duration in Hours/day								
X_4	Daylength - Hrs.								
X_5	Wind Index - Wind Speed x Duration(Knots x Hours)								
X_6	Mean Calorific Value of Available Prey								

confirmed by the linear correlation coefficients where Rainfall, Daylength and Wind Speed and Duration are all correlated at the 1% level or less ($p = 0.001$, $p = 0.001$ and $p = 0.01$ respectively). Insect abundance is correlated only at the 5% level. It therefore appears that limitations imposed on growth rates of second broods by food shortage has been effectively minimised partly by the involvement of first brood young in the feeding of the second brood in the nest, (see section 12) and partly by changes in the abundance of insects at the two seasons. Examination of the data in table 4.1 & 8.3 in section 8 reveals the relatively greater total abundance and mean size of insects during August when most second broods are reared. Therefore in the absence of the food shortages encountered earlier in the season, dependance of growth rates on changes in food abundance will be less intense. Although the relative influence of the weather factors in the second brood, when compared with the influence of food abundance in the first brood (see (B)² weightings) is considerably less, the total variance accounted for ($r^2 = 33\%$) is only reduced by 9%. It appears therefore that while the influence of food abundance largely determines growth rates in first broods, an influence involving the interaction of rainfall, daylength

and wind is important in the second broods.

When growth rates were examined separately in different brood sizes, there was broad support for the above results (Appdx IV). The relative importance of insect abundance in first broods is confirmed for all brood sizes, though there is no indication that the relative importance of temperature or any other parameter changed as brood size changed. Note however that the Variance Ratio (F) is insignificant for all brood sizes except broods of 4 indicating that the fit of the multiple regression equations is poor in all except the broods of four. The results are presented however because they provide to a certain degree, confirmatory evidence for the findings detailed above. It will be noted that the coefficient of determination (r^2) varies considerably between different brood sizes and this will be discussed in the context of limitations on brood size in section .9. . In the second broods the results indicate that food abundance is only important in broods of one, and this anomaly is difficult to explain. The thermoregulatory properties of small broods are possibly so inefficient that when food is very short growth is drastically reduced, because of excessive maintenance requirements in the absence of parental brooding. There is no constant implication

of any other environmental factor, though all are involved in one brood size or another by either the linear correlation coefficients or the $(B)^2$ weightings. However it may be noted that the results for the combined broods of 4 and 5 (consisting of some artificially supplemented broods of 5) assign primary importance to daylength variation and secondary importance to food abundance. This point is of interest in the context of brood size limitation and will be discussed in section .9. .

In general the results confirm those for all second broods together (though again the Variance Ratio is only significant for a single brood in the second broods) and indicate that in all naturally occurring broods, emancipation from the effects of food shortage is very efficient. However the implication of weather factors suggests that they may affect the availability of food to such an extent (while the sampled abundance remains constant) that limitations on growth are imposed. It may be noted for example that the incidence of rainfall (Duration) in the sample period for broods of 2 was higher than in any other period. It is probably no coincidence that rainfall is rated of greatest importance by the $(B)^2$ weightings for those broods. It is

not considered that rainfall, wind or daylength can have a direct effect on nestling growth, but act by disturbing the availability of food.

In summary therefore evidence from the first broods suggests that when nestling growth is dependent on the provision of food by only two adults, variation in growth with respect to the mean rate for that brood size is principally a function of food availability. However it is evident that contributions may be made by other factors not taken into account in this analysis, which are reduced in certain brood sizes, as demonstrated when the broods were examined individually. For example r^2 for second brood of one, was 99% leaving only 1% residual variance.

The accuracy of the aerial insect sampling is therefore, validated to a large extent for the first broods and the influence of extraneous factors on production rates in House Martins can therefore be effectively disregarded. The second broods are evidently extensively influenced by weather which probably disturbs the availability of food. The demonstrable importance of each of these weather factors apparently depends on their chance incidence in the sample period.

SECTION 7

The factors influencing nestling quality

Any nestling may be influenced by both prehatching and posthatching factors. In some species, for example the Partridge (P. perdix) (Southwood and Cross, 1967) posthatching factors appear to be a dominant influence on mortality of the chicks while in others prehatching factors predominate as for example in the Red Grouse (L. lagopus scoticus) studied by Jenkins et al (1963). Prehatching factors primarily affect the absolute and relative (within the brood) quality of nestlings at hatching but may also affect subsequent quality, where this quality is estimated in terms of wet weight and primary length at chosen intervals. It is necessary to examine if prehatching factors can influence posthatching performance and whether such affects persist or whether they are swamped by the effects of the posthatching factors. The analysis firstly involved isolating the influences on egg quality (namely egg weight) and secondly examining the correlation between egg weight and chick quality at hatching. Thirdly the influences on nestling development suggested further potential causes of variation in nestling quality and selected variables were examined in a multiple regression analysis to

extract the most important influences on nestling quality.

THE FACTORS INFLUENCING EGG QUALITY

House Martin eggs from the 1969 breeding season were weighed within 24 hours of laying. It is necessary to standardise the weighing time because the weight declines throughout incubation due to the evaporation of water (Smith, 1930; Romanoff and Romanoff, 1943). This decline represents on average 8.2% of the initial egg weight with a mean loss of 0.145 gms over the 14 day incubation period in the House Martin. The egg weight was used as an index of egg quality and the implications of this are examined below.

The weight of the eggs of the domestic fowl have been shown to be influenced by hereditary factors and age and experience of the laying adult (Clark, 1940; Hadley and Caldwell, 1920). These factors were not examined in the House Martin but are probably of similar importance. Also the size of the laying adult is known to influence egg size in the fowl (Robertson, 1931) but because of the paucity of data on the weight of the adult House Martins at laying, no analysis was possible. Potential difficulties arise because of the subjective choice of time of weighing of the adults

which varies considerably at this time (Petersen, 1955) as demonstrated in the Sand Martin (R. riparia). Also because of the unknown contribution of the male and female birds to variation in egg weight (Waters, 1945 and Olson and Knox, 1940) However this does furnish the possibility that some of the seasonal variation in egg weight (see below) is a function of the the seasonal variation in the size of the laying birds, where this may or may not be influenced by proximate environmental factors. However for the present time this point is disregarded. Egg weight will also be influenced by adult nutrition, environment and season (Tangl, 1939; Hendricks, 1934; Romanoff and Romanoff, 1949); these aspects will be discussed here as sufficient data was collected to make useful generalisations. The House Martin egg weights were examined in relation to the eventual clutch size of which they were a part. No significant correlation was established for either first or second broods. (Respectively $r = -0.21$ N.S and $r = 0.13$ N.S). Similarly when the sequence of laying within a clutch was examined in relation to egg weight no significant correlation was apparent. ($r = -0.21(1st/4)$; $r = -0.22(2nd/3)$). Also when each egg weight was examined in relation to the time of laying (where this is the number of days from the

first egg laid in the breeding seasons of 1968 and 1969) a significant positive correlation was apparent for the first but not the second broods. ($r=0.26$ $p<0.05$ /1st. ($n=68$) ; ($r=0.31$ $p=N.S$ /2nd ($n=18$)). This contrasts with Perrins' findings for the Great Tit where he noted a seasonal decline in egg weight.

The egg weights were then examined in relation to the environmental conditions under which they developed. An important aspect of the environment at least during the development time of the first broods, is variation in food abundance (see later section). Therefore, if production rates in nestling birds can be affected by food shortage, and given the necessity of laying one egg each day, (for reasons discussed in section 8), can the Martin lay down sufficient reserves in all eggs for the adequate development of the embryo? There are two possible mechanisms. Either that egg weight might behave as a linear function of food abundance or that if the food abundance falls below a critical level the weight of the egg will be affected, but will remain unaffected above this critical level. The egg weights were therefore examined in relation to the mean food abundance in the five days preceding hatching (the probable development period see section 8.). A similar period was suggested by Perrins for the Great Tit.

No significant correlation was found. Correlation was also attempted for a single (presumed critical) day for each egg both two and three days before hatching. Again no correlation was found. The twenty lightest eggs were then contrasted with the twenty heaviest eggs to see if there was a significant difference in the mean level of food abundance during their respective development periods. There was no indication of significantly lower food abundances preceding the lightest eggs in these groups, and nor in smaller groups of down to 5 eggs. It can therefore be concluded that nutrition of the adults during laying does not affect the weight of the eggs under development. However, it is possible that egg quality may be affected in other ways as demonstrated in the fowl (Romanoff & Romanoff, 1949). A shortage of fat in the diet results in more saturated fatty acids in the egg than normal (Russel, Taylor & Walker, 1941). The implications of this regarding chick weight at hatching is not known.

Bennett and Warren (1933) describe how in the domestic fowl, egg weight declines when temperature rises above a critical level of 21°C . However an analysis similar to the above but with temperature instead of food abundance as the independent variable did not suggest a similar process in the House Martin.

It is instructive to determine which of the components of the egg contributed most significantly to variation in fresh egg weight. A sample of 13 eggs was collected and analysed for dry egg shell weight, water content, lipid content, and protein content. All the eggs collected were the first laid in each clutch and were taken within 24 hours of laying. Ideally the key contributant to variation in egg weight could have been isolated by multivariate analysis. However many of the constituents were intercorrelated, therefore partially invalidating the results. Thus the most significant correlate of egg weight was sought. The results are presented in Table 7.1. Both water content and protein content are correlated because unit weights of protein are naturally associated with constant units of water. They in turn are both significantly correlated with total fresh egg weight. It is therefore evident that the variation in total water and protein content of the eggs is the immediate cause of variation in fresh egg weight. It would be of interest to determine if the relative abundance of egg constituents is affected by variations in the food supply. The problem might be of particular interest in the House Martin because of the apparently restricted availability

Table 7.1

The Relationship between Fresh Egg Weights and the constituent fractions.

	r	N	Sig.
Lipid Free Dry Weight (Protein)	0.702	9	p = 0.05
Lipid content	0.385	9	N.S.
Shell weight	0.000	7	N.S.
Water content	0.998	7	p = 0.001

of calcium in its food for shell formation, though it is possible that it mobilises calcium associated with the skeleton (Deobald, Lease, Hart & Halpin, 1936).

THE RELATIONSHIP BETWEEN EGG QUALITY AND NESTLING QUALITY AT HATCHING.

The question arises therefore, does the weight of the egg affect the nestling at hatching or do the principal determinants of nestling quality occur entirely during the nestling period? If the physical nature of the egg is reflected in the young produced then the effect is possible. It has been shown in the domestic fowl by Morris et al (1968) that chick body weight at 12 weeks was strongly related to fresh egg weight, though the influence declined with age. Other factors that could contribute to variation in nestling hatching weight are also examined.

Hatching is usually synchronous and it is therefore impractical to determine which egg produces which nestling in the natural state. The mean weight per egg of 14 clutches and the mean weight per chick at the first sample visit after hatching are presented in Fig 7.1. The first weighing was therefore never more than 24 hours after hatching. In the

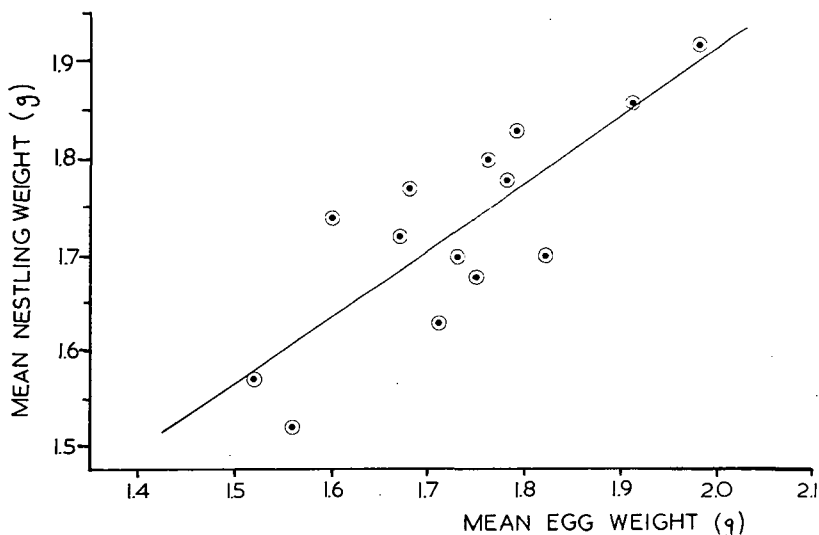


FIG. 7.1. The mean weight of each nestling on the first day after hatching (i.e. < 24 hours after hatching) in relation to the mean weight for each egg laying, of the clutch from which they hatched.

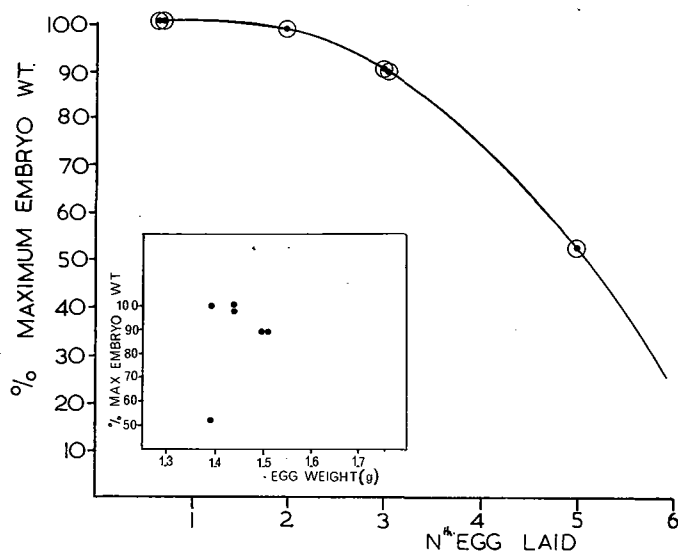


FIG. 7.2. The relative embryo weights after 12 days incubation (where this is 12 days after the laying of the final egg) in relation to their order of laying.

knowledge that the heaviest eggs have the highest protein and water content it is not unexpected that the heavier clutches produce the heaviest nestlings. It would appear to follow therefore that the heaviest eggs produce the heaviest chicks within each clutch. Ghany et al (1966) demonstrated a highly significant correlation between egg weights of Quail (C. corturnix) and the weight of the corresponding chicks at hatching. The correlation decays with time and is not significant two weeks after hatching. ($b = 0.70$, $r = 0.81$) In order to examine this latter point, eggs were taken from two clutches of known history shortly before hatching (on the 12th day of incubation). Only six eggs were collected but this was sufficient to clarify the point at hand. It was found that rather than the heaviest egg within a clutch producing the heaviest nestling, the sequence of laying determined the order of size. The first laid eggs contained the larger embryo, which if all the eggs hatched synchronously would be reflected in the nestling weight at hatching. The relationship between embryo weight at day 12 (/^{using} Moreau's (1946) definition of incubation period), expressed as a percentage of the heaviest embryo in each brood, and laying sequence is

shown in Fig 7.2. The coincidence of the points for the 1st and 3rd laid eggs supports the generality of the relationships. In summary therefore, it appears that the broad area of nestling weight at hatching is determined by the weight of the egg at laying, but that the relative weight of the chick within the brood at hatching is determined by the sequence of laying (where hatching is synchronous). Egg weight was not related to relative embryo weight within a clutch on the 12th day ($r = 0.27$ N.S). This state of advanced development of certain eggs in the brood is probably the result of incidental incubation during laying when the adults are roosting in the nest at night. In all cases examined the order of hatching was the same as the order of laying. Therefore the competitive ability of the young within the brood (assuming this is related to size) is apparently established at conception and during the laying down of yolk. To examine this, nestling weight at hatching were compared with various indices of growth performance for each chick, such as wing length and weight at different ages. The results within a single brood size (1st broods of four) indicated that the nestling weight at the first day of hatching (where hatching refers to the hatching of individual eggs rather than to the hatching of the

whole brood though usually this is one and the same) was not correlated with the weight on any other day (including day 2) nor with the wing length on days 15, 20 or 25. In contrast however the nestling weight on day 3 was correlated at the 5% level ($r = 0.45$) with the wing length at day 25, but not with the relative size of the wing length within the brood (expressed as a percentage of the largest in each brood) nor with the absolute weight after the sixth day. So it appears that within broods of 4 the weight at hatching is uncorrelated with nestling performance in absolute or relative terms ($r = 0.09$ for weight at hatching and order of wing lengths at day 25) but by the 3rd day (but not the second) that nestling's performance affected the wing length at day 25 but not the relative size within the brood at the same age. However it was found that the relative size at hatching (i.e. the order of hatching) was significantly correlated with the absolute weights on the second and third nestling days but thereafter with no other indices of growth performance ($r = 0.57$ - 1st and 2nd days weights; $r = 0.50$ - 1st and 3rd days weights). Hence in broods of four order of hatching rather than weight at hatching affects nestling weight on the 3rd nestling day and in turn this/is shown to be correlated with one index of growth; wing

length at day 25, but not with weight on day 12 or 25. Perrins (1965) demonstrated that the weight of Great Tit (Parus major) nestlings on the 15th day is a close correlate of survival potential. Hence although the order of hatching can affect the winglength on day 25 the influence must be minimal as there is no direct correlation between order of hatching (and relative hence/weight on the first day) and wing length ($r = 0.16$) or relative wing lengths within the brood ($r = 0.22$). The influence on survival potential is therefore not known. If order of hatching could be correlated with weight at a chosen age, and assuming the validity of the application of Perrins studies on the Great Tit to the House Martin, it would be possible to establish an influence on survival potential in this way. It has already been demonstrated that this did not occur within the first broods of four, but examination of other broods might provide information to contrast with or support the findings for broods of 4. Difficulties in interpretation arise because of the influence of brood size itself on nestling growth. Nevertheless the evidence is presented as suggestive rather than confirmatory data. Here the order of hatching is highly correlated with the absolute weight at the third day $r = 0.86$ ($p = <0.01$) and this in

turn is again significantly correlated with winglength at day 25 ($r = 0.42$ $p = 0.01$). However no correlation was found with either the relative wing lengths within the brood or with the weight at day 25. There was a correlation with the weight at day 12, $r = 0.63$ ($p = <0.01$) which indicates a possible influence of order of hatching on survival potential. This contrasts with the results for broods of four alone, and presumably acts by influencing the competitive ability of the nestlings in the 1st 3 days of growth, which thereafter maintain their superiority in brood competition and hence growth performance though not beyond the 25th day.

In summary therefore broad differences in the quality of nestlings at hatching are apparent, which are primarily a function of their sequence of laying within the clutch. The absolute weight of the nestling at hatching was not shown to affect any index of nestling quality that related to survival potential, though when all broods were examined together the order of hatching and thus the relative size of any nestling in relation to other members of the brood was shown to influence indices of growth performance that probably were related to their survival potential (my own results on fledging weight^s & the associated / post fledging mortality are inadequate but are presented in

section 10. There are however no direct and highly significant correlations between quality at hatching and quality of the nestling at either day 12, 20 or 25 and therefore their influence must be minimal.

THE INFLUENCES ON NESTLING QUALITY DURING DEVELOPMENT

If therefore inherent differences are not important it is probable that environmental differences are. Where this includes the immediate nest environment (i.e. brood size) and the external environment (i.e. food abundance). All first broods from 1969 were examined together and it was found that the most significant correlate of weight differences at the 25th nestling day were accounted for by variation in total food abundance over the 15th to 25th nestling day ($r = 0.62$ $p = <.001$). A multiple regression analysis was then carried out to ascertain the relative influence of a. the nestling weight 3 days after hatching, b. the sequence of hatching, c. brood size and d. insect abundance, all of which have been demonstrated in isolation to contribute to variation in nestling weight, at some stage of the growth cycle. The results are presented in table 7.2. The relative importance of the factors is given by the (B wts)². It illustrates the dominant role

Table 7.2

Multiple Regression Analysis to assess the factors influencing both nestling weight and wing length on the 25th nestling day.

(a) Factors influencing nestling weight on day 25.

	r	β Wt.	$(\beta \text{ Wt})^2$	B Wt.
Weight on third nestling day	-0.02	-0.44	0.19	-1.35
Hatching order	-0.08	-0.28	0.08	-0.52
Brood Size	-0.38*	-0.27	0.07	-0.63
Insect Abundance	0.62**	0.55	0.31	5.02

Variance Ratio $F = 8.46$ ($p = 0.001$)

Partial Correlation Coefficient $r^2 = 48\%$

Intercept Constant = 13.4

(b) Factors influencing wing length on day 25.

	r	β Wt.	$(\beta \text{ Wt})^2$	B Wt.
Weight on third nestling day	0.41**	-0.13	0.02	-0.98
Hatching Order	-0.50**	-0.46	0.21	-2.07
Brood Size	-0.51**	-0.28	0.08	-1.59
Insect Abundance	0.45**	0.32	0.10	6.93

Variance Ratio $F = 7.9$ ($p = 0.001$)

Partial Correlation Coefficient $r^2 = 46\%$

Intercept Constant = 83.5

N.B. Significance $p = 0.05^*$
 $p = 0.01^{**}$
 $p = 0.001^{***}$

of insect abundance, but ranks the weight on the third nestling day in the second order of importance. This is itself highly correlated with the hatching order $r = 0.86$ and so it is surprising that this is not reflected to a greater extent in the B Weighting for the hatching order. However it is of importance with respect to wing length growth. It is ranked as the most important influence on wing length at day 25, followed by variation in insect abundance. It is interesting to note the subsidiary role played by brood size in its affects on nestling quality. However although it is ranked low on the B Weighting, it is the only independent variable examined which is significantly correlated with regard to both weight and wing length ($r = -0.36$ $p < 0.05$; $r = -0.51$, $p < 0.01$) apart from insect abundance. It may be noted that the total variance explained in both analyses was very similar, 48% in the former and 46% in the latter. It can therefore be concluded that the nestling's environment exerts a similar influence on both these aspects of growth and that much of the difference in the quality of nestlings as demonstrated by the indices used can be accounted for by variation in food abundance. This difference in quality was presumed to reflect directly on survival probability. Identical

analyses were run, including temperature as an independent variable. It was found in both cases that it was ranked at the bottom of the (B Wts)² and it was therefore excluded from the final analysis. It did demonstrate however the apparently insignificant direct effect of external temperature changes on enclosed nidicolous young.

The importance of these results is that they strongly contrast with those obtained by Parsons (1970) in his study of the Herring Gull (Larus argentatus). He established the dominant effect of egg size on chick weight at hatching which was subsequently highly implicated in chick mortality. He proposed that this was due to a shortage of yolk in the lighter chicks which hence had less reserve food. In the Herring Gull, mortality of the young is concentrated in the first week after hatching and is therefore ultimately attributable to the quality of the chick at hatching ($p = <.001$), though is proximately precipitated by exposure. However in the House Martin (a nidicolous as opposed to a nidifugous species) such mortality soon after hatching has been ^Psuppressed by the nature of parental care. Mortality, or the reduced survival probability of this study, is then primarily induced by environmental factors acting on the nestlings well after hatching, and usually after

fledging. This subordinates the influence of prehatching factors which are of such great importance in the Herring Gull and other nidifugous species in the natural state. (Jenkins et al 1963; Silvonen, 1957).

SECTION 8

THE TIMING OF THE BREEDING SEASON.

It is well known that the size of an animal population is partly dependent on the abundance of the resources on which it depends. Usually conditioning processes set a general level, about which populations fluctuate under the influence of density dependent and density independent factors (Richards & Southwood, 1968). Many animal populations utilise seasonal changes in the abundance or availability of resources and increase the standing crop by growth and/or reproduction. This is the case in many birds where the total population biomass in any one area bears some relation to the total biomass of available food. This has been shown by Johnson (1967) for the Purple Martin (Progne subis), and is strongly suggested by Gibbs' (1950) data for the Great Tit (Parus major) and Blue Tit (Parus caeruleus), when it is combined with the knowledge that Tit populations are at a minimum immediately prior to the breeding season at the time when food abundance is probably also at a minimum (Perrins, 1970). The same basic principle has been discussed by Lack (1954), Gibb (1950) and Perrins (1970), where they express the view that in many species the young are in the nest when food is most abundant.

The increase in the total population then (i.e. standing crop of avian population including nestlings) coincides with an increase in the total biomass of utilisable food (standing crop of food resources). This is graphically illustrated by Gibbs' (1950) data for the Tits in relation to the abundance of Lepidopteran larvae on which they feed the young, where a peak in the number of nests containing young coincides with the peak abundance of larvae. With a precise knowledge of both food abundance throughout the breeding season and of the standing crop of the Martin population, the timing of the breeding season in relation to the abundance of food was investigated in the House Martin over the breeding seasons of 1968 and 1969.

There are in practice two distinct approaches to the problem where either the biomass of the population within nests (i.e. the young) is investigated, or the biomass of the whole population is considered. Firstly the biomass of eggs and nestlings in each month within the nest was examined in relation to the abundance of food. Both parameters were expressed in terms of the mean daily total energy value (Kcals) for each month of the breeding season (May to September). It can be seen in fig.8.1. that the maximum energy content of

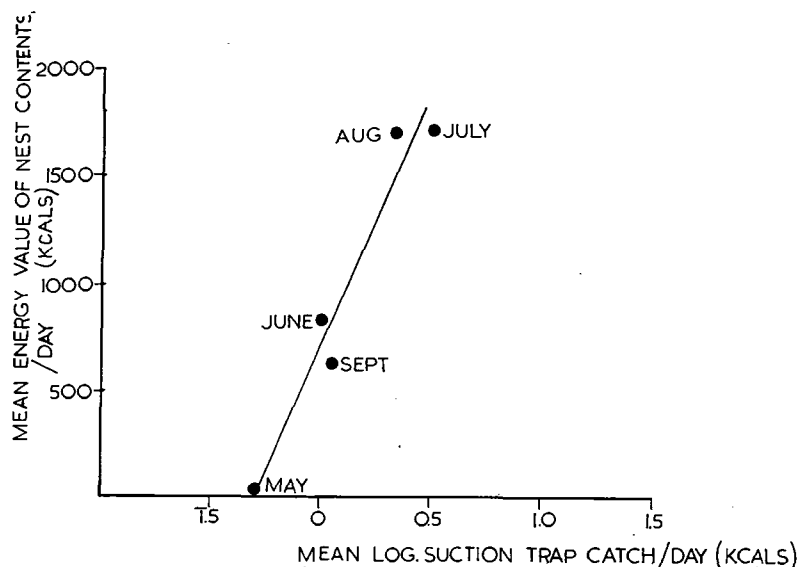


FIG. 8.1. Mean monthly standing crop of nestlings and eggs throughout the breeding seasons of 1968 and 1969 in relation to aerial insect abundance.

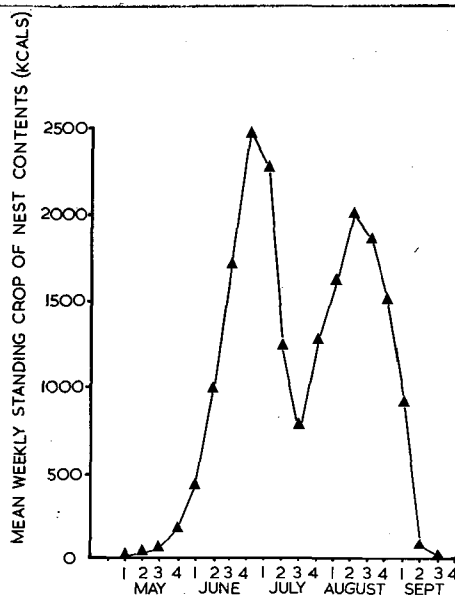


FIG. 8.2. Mean weekly standing crop of nestlings and eggs throughout the breeding seasons of 1968 and 1969. The 1968 data is from the kennels colony, while the 1969 data also includes the Sunninghill Park colony.

reproductive material occurs in July and August when the abundance of food is also at a maximum. Also the lowest nest population energy content is in May when food is also at a minimum. It appears therefore that the bulk of the House Martin population is timing its reproductive effort so that the young are in the nest when food for rearing them is most abundant and in this respect it resembles the single brooded species of Gibb (1950) as discussed by Lack (1952). However this method of monthly analysis obscures some of the detail of the life cycle. The whole breeding cycle is therefore illustrated in fig.8.2.in terms of the weekly means in the same units as above. There is an obvious period of under utilization of resources in mid season between broods, when this figure is viewed in conjunction with the scatter diagrams of daily catches which demonstrate that food abundance remains relatively constant throughout this period (See section .4. on food and food selection). This underutilization is obviously an integral part of the breeding biology though it may incidentally serve an accessory function, because the first brood young are able to feed in the proximity of the colony without the competition for food that may occur if young were being reared in the nest at the same time. It seems probable

that many of the first brood young, not involved in feeding the second broods leave the colony at the time when many of the second broods are in the nest in late August. However I have little quantitative data on this topic. Whether this exodus is caused by increased competition for food is not known. In conclusion therefore this data broadly supports Lack's (1952) contention that birds' breeding seasons are so timed that the young are in the nest when food is most abundant and this time is therefore the best time for breeding i.e. breeding success is likely to be highest. However there is an anomaly in such a situation, where the majority of birds apparently attempt to rear their young when food is most abundant. Because in nearly all species studied critically (Klomp, 1970), except the Herring Gull (Larus argentatus) Harris (1969), there is a greater survival potential for the earliest fledging young, and these "early" young are in the nest before the peak in food abundance is reached. Also these broods are larger, which should theoretically be an additional reason to suppose that rearing should take place at the time of maximum food abundance (Perrins, 1966). It therefore seems that the coincidence of biomass peaks is not necessarily demonstrating that the birds are breeding at the best time.

It seems probable that the earlier breeders are breeding at the best time because of their better survival, and these broods are in fact fledging when food is most abundant. Why then do not more pairs breed early enough for a similar enhancement of the survival of their young. Perrins (1970) has suggested that there is indeed strong selection in many species to breed as early as possible, but food shortage prevents the adults from collecting sufficient food for the process of egg formation and hence prevents them breeding earlier than they do. Then the rapid build up of the breeding season food supply is such that it is impossible for all pairs to so time the rearing of their young that the most critical phase of nesting coincides with the maximum food abundance except possibly for the very earliest breeders. I investigated the initiation and distribution of egg laying in the House Martin in relation to the food supply in an attempt to examine Perrins' proposal.

The Timing of the First Clutch.

An investigation of the factors limiting the earliness of the laying date of the first clutch ideally involves both a knowledge of the energy requirements of the female while

forming eggs and of the levels of food abundance at which this energy can be obtained. Then by reference to the observed abundance of aerial insects through the spring, the extreme limits of the laying period could be predicted. However no sufficiently precise information is available for the energy requirements of wild active passerine birds and this approach is therefore not possible at this stage. In fact the energy requirements specifically for laying in the domestic fowl are only imprecisely estimated at 40% in excess of the basal requirements (Perek & Sulman, 1945), though of course the total food requirements at this time are well known (Brody, 1945). However the differences in biology between the Martin and the Fowl make any direct comparison in this context impossible.

I therefore formulated an alternative approach based on observations of nestling growth in relation to food abundance. The basic assumption was made that a unit of energy content of egg material was laid down within the female, with the same efficiency as a unit of energy content of nestlings during the period of maximum growth rate, providing the abundance of aerial insects was the same in both situations.

In other words a brood increment of 1 gm, expressed in terms of the calorific value of that increment, is equivalent to the same calorific increment of an egg under the same food conditions, and can be laid down by the breeding birds with similar conversion efficiencies and similar adult maintenance requirements. The product of this assumption is an attempt to predict the pattern of egg laying from observations on the growth of nestlings by assuming that nestling weight increases are equivalent (with the appropriate adjustments) to egg material increments.

It must first be pointed out that nestling increments will vary with nestling age and brood size, because it is known that the absolute and relative contributions of daily food intake to growth and maintenance varies with surface/volume characteristics which are themselves a function of age and brood size. Theoretically the maximum amount of food that can be collected is that which encourages the maximum rate of growth in the largest brood sizes. However it is possible that all individuals may not be capable of the same feeding performance as those rearing broods of five. Therefore rather than deriving a relationship between nestling increments in relation to food abundance for the largest broods, ^{energy} values were derived

for the most frequent brood size (1st broods of 4) because this would be more representative of the whole population, while the slope of the regression relating growth to food abundance was derived on the basis of all first brood sizes. For this regression a highly significant correlation was obtained ($r = 0.73$ $p = <.001$) ($b = 44.29$ $a = -2.53$). The regression was notable in that a reduction of food abundance by 50% (on a log. scale) resulted in a corresponding reduction in growth of 51.2%. So effectively, a halving of the (log.) abundance of food reduced potential growth by 50%. On the basis of this regression the growth indices were converted to their weight equivalents (and thence their calorific equivalents) for broods of four. The data for the calorific equivalents for the wet weight of nestlings and eggs were those given by Pinowski (1967) in Petruszewicz (1967).

It is evident that the growth of 1st brood nestlings depends on feeding by both adults, whereas egg formation is largely by the female, though the female is fed to a certain extent by the male in "courtship feeding" and the value of this may be important as in the Great Tit (Royama, 1966). However because the extent of this habit in the House Martin

is not known it had to be excluded from the calculations.

It must also be noted that for nestling growth, food must be delivered to the brood for assimilation, and the energy cost to the adult for this process must exceed that for egg formation where the food has merely to be collected and assimilated. Possibly the energy cost of actually ~~formulating~~ the egg might compensate to a certain extent for the energy cost of collecting and delivering food to the nest, because as mentioned above the energy requirements of a laying hen are 40% greater than that of a non-moulting bird's basal requirements.

It would be possible to formulate a much more complex predictive model, indeed this was done, but I felt that the necessary assumptions made, invalidated the additional predictive power. The principal virtue of the present method is its simplicity, and it did provide a figure, that was preferable to an arbitrarily evaluated one, that allowed a prediction of the laying opportunities to be made.

The relationship between growth of all broods and food abundance is shown in fig.8.3. The mean calorific increments that such growth is equivalent to for broods of four is shown

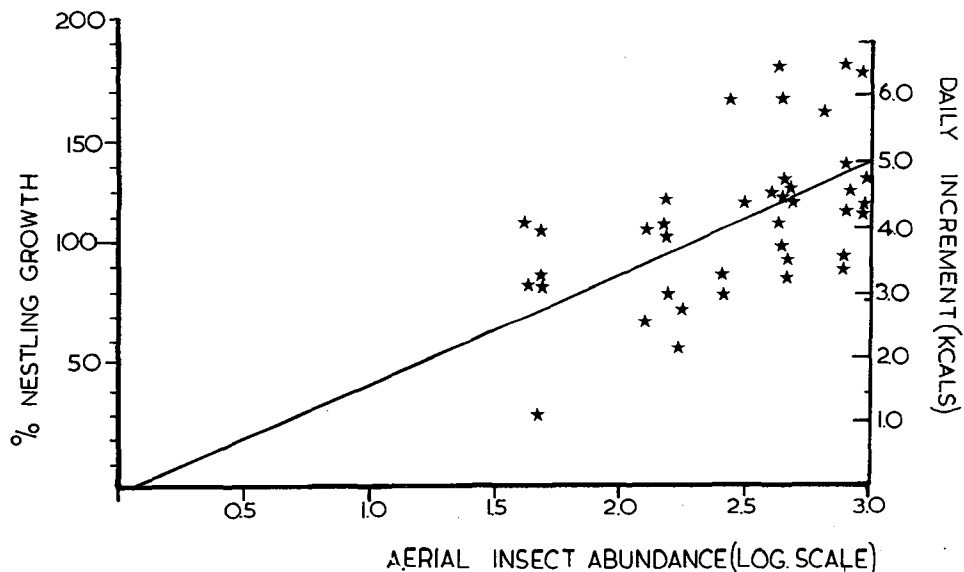


FIG. 8.3. The relationship between observed nestling growth (expressed as a percentage of the expected growth), and aerial insect abundance. See text for details of the method.

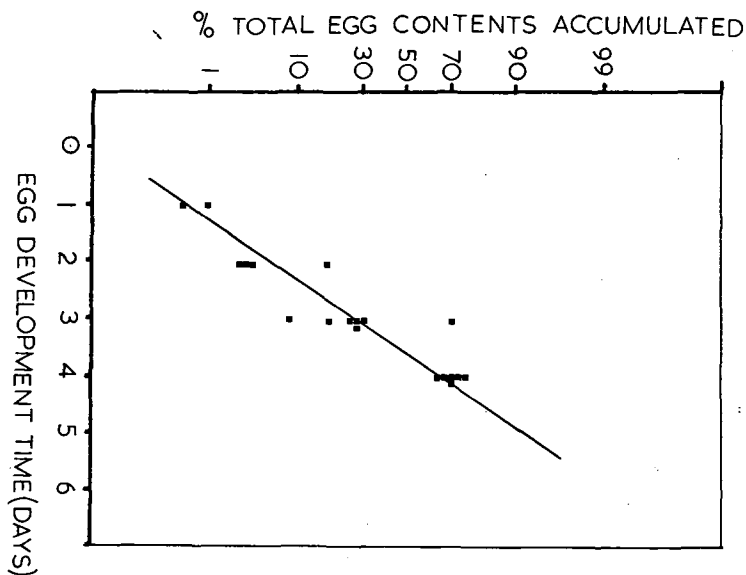


FIG. 8.4. The development of the contents of a single egg in the Sand Martin, Riparia riparia. The derivation of the values is described in the text and utilises the data presented by Petersen (1955).

on the right hand axis. The growth values were derived as follows. The observed weight increment of each brood on each day was expressed as a percentage of the expected increment for nestlings of that age in broods of that size. This expected increment was derived from a smoothed curve for each brood size estimated from data from the breeding seasons of 1968 and 1969. This smooth curve was obtained by plotting the daily brood weight values, expressed as a percentage of the asymptote, on probability paper. The method is described in section 6 and 9. On the basis of the regression illustrated in fig 8.3 the potential calorific increments for the laying down of yolk can be estimated from a knowledge of the food situation before and during the observed laying period.

However before the final analysis it remains to examine the mechanism of yolk deposition in the knowledge that the response of the laying bird to adequate food being available could never be instantaneous, and also that laying must occur on consecutive days to ensure synchrony of hatching. The time interval between the initiation of ova development and the laying of the egg must also be estimated. The deposition of yolk is spread over a period of several days and in the

domestic fowl the increase in the size of the ova begins 10 days before ovulation (Jull, 1952) while von Haartman (1956) suggests that the process of egg formation takes 5 days in the Pied Flycatcher (Ficedula hypoleuca) 4 days for ova maturation and one day in the oviduct for each egg . The Great Tit (Kluijver, 1951) takes one day less than the Pied Flycatcher. Petersen (1955) examined the ovaries of breeding Sand Martins (R. riparia) and deduced that ova maturation took four days. The egg then passed down the oviduct over the next day and appeared in the nest on the sixth day. The same situation was assumed to pertain for the House Martin.

Petersen (1955) also observed the sizes of the developing ova and from these I was able to calculate the relative rate of maturation of the ova over each day of the 4 day development period. Petersen expressed ova size in terms of the diameter, and I converted these values to volumes (on the assumption that they were ^hspherical) and plotted on probability paper ^aovulum volumes ($\equiv$ weight), as a function of the maximum ova size, for each of the (fig.8.4) development days. I estimated the development time over a five day period, because the principle^a interest was the rate of deposition of nutrients, and these are added to a certain extent in the albumen which is deposited

in the oviduct on the fifth day. It was found that a straight line (actually slightly skewed) was generated indicating at least an approximation to a sigmoid rate of deposition, being most rapid on the mid day of development, the third day (fig8.4).

Then on the assumption that deposition of yolk for each egg was described by a regular sigmoid curve the total yolk deposited each day for concurrently developing eggs could be calculated. It seems reasonable that they develop at similar rates, but one day apart, because they are laid at this interval. The methodology for this calculation is shown in fig. 8.5

Over the 5 day period, within, the female, the egg is presumed to increase from 0.01% to 99.99% of its final volume. The calorific value of each unit volume of increment is presumed constant. Therefore by cumulation of the values of the increments on each day, the total energy value of the whole clutch increment on each day can be calculated. The total calorific value of whole eggs was presumed constant, and was calculated on the basis of the mean egg weight and data in Petruszewicz (1967) [Wet egg weight (mean) - 1.722g(my data) Calorific value of wet egg - 1.02 Kcals/gm.] Therefore total calorific value of 1 egg is 1.77 kcals . It was found that

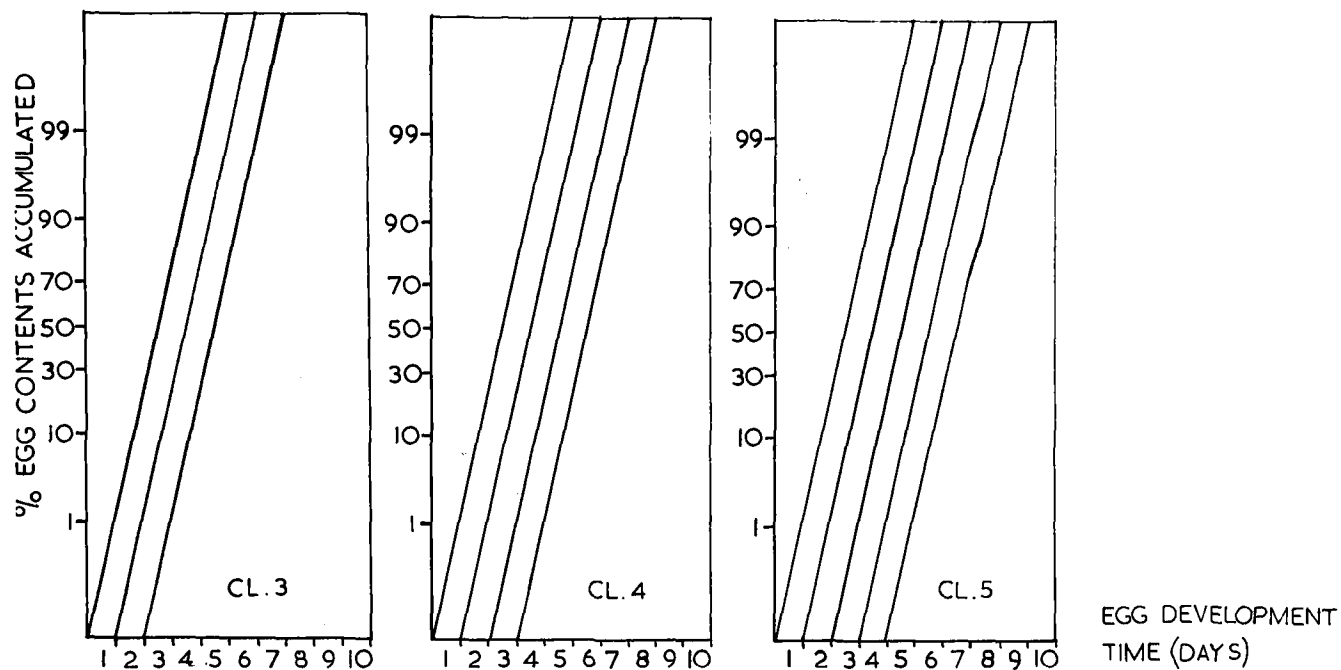


FIG. 8.5. The development of the egg contents of whole clutches in three commonly occurring first clutch sizes.

irrespective of clutch size the total energy value of the increment on any one day never exceeded the energy value of one egg for clutches of 2 to 5. Calculations based on an egg development period of 5 days suggested that for a 5 egg clutch a maximum of 1.77 kcals would be laid down on the 5th day after developmental initiation of the first egg. The same held for a developing clutch of 4, though here only 98.7% of the total calorific value of one egg is required on the day of maximum total requirements, which is 1.75 kcals.

By direct comparison with nestling increments (see Fig 8.3.) where Increment (Expressed as a percentage of mean increment in known food conditions) = $-2.53 + 44.29x$ where x is the logarithm of the Insect Catch for the day concerned), the expected increment for an observed level of food abundance can be calculated. These egg increments of 1.77 Kcals and 1.75 Kcals require an abundance of food of 1.10 (Log. Catch) and 1.098 (Log Catch) respectively. For example:-

$$\frac{1.77}{3.81} = -2.53 + 44.29x \quad \text{and} \quad \frac{1.75}{3.81} = -2.53 + 44.29x$$

$$\therefore x = 1.10 (\log. \text{Catch}) \quad \therefore x = 1.098 (\text{Log. Catch})$$

where increment of 100% of expected = 3.81 Kcals.

Effectively the same figure. With clutches of 3 the value for maximum daily requirements is slightly reduced to 97.4% of the calorific value of one egg i.e. $\frac{97.4}{3}$ % of the calorific value of the whole clutch of 3(= 1.77 x 3), which is 1.72 Kcals. This is available to the feeding female at an insect abundance (catch) of 1.08 (Log. Catch). It can be seen that for all the 1st clutch sizes normally encountered, an abundance of insects in excess of 1.08 (Log. Catch) is essential if the maximum energy requirements during egg formation, are going to be satisfied. I believe that it is essential that such an abundance of food should be available before laying is initiated for the following reasons. It can be seen from fig.8.5. that the duration of the period of high energy requirements varies with clutch size, and is in fact equal to the number of eggs in the clutch, being five days for a five egg clutch and so on. During this period food abundance must be in excess of at least log 0.86 (i.e. an increment of 1.77 x 78/100 Kcals can be cumulated when food abundance is equal to or in excess of Log Catch 0.86, see fig 8.3) for these requirements to be satisfied.

It is therefore evident that if egg development is to proceed normally, levels of food abundance such as these must be available. If food shortage occurs for example just before

or during the laying of the first few eggs, development of those eggs will be affected and possibly either low quality eggs will be laid or there will be a suspension of laying (see below) until sufficient food has been accumulated. Or if food is sufficiently short during incubation, the eggs will be left unattended and they become chilled. As evidence of this, in 1969 when regular checks were made on the eggs to determine if they were being incubated or not, it was found that in the period of this investigation, May 15th to June 15th, the only days on which more than one clutch was chilled was June 4th and 5th. The abundance of aphids on these days were respectively: Catch = 4, (Log Catch = 0.60), and 3, (0.48) while total/insect abundance was 0.80 and 1.6 respectively, both very low figures; though of course the latter figure does in fact exceed the calculated critical level (=1.03) On no other days during the period, where clutches were also checked, did nearly such a low level of food occur. Evidence of a reduction in quality is not forthcoming, though it must be emphasised that the situation is complex and awaits a more searching analysis. There is evidence however that in extreme food shortages laying may be suspended for some days during the laying of a clutch. Of 5 clutches in 1969 (1st brood) where laying was suspended for a day or more, all had a period

of extreme food shortage during laying, on or immediately prior to the suspension of laying. The information is tabulated below. (Table 8.1.)

Table 8.1. Suspension of egg laying in relation to aerial food abundance.

No	Date when expected egg did not appear (x)	nth egg in clutch suspended	Clutch size (eventual)	Insect Abundance (see key below) (I)							
				1	a	2	b	3	c	4	d
1	May 20th	3	5	3.46	2.5	3.06	2.15	<u>1.04</u>	<u>0.3</u>	1.68	1.0
2	May 27th	2	4	2.60	1.87	<u>1.75</u>	<u>0.84</u>	2.96	2.24	3.02	2.51
3	May 29th	4	4	2.54	2.02	2.92	2.17	2.60	1.87	<u>1.75</u>	<u>0.84</u>
4	~~June~~ 4th	2	3	<u>1.04</u>	<u>0.6</u>	1.89	1.41	2.90	2.39	2.76	2.16
5	June 4th	2	4	<u>1.04</u>	<u>0.6</u>	1.84	1.41	2.40	2.39	<u>2.76</u>	2.16

Column 1 = Log. I on day (x)

Column 2 = Log. I on day (x-1)

Column 3 = Log. I on day (x-2)

Column 4 = Log. I on day (x-3)

Column a = Log. Aphids on day (x)

Column b = Log. Aphids on day (x-1)

Column c = Log. Aphids on day (x-2)

Column d = Log. Aphids on day (x-3)

N.B. The hypothesised critical days are underlined.

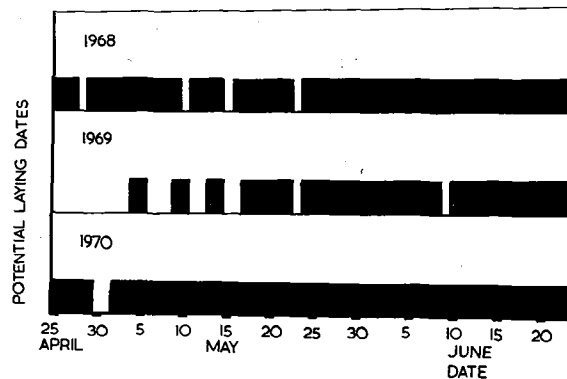
It can be seen that depending on which egg is suspended so the critical day appears to be successively earlier before the laying

of that egg. It is therefore either the same day or one day before for the 2nd egg, two days for the 3rd egg and three days for the fourth egg. The fate of the products of these eggs is of interest. Egg No. 1 and No. 4 were normal while 3 produced a / ^{nestling} which fledged considerably under the mean fledging weight, though this may be associated with being the last egg to hatch rather than the character of the egg. Egg 2 was the second lightest egg recorded in the study (1.49 gms) ^{nestling from} Egg. 5. survived, but the / last egg to hatch died of starvation through brood competition because it hatched later than the rest of the brood. Its poor competitive ability was probably aggravated by the much earlier hatching and hence comparatively larger size of the first nestlings. There is some evidence therefore, albeit tentative at this stage, that extreme food shortage may precipitate suspension of laying, which may have a deleterious effect on the survival potential of the young hatching from the eggs or clutch concerned. However this evidence requires further examination. There is also an indication in this data that a higher level of food abundance than estimated is necessary for the satisfactory formation of eggs by certain females (Egg 2.- May 27th; Egg 3-May 29th. Table 8.1)

On the basis of the predictive model outlined above, the

dates when laying could theoretically begin is demonstrated in fig 8.6. It can be seen that laying was potentially possible in April in 1968 and 1970. And from this it can be concluded that food was sufficiently abundant for egg laying to take place considerably before it actually did in these two years (Fig. 8.8) However examination of the total food abundance data (Fig 8. reveals that if breeding had begun at or during these predicted times, periods of extreme food shortage would have been encountered. I suggest that any eggs laid at this time would have become chilled, due to the consequent lack of brooding, or laying would have been suspended with the adverse consequences associated with extreme non synchrony of hatching. In no year did the total daily catch fall below Log 1.0 after May 10th, and this figure was only approached on 5 occasions in 1968 - 1970. Therefore it seems reasonable to propose that House Martin breeding is not initiated immediately sufficient food is available, but rather that a proximate factor such as daylength inhibits breeding before about May 10th because of the high probability of harsh food conditions before this time. For breeding to begin at this time food must be sufficiently abundant to satisfy the dietary requirements for egg formation.

FIG. 8.6. The hypothetical pattern and limits of first clutch egg laying. The solid areas indicate those days that the first egg of a clutch of any size may appear. The open areas refer to



those days that it is predicted that laying will not be initiated. Refer to the text for methodology.

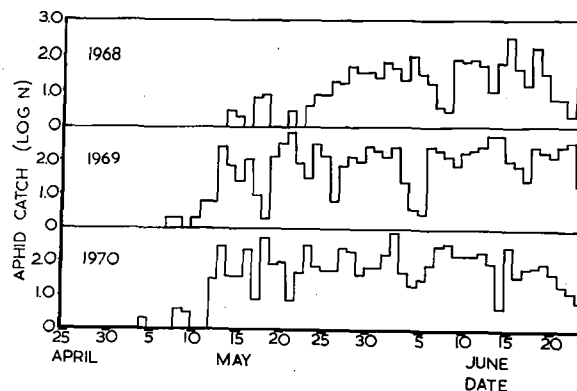
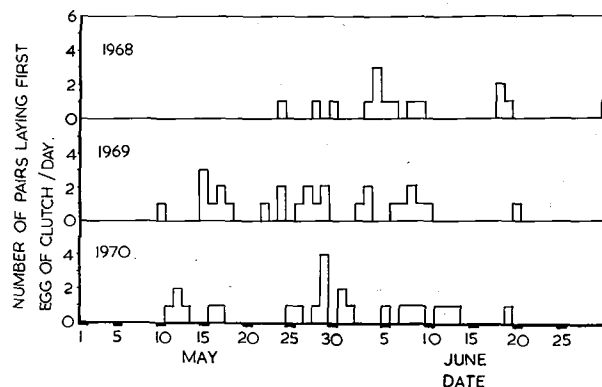


FIG. 8.7. The aerial abundance of Aphids in the early part of the breeding season in 1968 to 1970.



Mean Laying Dates

June 8th

May 28th

May 27th

FIG. 8.8. The observed distribution of the laying of the first egg in each clutch at both the study colonies in 1968 to 1970 during May and June.

However laying does not usually begin until Aphids become available. Examination of fig. 8.7 in conjunction with fig 8.8. illustrates this (See Fig 10. also) . . . The former illustrates the aerial aphid abundance (log catch) and the latter the observed distribution of laying of the first egg association in each clutch. This may be because aphids form a dependable and accessible food supply once they appear in the aeroplankton. . . Indeed from the study of food and food selection it is known that the principal source of food to the Martins at this time is Aphids, and it is likely that they are the principal food source for the formulation of eggs. Aphids constitute 50.4% of the total energy value of the food ingested in May, and undoubtedly constitute a proportionally greater amount in the latter half of the month, because the above value is expressed as a percentage of the whole month's food and aphids are not available early in the month. [N.B. The mean date of laying in each year is shown on fig. 8.8., and is approximately a constant cumulative sum of aphids (Log catch i^{th} day + log catch $i+1$ + $i+2$.. $i+n$) from the onset of their appearance each year. (See Table 8.2)

Table 8.2. Mean laying date and cumulative Aphid catches. (Sum of catches from date of first egg to the mean laying date)

Year	Cumulative Log. Aphid Catch
1968	25.80
1969	32.20
1970	35.52

The deviance of the 1968 data may be due to the fact that 80% of the layings occurred in June when aphids only form 13.6% of the energy ingested] . In the light of this association between aerial aphid abundance and the onset of breeding it becomes of interest to compare the predictive data for egg laying with the observed pattern of laying. It is apparent that the observed onset of laying coincides with the predicted possibly onset providing that aphids or/another component of the aerial fauna with a similar temporal distribution and abundance are available. The only exception to this is the first laid clutch of 1969, which must have started development before aphids appeared in the suction trap. However it appears that the relatively high level of total insect abundance on the 5th May (see fig 8.9) was sufficient stimulus to initiate yolk development. Also, it may be that a local occurrence of insects was encountered by the Martin, that was not monitored by the suction apparatus. The predicted distribution of laying

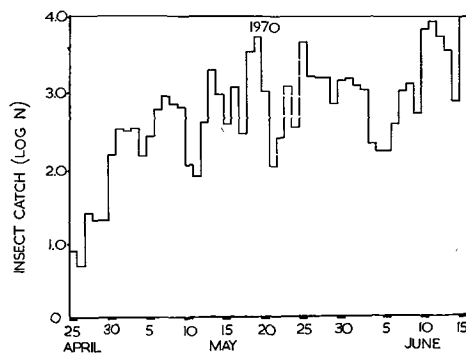
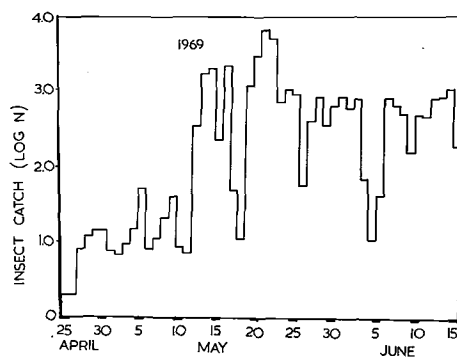
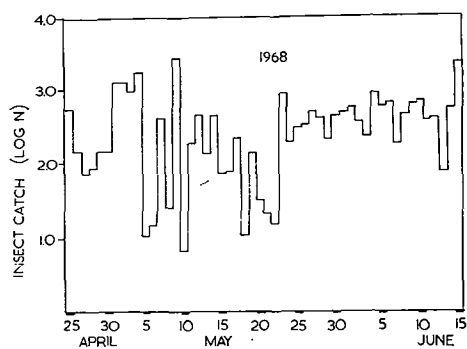


FIG. 8.9. Total aerial insect abundance in the early part of the breeding season in 1968 (a), 1969 (b) and 1970 (c).

is also largely in agreement with the observed situation. The exceptions again are of interest and all occur in 1969 (Cross Hatched= Exceptions) (see Fig.8.10). The clutch of which the first egg was laid on the 16th May was deserted after 3 eggs had been laid, presumably because the eggs had chilled or were inadequate in some other way. Relaying began successfully in the same nest on the 24th May, after ejection of the first clutch. Similarly one of the clutches laid on the 15th May was also deserted after two eggs had been laid. The other two clutches were successful but may have in fact been laid on the 14th May as no check was made on that day, and laying was maybe then suspended over the 15th, the second egg being laid on the 16th. However there is no evidence for this suspension of laying and all the young fledged successfully. These two clutches were however the mean lightest recorded in 1969 and contained the lightest individual egg 1.41 gms (Lightest clutch - 1.55 gms mean/egg) of the whole study.

In summary therefore a knowledge of the ability of the female House Martin to exploit the aerial insect food supply from observations of the developing young, enabled a crude prediction of the pattern and onset of egg laying to be made.

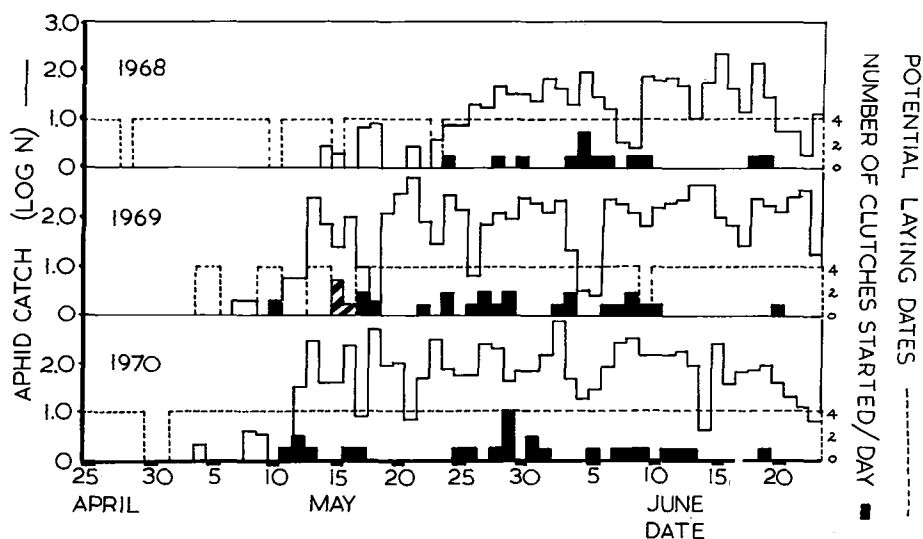


FIG. 8.10. Total aerial insect abundance, aphid abundance and the distribution of laying of the first egg in each clutch during May and June (1968 to 1970).

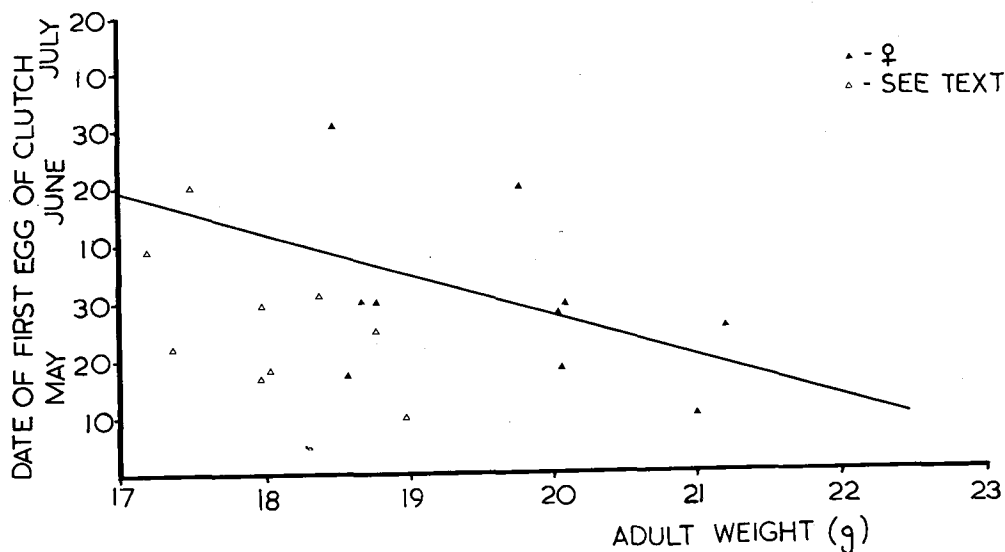


FIG. 8.11. The body weight of adult House Martins in relation to the date of laying of the first egg of the clutch with which each was associated.

This prediction was however of little value except for 1969. A closer examination of the actual components of the aerial food supply exploited by the Martins, in effect, implied that the suction trap was not sampling precisely that food exploited by the Martins at this time. It appeared that Aphids or other taxa and conditions closely associated with the appearance of aphids in the suction trap are a key to the initiation of breeding, such that their appearance in the air was either associated with or directly disposed some members of the population to start laying.

It is interesting that the clutch size in each year was closely correlated with aphid abundance, and it is suggested elsewhere (section 5.) that this has the adaptive function of /
of facilitating adjustment/ the clutch size to the most profitable clutch size for the prevailing conditions. Possibly therefore this provides a reason for delaying laying, so that an accurate "prediction" can be made of conditions in June and the clutch size adjusted accordingly.

In general therefore the timing of the start of laying seems closely associated with the points outlined above. There remains the question of the distribution of laying over the succeeding weeks. This apparently involves the jeopardisation

of reproductive potential by some members of the population, because of the seasonal decline in clutch size and a consequent reduction in the number of young reared. I propose that this decline is partly due to a difference in the efficiency by which different sized females can collect sufficient food to form eggs mainly because differences in body size endow the aerial feeding birds with marginally different flight characteristics (see section 11.). This results in slightly different optimal prey sizes for each size of bird. There is some evidence that the body size of early breeding House Martins is larger than the late breeders (fig.8.11) though the differences are not significant. This confers a higher economic cruising speed on the larger Martins which enables them to collect more food per unit time, or on average larger items (approaching the niche occupied by the Swallow) . The mean size of prey available declines throughout May and June (table 8.3) and this observation provides a foundation for this theory. The question then arises, why does not a larger Martin evolve? There is an increase in total energy requirements which will be disadvantageous when food is short. This could be particularly important outside the breeding season when the mortality is greatest, probably as a result of food

Table 8.3.

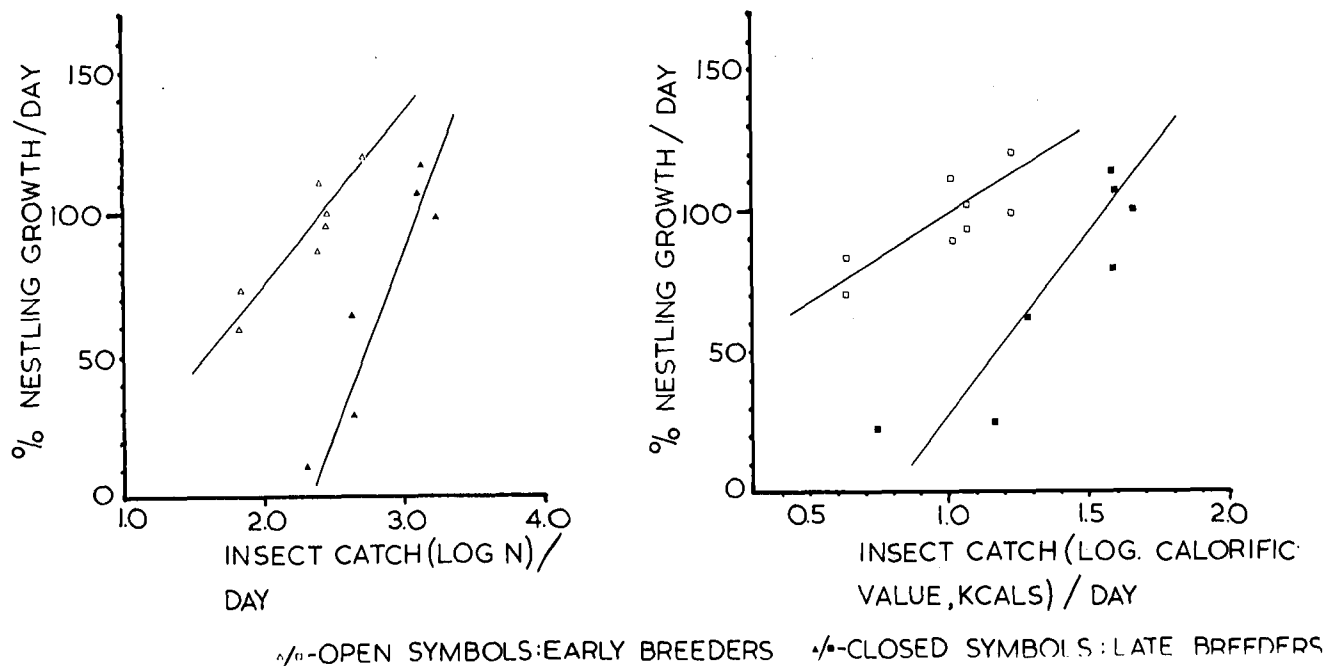
The mean energy values of items in the aeroplankton in
May and June. (1968 and 1969 data)

<u>Month</u>	Mean energy values of individual insects
May	3.42×10^{-3} Kcals/item.
June	3.13×10^{-3} Kcals/item.

shortage. Two balanced selective forces will then pertain in the population, One tending to enhance reproductive potential and the other minimising mortality due to food shortage.

While emphasising that the evidence for the following is also very slender and requires further study, it is possible that this difference in feeding efficiencies is reflected in the nestling growth rates. Four broods of 4 nestlings from 1969 were examined. Growth rate figures for the mid period of nestling growth were derived and plotted in relation to the concurrent food abundance. It was found (fig.8.12) that the early breeding birds were able to achieve a growth form equal to the mean growth of all broods of 4 at a much lower level of food abundance than the late breeders. This is not due to a change in the quality of the food available at the two times because the same relationships are revealed when growth is plotted against the calorific value of the catch on the appropriate day (though the correlation is less close). There are therefore grounds for believing that individual birds do differ in their abilities to harvest food and this may account for the observed distribution in laying times. Also it could possibly account for observed differences in clutch size in

FIG. 8.12: Nestling growth (expressed as a percentage of the expected growth) in relation to aerial insect abundance, in two broods reared early in the season and two broods reared at the end of the first brood laying period. Aerial insect abundance is expressed both (a) numerically (log. scale) and (b) in terms of the energy value of the catch (log. calorific value).



different individuals. The smaller individuals are better adapted to exploit smaller prey and lay appropriately smaller clutches. They may survive better at another season, so balancing mortalities and hence the representation of the different morphs within the population. Other explanations are available to explain why laying is dispersed over a period of several weeks. Late laying may reduce adult mortality or egg failure and may influence nestling survival after fledging, though little data is available to examine these possibilities. In the long term therefore reproduction rates may be maximised, albeit if in certain years it is at the expense laying the largest possible clutch.

To sum up therefore, the evidence suggests that breeding is ~~not~~ occurring as early as possible, with absolute limits imposed by food shortage. However there is evidence that breeding occurs at the earliest time at which food availability is stable enough to give eggs a reasonable chance of survival and probably results in the young of the earliest breeders developing during the most favourable period. This hypothesis is summarised graphically in fig. 8.13.

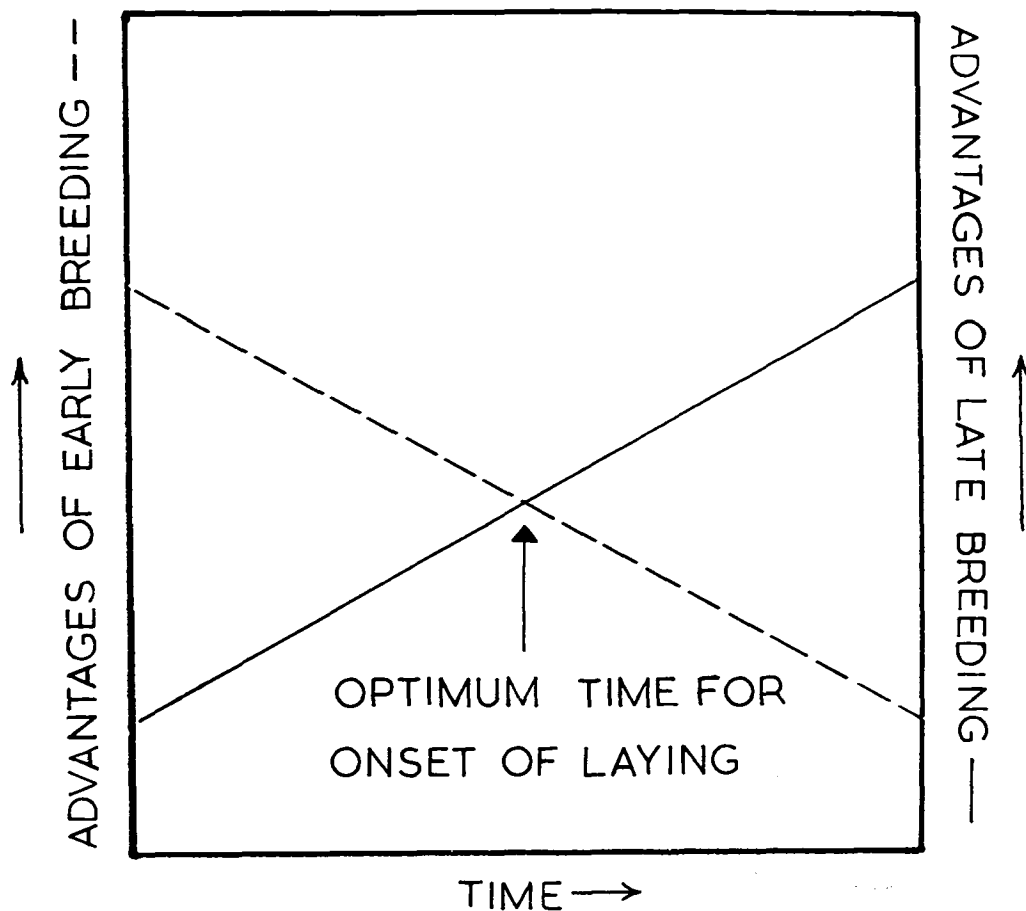


FIG. 8.13. A schematic model to describe the optimum time for the onset of laying, for individuals within a population of House Martins. The model illustrates two conflicting components, where the intersect indicates the optimum time for the onset of laying.

SECTION 8

THE DETERMINATION OF CLUTCH SIZE

Introduction

In section 5. I discussed the proximate influence of food abundance on the yearly variation in clutch size. This involved an annual modification of the first clutch size apparently as a direct response to the current food situation, which was itself correlated with the food abundance one month later when the nestling energy requirements were at a maximum. The adaptive significance of this modification was therefore clear. However in addition to this annual modification, the clutch size of most bird populations lies within well defined limits, and remains within this range in successive years. I therefore discuss in this section the evolutionary processes that might have acted to determine the relative frequency of the observed clutch sizes in the House Martin. These are the ultimate factors determining clutch size.

Lack (1947-48, 1950, 1964, 1966) has discussed the subject and concluded that the most frequent clutch size has become established by natural selection, because it on average produces the largest number of surviving offspring. Clutches smaller than the most frequent, are selected against because

the birds laying such clutches will contribute successively less to succeeding generations. While in clutches larger than the most frequent the mortality is such that the number of young surviving to breed is less than that produced by the most frequent clutch size. The observed variation in clutch size remains because the variability of the environment is such that in some years clutches of other than the most frequent size are favoured. Lack supports his theory principally by reference to studies of nidicolous species for example the Swift (Apus apus) (Lack, 1956, 64) and the Titmice (Parus sp.) (Lack et al, 1957) and a number of long term studies (Lack, 1966).

On the basis of these studies Lack proposed that because the parents had a finite capacity to deliver food to the young, the nestlings in the larger broods suffered from food shortage and subsequent starvation to a relatively greater extent than those in the most frequent brood size. As evidence of a reduced food supply per nestling in the larger broods Lack examined the feeding frequencies of different brood sizes and by implication the total food delivered to these broods. He found in the Swift (Lack, 1951) and the Robin (Lack and Silva, 1949), and drew on evidence from a wide variety of sources

(Gibb 1950, 1955) . . . to demonstrate that larger broods received less feeds per nestling than smaller broods. Lack supposed that this indicated that the larger broods were less well nourished than the smaller broods. However Royama (1966) suggested on the basis of his work on the Great Tit (P. major) that the food requirements per nestling in larger broods were anyway reduced, because of a reduced surface volume ratio and hence heat loss, which decreases the maintenance costs of individual nestlings in larger broods. It was evident therefore that the data on feeding frequencies were not themselves proof of relative food shortage in larger broods. It follows that while the hypothesis itself is not necessarily invalidated by such a demonstration, the process by which the observed clutch sizes are selected for, and mortality induced must be examined in the possibility that Lack's evidence of food shortage was not causal. There is an abundance of evidence that does not agree with Lack (Wynne Edwards 1964) and it therefore becomes a possibility that in many species Lack's hypothesis is not applicable. However the annual modification of clutch size in the House Martin in direct response to food abundance is strongly suggestive of a direct relationship between food abundance and the ability to rear

broods of certain sizes. In order to investigate the problem in the House Martin the critical question of nestling energy requirements in relation to brood size was examined. Also feeding frequency in relation to brood size was investigated. The significance of the findings will be discussed below after the examination of the relevant topics in isolation.

I. METABOLISM OF NESTLING HOUSE MARTINS

The heat production of nestling House Martins, and by implication the food requirements of those nestlings, was investigated by the following method. Nestlings of known characteristics were confined in a compensating respirometer as illustrated in Fig. 9.1. The rate of oxygen consumption in each situation was recorded and using the methodology of indirect calorimetry, the heat production of different brood sizes and different aged nestlings was examined. The runs were carried out at two different temperatures by placing the respirometer in a water bath at 15°C and 22°C. These temperatures correspond to the mean breeding season temperature and the mean daylight breeding season temperature respectively. However, the heat production of the nestlings probably influenced the internal respirometer temperature. This will be further discussed below. The nestlings were acclimated prior to examination for a 0.25 hr period in the respirometer during transit, and oxygen consumption monitored for a 0.50 hr period in the respirometer at the appropriate temperature. This period was demonstrated to be the optimal compromise between the need for the bird to be in a post absorptive state and the

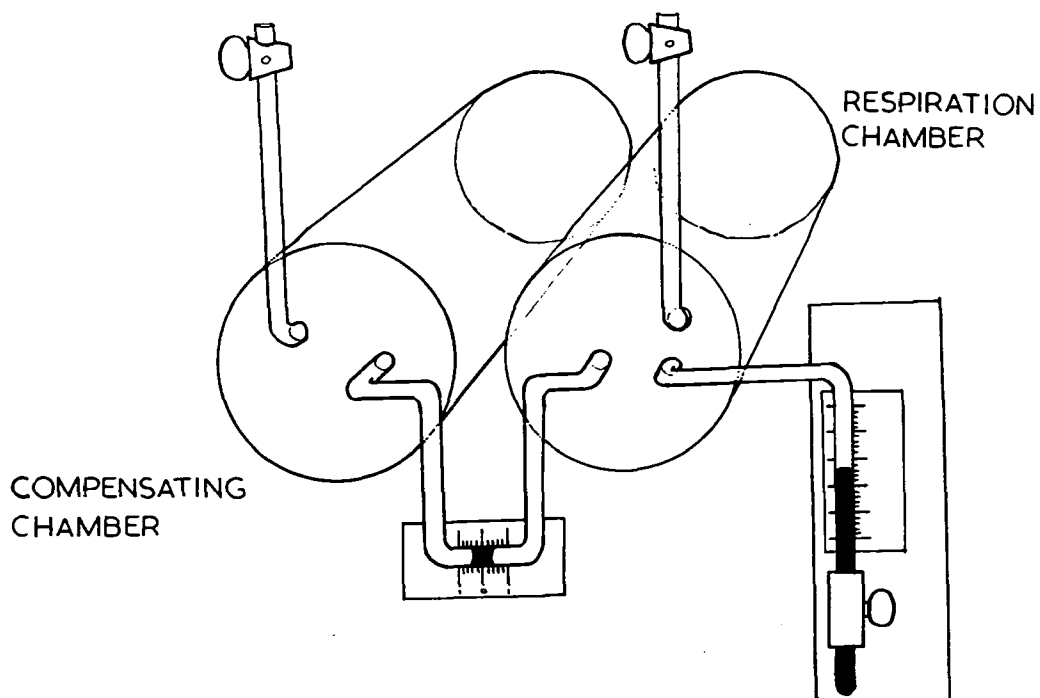


FIG. 9.1 The compensating respirometer used to measure oxygen consumption of nestling House Martins in relation to nestling weight and brood size. The apparatus was constructed from perspex and glass.

influence of stress due to starvation both of which would elevate the metabolic rate above the standard rate, the latter principally by intense begging. The nestlings were removed from the nest for study, at the same hour each day (18.00) to eliminate the potential influence of ^{diel} variation in rates. Therefore even if the results may be criticised on the absolute scale, they are satisfactory for comparative purposes. The whole experimental programme was conducted with the second broods in 1969 to reduce the influence of gross seasonal variation though this is unlikely to be important in nidicolous nestlings.

Results

Heat production as a function of nestling age at 15 and 22°C is presented primarily to indicate that the period of maximum heat production coincides approximately with the period of peak nestling weight and lies between the 10th and 18th nestling day in broods of one. The results for broods of 3 are inadequate for critical analysis. This is primarily of interest in relation to nestling mortality and is discussed in that section. (see Fig. 9.2 and 9.3).

The relationship between brood weight and heat production

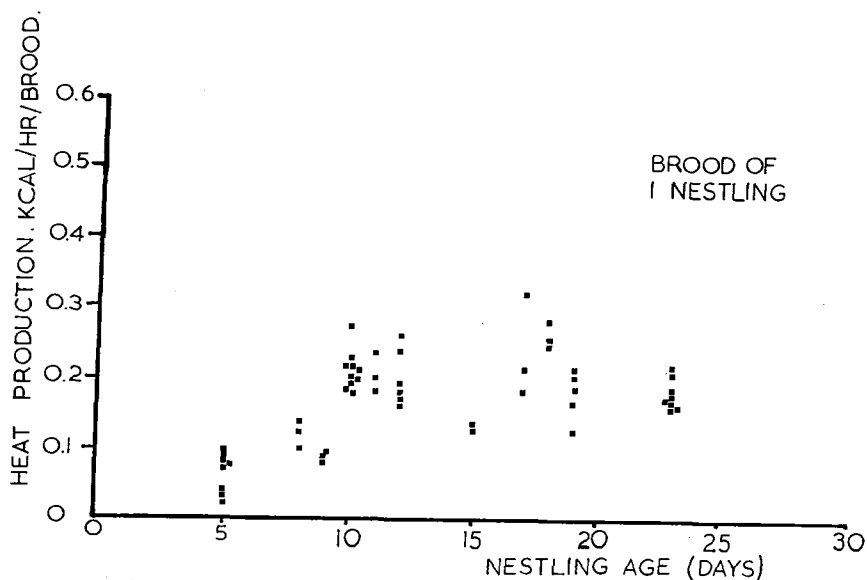


FIG. 9.2 The metabolic rates of single nestlings in relation to nestling age.

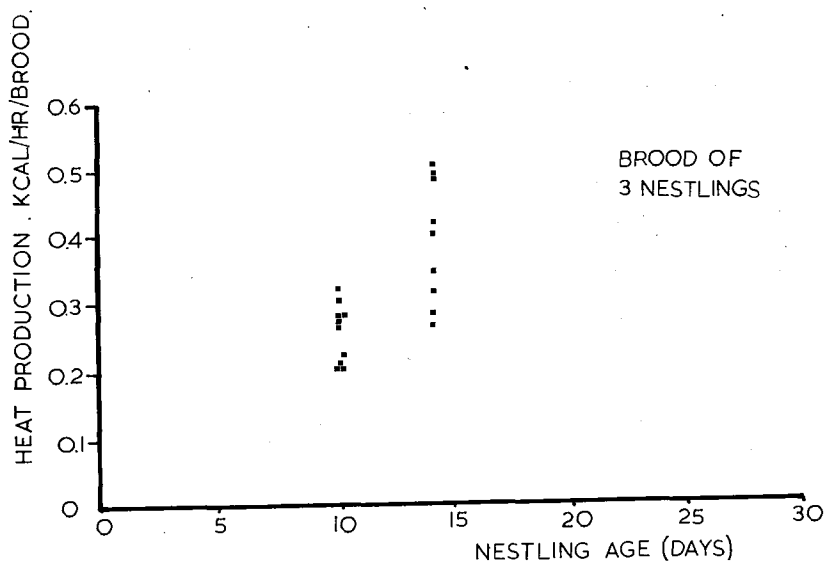


FIG. 9.3. The metabolic rate of broods of three nestlings in relation to age.

in different brood sizes is shown below at both 15°C and 22°C (Fig 9.4 a,b,c). The relationship can be described in terms of the power law $Y = aW_B^b$ where Y is the metabolic rate in terms of heat production, W_B is the brood weight in grams and a and b are descriptive coefficients. The value of b describes the percentage change in heat production with changes in weight. Examination of each brood size reveals generally a decrease in the b value as brood size increases. There is therefore a relatively greater increase in metabolic rate with weight increase in the smaller broods. As there was no significant difference in the slope of the regression at different temperatures the data from these two temperatures were combined and this increased the significance of the regressions. It is considered that this is legitimate, because the heat production of the nestlings during acclimation was such that the internal respirometer temperature was likely to be approximately equal at both temperatures, though this was not investigated directly. Both temperatures therefore probably lay in the thermoneutral zone, and both slightly higher than the water bath temperature. From this combined data comparative values for the heat production of each brood size was derived, and for each nestling within those broods. The calculated values for nestlings of 20 gms

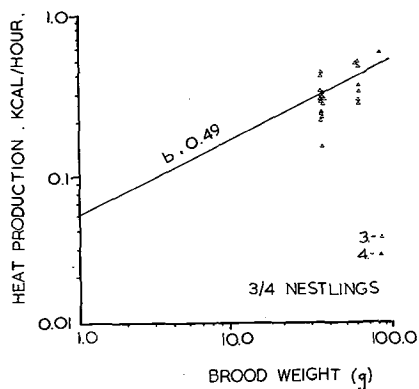
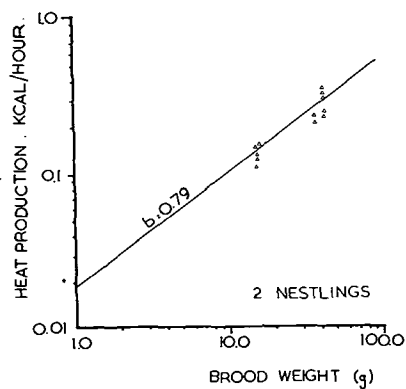
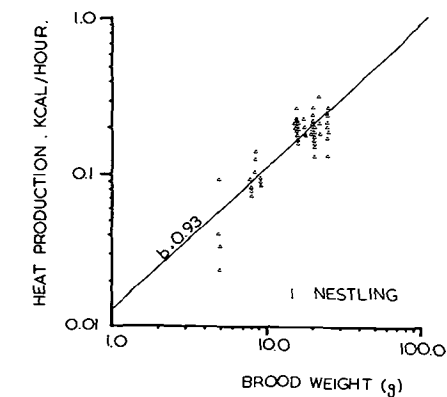


FIG. 9.4. The relationship between whole brood metabolism and brood weight for broods of one, two and three nestlings (a, b, c).

are shown in table 9.1. (The data for each temperature is also displayed). It can be seen that the increase in heat production in these broods is not absolutely related to brood size, as the heat production per nestling declines as brood size enlarges. In fact the total heat production is a direct function of brood size on a double log scale and can be described by the equation $Y = aW_B^b$. Where the symbols are as above except that W_B refers to the whole brood weight. The value of the exponent $b = 0.61$ approximates to the general value relating weight to surface area where $b = 0.66$. This indicates that the reduced heat production per nestling with increasing brood size is a function of the reduced surface/volume ratio in the larger broods. The relationship is illustrated in fig 9.5. On the basis of the empirical data for broods of 1 to 4 nestlings it is possible to predict the heat production for broods of 5, 6 and 7 from the derived values for 'B' and the power law $Y = aW_B^b$. This assumes that the reduction in surface volume ratio is constant with unit increases in brood size. This is apparently true of the nestlings in the respirometer, but may not be true of nestlings within an enclosed nest, where contact with the nest walls may reduce the exposed surface area in a similar way as contact with another

Table 9.1.

Heat Production of 20 gm nestlings in different brood sizes
(kcal/hour).

Brood Size	Brood Weight (gms)	Temperature	kcal/brood	kcal/nest ling
1	20	15°C	0.1853	0.1853
2	40	"	0.3315	0.1657
3	60	"	0.3060	0.1020
4	80	"	-	
1	20	22°C	0.2040	0.2040
2	40	"	0.2465	0.1224
3	60	"	0.4165	0.1445
4	80	"	0.5440	0.1360
Combined Results				
1	20	15°C & 22°C	0.2040	0.2040
2	40	"	0.3040	0.1520
3	60	"	0.3951	0.1320
4	80	"	0.4743	0.1185

Values for brood of 4 calculated from the combined results of broods of 3 and 4.

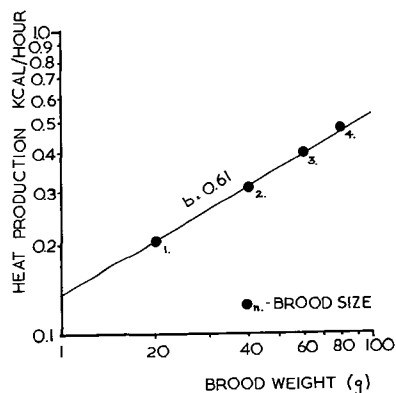


FIG. 9.5. The relationship between whole brood metabolism and brood weight where individual nestlings within each brood of one to four weigh 20 grams.

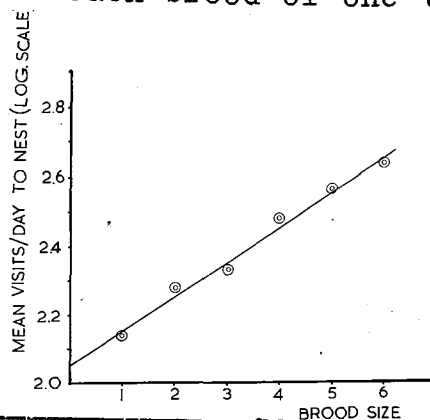


FIG. 9.6 The mean number of visits (presumed feeding visits) to the nest by adults each day (logarithmic scale) in relation to brood size (linear scale).

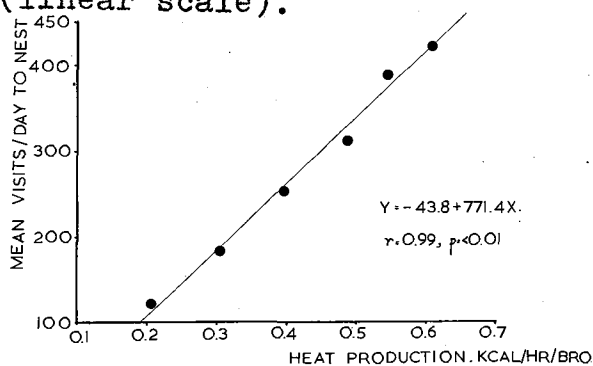


FIG. 9.7 The mean number of visits (presumed feeding visits) to the nest by adults each day for broods of one to six nestlings in relation to the energy requirements of those broods.

nestling. Also hyperthermia may develop in the larger broods which is unfavourable as they then increase their evaporative water loss in an attempt to eliminate this hyperthermia, and thus increase heat production and hence energy consumption. Mertens(1969) found in the Great Tit that such hyperthermia probably developes in broods of 12 to 13 or more nestlings, to a considerable degree, though the level of its development in the House Martin is not known. The estimations made below were unable to take these factors into account. The effects of brooding are discussed later.

In order to derive a value for heat production in broods larger than those examined experimentally, where each nestling weighed 20 gms, the values for broods of 1 to 4 nestlings were plotted and the data extrapolated so that heat production values for broods of 5 (100 gms) 6 (120 gms) and 7 (140 gms) could be derived. (Table 9.2) The calculated values for broods of up to seven young are shown in table 9.3. It then remains to examine these values for heat production in relation to the abundance of food delivered to the nest expressed in terms of the feeding frequencies. Discussion will therefore be postponed until after the section on feeding frequencies.

Table 9.2

Values of the exponent b in the broods examined at 15°C and 22°C .
in the equation $Y = aw^b$

15°C

Brood Size	b
1	0.899
2	0.949
3	0.119
4	-

22°C

1	0.886
2	0.442
3	0.464
4	-

15°C & 22°C

1	0.929
2	0.790
3/4	0.495

Table 9.3

Calculated values for heat production of broods of up to 7 nestlings.

Brood Size	Heat Production of whole brood	Heat Prod/Nestling
5	0.5400 kcal/hour	0.1080 kcal/hr
6	0.6050 " "	0.1008 " "
7	0.6630 " "	0.0947 " "

II. FEEDING RATES IN RELATION TO BROOD SIZE.

The rates of feeding of nestlings by adult House Martins ~~was~~^{are} estimated by means of an automatic recording device. The device operated continuously and simultaneously on six channels. It was therefore possible to examine the frequency of feeding in different brood sizes or variation within the same brood size under different environmental conditions. Royama (1966) has emphasised the potential influence of changes in abundance and quality of food on the feeding rates of birds delivering food to nestlings, and therefore standardisation in this respect is desirable.

The recording device operated on a photoelectric principle, the adult bird ideally breaking the beam on arriving at the nest but not doing so when leaving. A considerable amount of adjustment was required to achieve this optimal operation state, and in certain cases the photobeam was adjusted so that two records were recorded for each visit. In each case the apparatus was calibrated against visual observations. The total number of visits in each half hour period in each 24 hours was recorded photographically. The data obtained could therefore be used to examine periodicity of feeding activity, (where each visit was assumed to be a feeding visit)/^{and} the time of initiation

and cessation of feeding each day in relation to environmental parameters, though the data remains to be analysed in this respect. However for the present purpose the total daily frequency of feeding was the principal interest. Results were obtained from a total of 11 nests consisting of at least one representative of broods from 1 to 6 young, the brood of 6 being an artificially enlarged brood of 4. The results are presented in Table 9.4 and Fig 9.6. It can be seen that mean feeding rate increases as brood size increases. However the number of feeds per nestling is less in the larger broods, as has been demonstrated by Lind (1960). The relationship between feeding frequency^(y) and brood size^(x) is described by the equation

$$\text{Log } y = 2.06 + 0.099 \log x (r = 0.99 \quad p = < .01)$$

The relationship however is possibly not linear and will be further discussed below. However the principal aim of this investigation was to examine feeding frequencies in relation to energy requirements. Therefore to estimate the energy requirements of each brood, when these were approaching a maximum the heat production of different brood sizes composed of 20 gm nestlings was calculated as discussed in the previous section. For the feeding frequencies to be absolutely comparable they should be the frequencies associated with

TABLE 9.4

The Number of Visits to the Nest by Adult House Martins in Relation to Brood Size.

BROOD SIZE (1st or 2nd BROOD)	1 2nd	2 1st	2 2nd	2 2nd	2 2nd	3 2nd	3 2nd	4 1st	4 2nd	5 1st	6 1st
"n"th nestling day											
5				67							
6											325
7	177	292	91								257
8	175	243	38	91		461			412	170	216
9	178	379	89	110		451	173		396	414	291
10		365	106	96		247		523	266	391	286
11		252	94	73			422	354	300	244	
12				140		212	474	526		200	
13							380	315			242
14			329								443
15		330	254		65				216		463
16		330	115	190	88		251			421	547
17		331	130	120	273	126	187	187	298	473	560
18		270		152	117	127	212	396	280	386	
19	128			144	265	99	231	297	187	609	
20	120		50					228			
21	112										
22	85			164		94			212		
23				91	240	85		179			646
24		191		121	244	99	106	335			670
25		265		157	318	175		338			
Mean (all readings)	139	295	130	123	201	198	259	339	285	367	412
Mean Day 16 to Day 25	139	295	130	135	301	171	259	321	285	367	436
Standard Deviation (all readings)	37	60	91	37	96	137	125	116	78	140	163

(ommissions indicate no reading because of electrical failure, component failure etc.).

nestlings of such weights. However this means utilising frequency rates from one or two days and as these are known to be highly subject to environmental conditions, a mean feeding frequency rate was derived for the period from the 10th to the 20th nestling day and expressed as a mean rate per day. The values of these two parameters were then plotted as shown in Fig 9.7. It can be seen that the feeding rates obtained behave as a linear function of heat production and hence food requirements. There is therefore no evidence to suggest that the reduction in the number of feeds per bird in any way reflects an effective shortage of food in these broods, but rather is a direct reflection of the energy requirements of those particular brood sizes (with the reservation that the energy requirements of broods of 5 and 6 were calculated rather than actually observed).

III PRODUCTIVITY OF DIFFERENT BROOD SIZES IN RELATION TO THE FREQUENCY OF LAYING.

As there is no indication from the study of energy requirements and feeding frequencies, that the larger broods are undernourished, it is not surprising that my data for the House Martin does not indicate that the production of young up to the stage of fledging is at a maximum in the most frequent broods. It was found that only in the second broods of 1969 did the most productive clutch size correspond with the highest frequency of laying. In all other broods, and also when the data for the three years was combined, there was no correlation between frequency of laying and productivity. The data is presented in table 9.5 and fig 9.8. It can be seen from the figure that productivity per brood in natural broods was linearly related to brood size. This data does not apparently support Lack's hypothesis (see next section for details), though it is possible that the mortality occurred after fledging, and it might then have conformed with the hypothesis. However neither the fledging weights nor the asymptotic weights or the wing lengths prior to fledging indicate (following the proposal of Perrins, 1965) that the mortality will fall more heavily

TABLE 9.5

Survival of House Martin Nestlings in relation to brood size (where this is treated as equivalent to clutch size).

Grouped results for 1968 to 1970

Brood Size	% Frequency of Clutch Size	Young Fledging per brood (Mean)		No. nests	
		Natural Broods	Artificially Adjusted Brood		
1st Clutch	1	0.0	-	-	
	2	7.0	1.80	-	
	3	21.1	2.47	-	
	4	52.2	3.22	-	
	5	19.7	3.64	-	
	6	0.0	-	6.00	(2)
2nd Clutch	1	0.0	-	1.00	(2)
	2	12.3	1.86	-	
	3	73.7	2.52	-	
	4	14.0	3.37	-	
	5	0.0	-	5.00	(2)
	6	0.0	-	-	

Results for each year

	% Frequency of Clutch Size			Young Fledging/Brood.		
	1968	1969	1970	1968	1969	1970
1	0.0	0.0	0.0	0.0	0.0	0.0
2	26.7	0.0	9.4	1.75	0.00	2.0
3	20.0	15.4	25.0	1.67	2.25	2.87
4	46.7	57.7	46.9	2.57	3.40	3.33
5	6.7	26.9	27.3	4.00	3.57	3.67
6	0.0	0.0	0.0	0.0	0.0	0.0
1	0.0	0.0	0.0	0.0	0.0	0.0
2	13.3	20.0	4.5	1.50	2.0	2.00
3	66.7	70.0	81.8	2.20	2.64	2.61
4	20.0	10.0	13.6	4.00	2.0	3.67
5	0.0	0.0	0.0	0.0	0.0	0.00
6	0.0	0.0	0.0	0.0	0.0	0.00

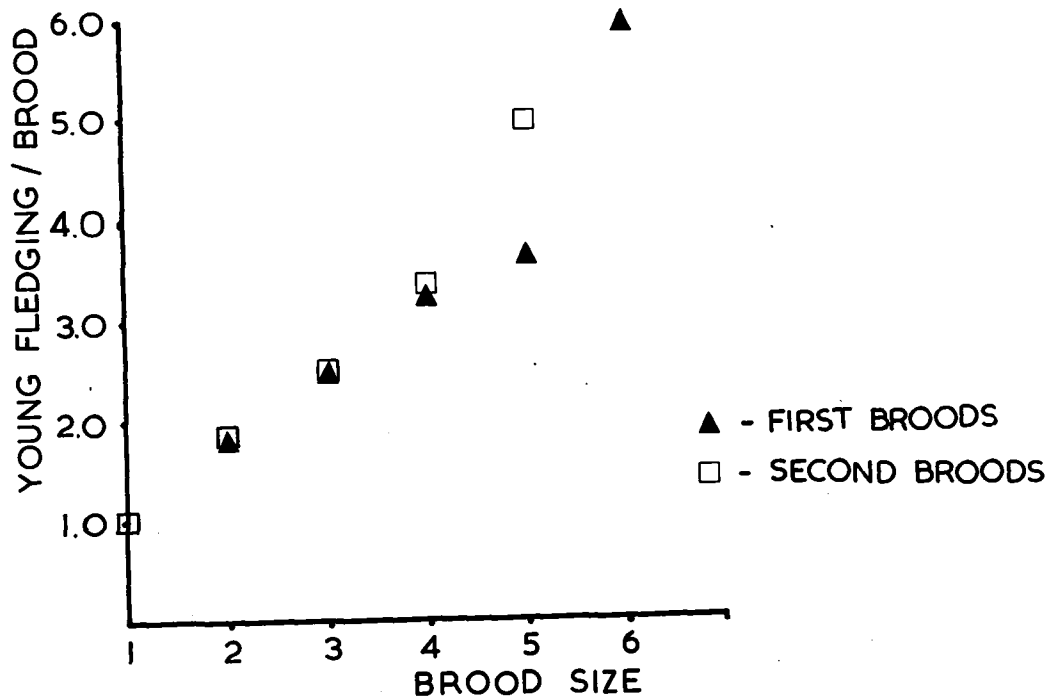


FIG. 9.8 The mean fledging success in relation to brood size for both first and second broods. The results refer to the period 1968 to 1970. The data for first broods of six nestlings and second broods of five nestlings were derived from small samples of artificially adjusted broods.

on the largest brood sizes. However this needs more critical analysis, because it is known that undernourishment in a brood is reflected in only a certain percentage of that brood, through the action of competition for food within the nest.

Therefore in the absence of positive evidence that clutch sizes are selected for by differential nestling survival within the nest, alternative explanations need to be found. The following section is an attempt to demonstrate that selective forces are probably acting to different extents on different brood sizes, which ultimately has led to the different frequencies of clutch sizes in the natural state.

IV DETERMINATION OF MEAN BROOD SIZE IN THE HOUSE MARTIN.

The factors determining brood size in birds have been extensively discussed by Lack (1947, 1954, 1966) and more recently by Klomp (1970) Royama (1969) and Haukioja (1970). They propose that the production of young is maximised within certain environmental limitations, principally that of food shortage, acting through the limited ability of adults to nourish their young. An alternative approach, that of Wynne Edwards (1962) proposes that the production of young may undergo imposed or voluntary restraints on behalf of some of the adult population to prevent overpopulation and the consequent depletion of resources. Brood sizes may therefore be less than the species concerned is capable of successfully rearing. On the initial premise that the genotype that produces the greatest number of offspring, which survive to breed, will prevail at the expense of less productive genotypes, Lack has suggested, with regard principally to nidicolous species, that it is the mortality acting on the nestlings within the nest and soon after fledging, in the largest broods that is the most important factor determining the differential survival of different genotypes.

Evidence for such food shortage in larger broods and its

consequent influence on nestling survival has been largely based on brood enlargement experiments and similar work. However it is possible that such experiments are essentially inconclusive for two reasons. Firstly, because the clutch size of any particular pair of birds is a product of both genotypic and phenotypic factors (Delius, 1968; Klomp, 1970; Håkioja, 1970) and, if a certain pairs clutch is adjusted this will possibly precipitate a mortality related to the difference from the original clutch size rather than to the adjusted size. (Wynne Wedwards 1964 discussed this). Secondly if mortality in the larger broods occurs after fledging it becomes difficult to estimate and further to distinguish it from dispersal. However it is possible to relate nestling condition to survival probability (if this is indeed mortality and not dispersal). Perrins (1965) demonstrated that young leaving the nest at relatively low weights had less chance than heavier young of being recaptured at a later date. The present work has assumed the validity of Perrins' conclusions in relation to the Great Tit and extrapolated to the House Martin situation. Therefore any factor that depresses growth rates will accumulatively contribute to fledging at low weights and

in turn influence the survival potential of that brood or at least certain nestlings within that brood. The hypothesis is therefore developed by reference to growth rates, of different sized broods. It is evident that if a bird is maximising its production of young within limits imposed by food shortage that (given the physiological necessity of non linear growth) there will be a stage during nestling growth when the energy requirements are at a maximum. This stage may or may not coincide with the period of maximum growth rate and in the House Martin does not. If evidence of food shortage is being sought it is therefore best to look at this time. Now bearing in mind that there is a maximum rate at which food can be collected (possibly at that point which if exceeded would be detrimental to the survival of the adult) then the potential effect of food shortage is likely to be most acute at this time, becoming increasingly acute as brood size enlarges. A difficulty arises in that it is possible in species not liable to heavy predation in the nest for the energy requirements of the nestlings over a unit period to be depressed by lowering the rate of growth. This furnishes the possibility of raising more young but over a longer period, or reducing the potential influence of food

shortage. In the majority of species a number of factors tend to shorten the nestling period and hence maximise growth rates. The most important factor is that there is a finite period in which food is sufficiently abundant for young to be raised each season. Therefore when the total breeding time of a pair, whether raising one or more broods in a season, approaches this available time for breeding there is a possibility that, as the total period available varies from year to year, they might be unable to complete their breeding cycle unless growth rates are maximised. A faster nestling growth rate would ensure completion of the cycle or will enable more broods than otherwise to be raised in a year. Also fledging will be earlier, which Perrins has demonstrated is advantageous for survival and there is a reduced possibility of predation on the adults during this vulnerable period because of the shorter exposure time. I therefore suggest that a multibrooded species, utilising the resources of a brief and intense season, will generally undergo selection for rapid nestling growth. If therefore brood growth can be shown to be increasingly dependent on adequate resources being available at or near this period of maximum energy requirements, it will provide to a certain extent support

for the food limited hypothesis because it is known that successive depressions of the growth rate will accumulatively depress nestling weight and result in either nestling mortality or a reduced survival potential, by reducing the fledging quality (i.e. weight). This is graphically illustrated in the Swift (Apus apus) Fig 9.10 and an example from the House Martin is shown in Fig 9.9 which illustrates the low fledging weight of individuals that have experienced low growth rates.

The present study therefore was primarily concerned with examining the food limitation hypothesis of brood size in birds by observing the change in dependence of nestling growth on changes in environmental conditions in different brood sizes. This was interpreted as the degree to which the environment influenced the growth of those brood sizes either directly or indirectly. The greater the influence the greater the difficulties of the adults in nourishing those broods under the influence of food shortage, and the greater the consequent nestling, and also possibly adult, mortality. The most frequent brood size is therefore, that which is a compromise between the most productive and the least susceptible to environmental vagaries. This tends to both minimise potential adult

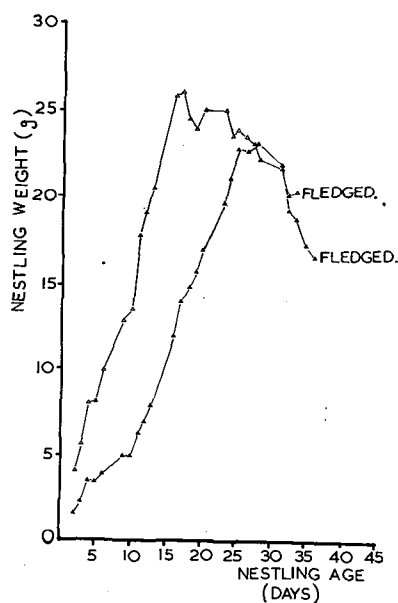


FIG. 9.9 The growth curves for individual nestling House Martins in a brood of two, where the growth rate of the smaller nestling has been considerably depressed.

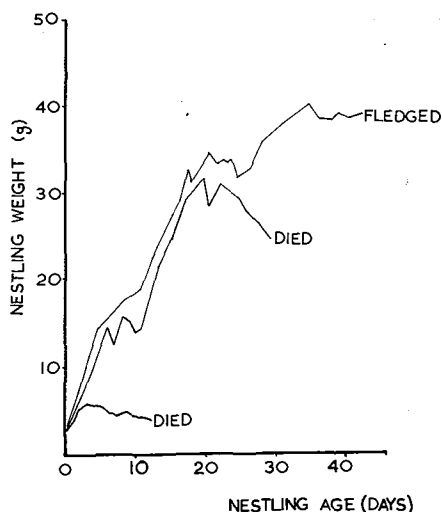


FIG. 9.10 The growth curves for individual nestling Swifts (Apus apus) in a brood of three, where the depressed growth of two nestlings precedes death. (Lack)

mortality and maximise nestling production. If it is to be demonstrated that the most frequent broods are indeed associated with low adult mortality rates adult mortality in relation to brood size needs to be studied (see section 10). However I have no significant data for the House Martin in this respect, though in the Great Tit (Kluijver, 1963) and the Pied Flycatcher (Lack, 1966, after B. Campbell) adult female mortality is apparently not significantly correlated with brood size though the data is suggestive. It would seem logical that the more difficult a particular brood size was to rear, so greater would be the detrimental effects on the adults involved and the greater their mortality rates. The main ways in which this mortality could occur in larger broods, is the extended exposure to predators, increased chance of complication with laying, and depletion of energy reserves with the consequent reduced resistance to adverse conditions.

Method

To investigate the growth rates of different brood sizes in relation to environmental influences the method described below was used. This is described briefly in an earlier section (6) Because growth rates of the majority of organisms is a constantly

changing function of age it is not possible to compare growth rate values for different days directly in such units as gms/day, weight increases. However in the House Martin the nestling growth curve is approximately sigmoid up to the asymptotic weight. Therefore using probit analysis or plotting the growth curves on probability paper as a function of the asymptotic weight, yields a straight line, the slope of which describes the rate of growth over the whole period from hatching to the asymptote. Alternatively the slope between successive points (or the difference between the points on the vertical axis on a linear scale) describes the growth rate over the daily periods. These daily rates were expressed as percentages of the rate over the whole growth period. The daily rates for each brood size were expressed as functions of the growth rate for that particular brood size rather than functions of the mean rate for all brood sizes because there is no evidence that the depressed rate, postponing fledging by a few days at the most, is in itself detrimental to nestling survival. However there is evidence that if weight increase deviates negatively from this mean growth on successive days, then the greater the deviation, the greater the detriment especially if such weight losses are cumulative. For example the precursor of nestling

mortality and reduced fledging weight in the Swift (Fig 9.9 & 9.10 and House Martin. Growth rates were derived from the growth period of the 5th to the 10th nestling day when the weight increment of each nestling was approximately constant at 2 gms per day. In order to investigate the influence of environmental factors on growth rates a multiple regression and correlation analysis was conducted on the daily growth rates for each brood size to determine respectively the proportionate influence of each factor and the total influence of all factors together. The influence of each factor has been discussed extensively in the section on the determinants of growth rates, though reference will also be made to these differences between different brood sizes below. The influence of all environmental factors acting together, in effect describes the dependence of each brood size on the environment. It might be expected that this dependence increases, as brood size increases, but the results are notable because they do not only show this.

Results.

The variance in nestling growth rates is dependent on both the environmental conditions during the sample period and the brood size of the sample concerned. The effects of environmental

TABLE 9.6

Multiple Correlation Analysis to Investigate the Effect of Six Environmental Parameters on Nestling Growth in Different Brood Sizes (n in days) See text for methodology.

Brood Size	1st & 2nd Brood	F Ratio	Signif.	n	$r^2 \times 100\%$	s^2 (Growth)	$r^2 \times s^2$	Residual s^2
1	2nd	65.3	10%	9	99	1704	1687	17
2	1st	0.6	N.S.	14	33	2611	867	1744
2	2nd	6.2	1%	17	79	1636	1289	347
3	1st	6.7	15%	9	95	697	655	42
3	2nd	1.2	30%	33	21	632	133	499
4	1st	6.2	20%	17	53	704	467	237
4/5	2nd	2.4	10%	14	67	288	194	94
5	1st	1.8	20%	17	53	1898	1002	896
6	1st	-	N.S.	6	72	1008	727	281
4	2nd	1.7	25%	12	58	271	157	114
5	2nd	2.5	<25%	10	76	267	203	64
5/6	1st	2.7	5%	23	51	2060	1035	1025

disturbances have been analysed in section 6, and it is clear that they are sufficiently intense for an analysis of the effects of brood size on growth rates to be disturbed by weather induced variation. This will be particularly important if the sample sizes are small, as is the case here. Therefore instead of examining the total variance in growth rates in relation to brood size, the percentage of this variance explained by the environmental variables supplied, was investigated. This value is independent of sample size and total variance, and will therefore be a more satisfactory measure of the influence of environment on nestling growth in different brood sizes. A multiple correlation and regression analysis was conducted to examine the percentage of the variance in growth explained (the coefficient of determination), while a multiple regression analysis was used to examine the relative influence of different environmental factors in different brood sizes. The results are presented in table 9.6. The coefficient of determination ($r^2 \times 100$) quantifies the percentage of the variance accounted for in the dependent variable, growth, by changes in Food Abundance, Mean 24 Hour Temperature, Duration of Rainfall (Daylight only), Daylength, Wind Index and Mean Prey Size. The frequency of laying of different clutch sizes (mean of 1968 to

1970 data), was then examined in relation to the environmentally induced variance in growth of the corresponding brood sizes. (Fig 9.11). There is a tendency for those brood sizes whose growth is most influenced by environmental disturbance (i.e. those with the highest $r^2 \times s^2$) to be the least frequent in the population. The second broods of four and five are obvious exceptions. However there are two operations that may be performed on these data in an attempt to increase the significance of the relationship. Firstly all artificially adjusted broods may be discarded because of factors discussed elsewhere (see Wynne Edwards 1962, and section 7). This includes first broods of 6 and second broods of 5. Secondly the results may be arbitrarily divided into those in which the fit of the regression equation is poor (i.e. F ratio significance, $p = 21\%$) and those in which the fit is reasonable to good (F ratio, $p = <20\%$). This results in the exclusion of the values for first broods of 2 and 6 and second broods of 3, 4 and 5. The remaining five points indicate a distinct tendency for the most frequent brood sizes to be least influenced by environmental disturbances, and this tendency is in fact strengthened by the other less satisfactory points, though with the exception of

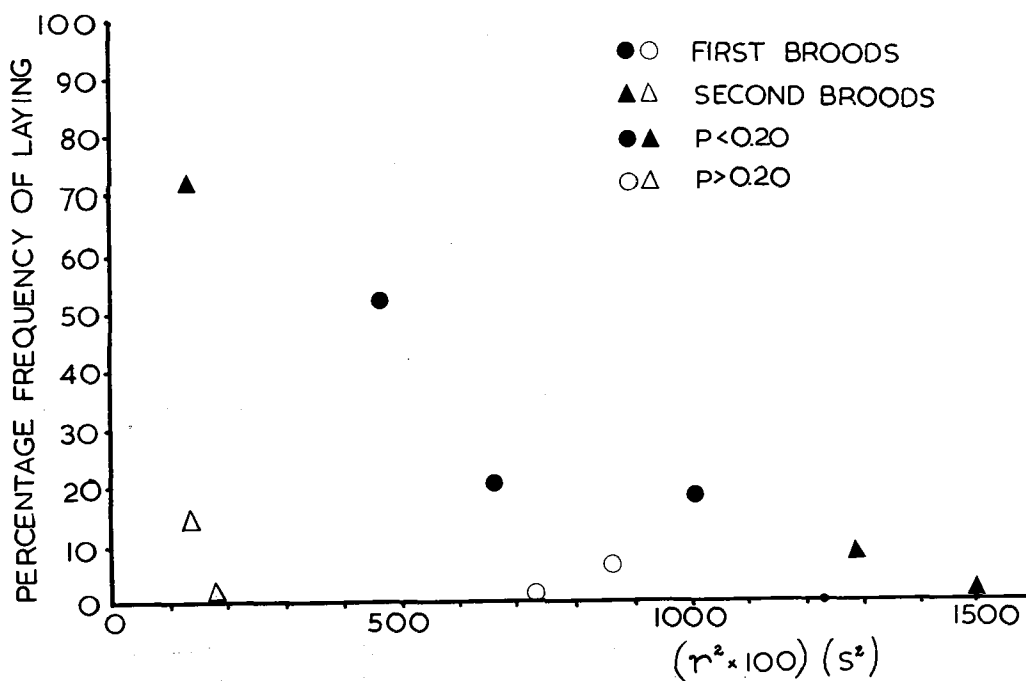


FIG. 9.11 The frequency of laying of different clutch sizes in relation to the association between nestling growth in different brood sizes, and several environmental parameters. The nature of these parameters is described in the text. The data refer only to the breeding season of 1969.

those for the second broods of four and five. It is interesting that the results for growth rates and fledging weights of these second broods of four and five, analysed in section 7, indicated a similar emancipation from food shortage effects (Table 9.7). Their final quality was similar to the smaller second brood sizes of two and three young. Assuming that this is not a biased sample, it is obvious that some members of the population are jeopardizing their reproductive potential, and raising smaller broods than can successfully be reared. This phenomenon was possibly restricted to this one year of study rather than being generally applicable, or alternatively post fledging mortality may act in a manner that doesn't accord with the scheme proposed by Perrins (1965) and discussed in chapter 7. Or it may be that some members of the population are undergoing reproductive restraints to prevent overpopulation and the consequent overexploitation of resources, as argued by Wynne Edwards (1964). However I tentatively propose that as daylength was demonstrated in section 7 to influence the growth of 2nd broods of 4 and 5 young to a greater extent than other broods, the rearing of such large broods could detrimentally affect the adults concerned, (by reducing the time they have available for feeding themselves).

Table 9.7

Nestling parameters used as an index of nestling quality
(Mean values)

<u>Brood Size</u>	<u>Fledging Weight</u>	<u>Asymptotic Weight</u>	<u>Wing Length</u> <u>on day 25</u>
	(grams)	(grams)	(m.m)
1 Brood	1	-	-
	2	16.2	25.8
	3	17.0	23.2
	4	16.9	23.4
	5	17.0	22.0
	6	16.0	23.6
2 Brood	1	16.8	25.2
	2	17.8	24.2
	3	17.5	23.2
	4	17.8	23.8
	5	17.4	21.8
	6	-	-

process of natural selection.

It appears from the B Weights associated with different brood sizes that the importance of food shortage in limiting growth rates is dominant in all the first broods while several factors are important in the second broods. (see Table 6.1) It is notable that food abundance does not become increasingly important as brood size becomes larger and this suggests that food shortage was not alone in causing the relatively more intense variation in growth rates in certain brood sizes. However it was probably responsible for the overall depression of growth rate observed in broods of six. In second broods food shortage was of less importance, possibly due in some cases, to the contribution of first brood young to the feeding of the second broods. Observations on natural broods, over hourly periods at midday, suggested that the contribution of first brood young could be considerable (Table 9.8). Broods of one, two and three young were observed. Only the brood of three received food from both adults and first brood young, the latter contributing 28% of the total feeding visits to the nest. Interestingly the difference in the average number of feeding visits to the second broods of 2 and of 3 is 60 visits

Table 9.8

The relative contributions of first brood young to the feeding of the second broods in the nest.
(Data refers to Feedings/Hour at Midday).

Nestling Age	<u>2nd Broods of 1</u>		<u>2nd Broods of 2</u>		<u>2nd Broods of 3</u>	
	<u>Adult</u> <u>Contri-</u> <u>bution</u>	<u>1st Brood</u> <u>Contri-</u> <u>bution</u>	<u>Adult</u>	<u>1st Brood</u>	<u>Adult</u>	<u>1st Brood</u>
7			13	0		
8						
9						
10						
11			28	0		
12						
13						
14			24	0	36	0
15					26	0
16						
17					34	34
18					20	29
19					26	0
20					56	0
21			26	0	30	14
22					33	17
23					46	24
24						
25					9	3
26			20	0		
27	16	0				
28						
29						
30			18	0		
% Contribution of 1st Brood Young	0%		0%		28%	
% Contribution of Adults	100%		100%		72%	

(Brood 3) 215/day - (Brood 2) 155/day = 60 , which is 27.9% of the total feeding to broods of 3 and equal to the first brood contribution.

In summary therefore there are limits to the ease by which energy can be supplied to the nestlings and this appears to be easiest in the most frequent brood sizes of three and four young. Birds laying such clutch sizes will therefore tend to have any detrimental effects on themselves minimised, and possibly therefore have their survival potential enhanced. Also nestlings in the most frequent clutch sizes are the least subject to environmental vagaries and are thus most likely to survive severe conditions. This latter point is not substantiated by the figures for nestling survival in relation to brood size (see section 10 and discussion), maybe because such catastrophes are irregular and did not occur in the study period. However the sample size was too small for positive conclusions to be made . If this analysis is valid it implies a maximisation of the total lifetime production of young at the expense of maximising the^{annual} rate of production of young.

It is easy to see why the largest brood sizes are relatively more influenced by environmental factors, namely because the abundance and availability of food can be limiting. The

environmental constraints on the broods smaller than the most frequent are difficult to explain, and I shall attempt to do this in the model illustrated in Fig 9.12 and Table 9.9 . Though they would not anyway be expected to be frequent in the natural state because they are less productive than the most frequent brood sizes. The model represents the time allocated by a pair of House Martins each day, to the two important activities of feeding and brooding the nestlings. The situation is examined in brood sizes from one to six young. The time allocated to each activity is presented as a percentage of the total daylight period available each day. The model attempts to demonstrate that given the necessity of certain minimum levels of feeding and brooding, a shortage of food, need not necessarily affect only the largest broods.

To evaluate the time spent brooding in different brood sizes I have used the data of Lind (1960). He observed the percentage of the daylight hours spent brooding by House Martins, with broods of 3 and 6 young. By extrapolation on a semilogarithmic scale (though there was little difference when the results were extrapolated on a linear scale) the percentage of each day that broods of one, two, four and five would be brooded was calculated. (See Table 9.9).

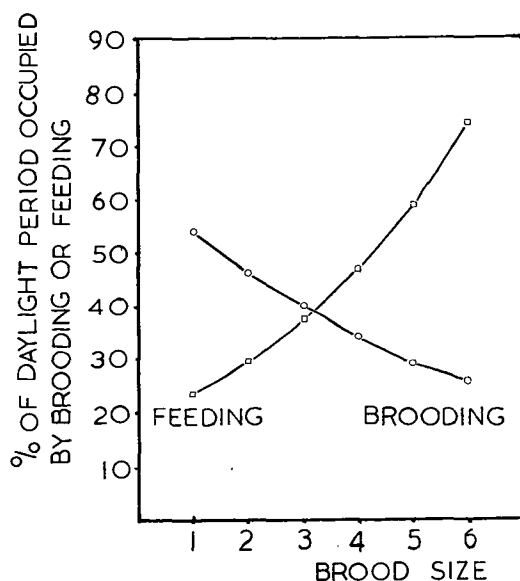


FIG. 9.12 A model which describes the percentage of each day invested in the activities of feeding and brooding by a pair of House Martins. The model illustrates variation of these parameters with brood size.

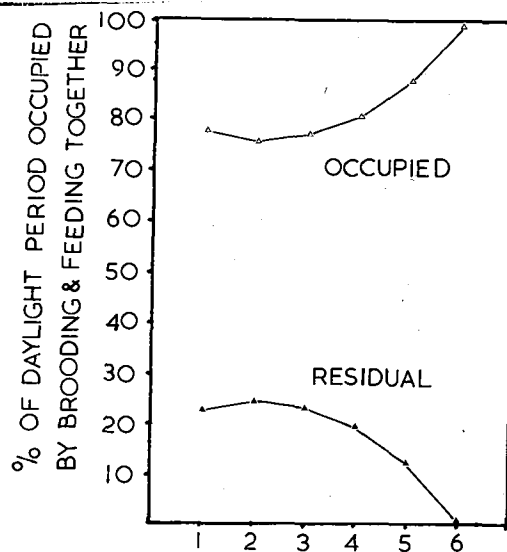


FIG. 9.13 The sum of the percentage of each day invested in feeding and brooding (see Fig. 9.12), illustrating the total percentage of each day occupied by these two activities in relation to brood size.

TABLE 9.9

The time spent each day by a pair of House Martins (expressed as a percentage of the total time available) on feeding and brooding activities in brood sizes of one to six young.

Brood Size	% of day spent feeding young	% day brooding	Total % day occupied	Residual time available %
1	23.4	54.0	77.4	22.6
2	29.5	46.2	75.7	24.3
3	37.1	*40.0	77.1	22.9
4	46.6	34.0	80.6	19.4
5	58.8	29.0	87.8	12.2
6	74.0	*25.9	100	0.0

* Data calculated from Lind (1960) and expressed as an average figure for the whole nestling period. See text for derivation of other figures.

The figures for the time spent feeding, I have derived from my observations on feeding frequencies. It is evident that broods of six experience a depressed growth rate and that the adults involved are fully occupied in an attempt to nourish the brood. I therefore, assumed that the total time allocated to brooding (25.9% of each day) plus the time allocated to feeding (433 feeding visits) accounted for 100% of the available time each day in broods of six. The time not available each day includes, time spent on other activities, such as adult maintainance. Therefore 74% of each day ($100 - 25.9 = 74.1\%$) is spent executing the 433 feeding visits. Then by proportion, with a knowledge of the mean feeding frequencies associated with other brood sizes, the percentage of each day necessarily spent feeding the brood can be calculated (Table 9.9). Now the sum of the time involvement in the two activities is presented graphically in Fig9.12 for each brood size. It can be seen that there is very little difference in the requirements of broods from one to three young, with the least demanding brood size being a brood of two. The percentage change in requirements increases geometrically above broods of three with a 4.5% increase between broods of 3 and 4, a 9.0% increase from 4 to 5 and a 13.9% increase from 5 to 6. Regarding total time

occupied each day therefore, broods of 2 are the least demanding and should allow a minimisation of the effects of food shortage or of adverse effects on the adults.

To examine the environmental constraints on the smallest broods it is necessary to investigate the relative contributions of brooding and feeding to the total daily requirements and their variation with brood size. The percentage of each day spent brooding and feeding in each brood size is shown in figure 9.13. The potential effect of food shortage on the larger broods is clear. A reduction in food abundance will also indirectly affect the smaller broods because with more time devoted to collecting the necessary food, beyond a critical point (for example, where feeding time is increased above 46% of each day for broods of one; $\text{Feeding time } 46\% + \text{Brooding Time} = 100\%$) insufficient time will remain to adequately brood the young. It has been shown earlier that a brooded nestling may have only half the energy requirements of a single exposed nestling, and therefore a period of exposure will in turn elevate the food requirements relatively more than in larger brood sizes. In the case of broods of one nestling, it would require only that the mean food abundance be halved for the feeding time to double

and brooding requirements to be at their absolute minimum for satisfactory growth. (Feeding Time $23.4\% \times 2 = 46.8\%$. Then Feeding Time + Brooding Time = $46.8\% + 54.0\% = 100.8\%$). The consequence of food shortage of this order would be a slight depression of the growth rate. That brood size which is least susceptible to similar or more extreme disturbances is that in which the requirements of each factor are not excessively elevated or depressed by a shortage of food. The intercept of the two curves in Fig 9.12 indicates the approximate value of this optimal brood size. The value of the brood size is derived by dropping a line from the intercept, and is a brood of 3.2 young. This is close to the mean size of all clutches and hence brood sizes observed 1968 to 1970, which was 3.23 eggs. However it does not accord closely with either the mean 1st brood or 2nd brood size. This is possibly because the fitted brooding curve is inaccurate when applied to the first and second broods individually. To examine this a correlation analysis between growth and temperature for each brood size, assigned the highest r to first broods of 2 and 3, and the lowest to all second broods. It is possible that because of a possible direct effect of temperature on the smaller first broods through

exposure when not being brooded (though I have no evidence for this view) that the fitted curve for brooding should be elevated for these first broods and depressed for the second broods. This would have the effect, in the model of shifting the intercept towards the right for the first broods, bringing it closer to the mean value for 1st broods (4.46 eggs) . While a shift to the left would bring the predicted value closer to the observed value (2.95) for 2nd broods. This model therefore described graphically the mode of action of the limiting environment described by the multiple correlation analysis, where the least frequently observed brood sizes were generally the most subject to a disturbed environment. It seems probable therefore that such susceptibility may in some years (or in all years though after fledging) reflect in the relative survival of these nestlings or the survival of the adults rearing these broods. This will ultimately lead to selection against such brood sizes, and the appearance of a most frequent brood size which is on average the one that ensures that the individual adults concerned will maximise their total lifetime production of young, even if in some years this is at the expense of maximising their annual production of young.

SECTION 10

ANNUAL MORTALITY

Adults and nestlings were ringed in each colony in each year of the study. However this involved only a few birds at the farm colony in 1968 though otherwise effort was directed similarly towards each colony in each year.

A mean adult mortality of 32.3% was calculated and a mean mortality of the young in their first year ^{of} ~~as~~ 83.3%. The values for each year of the study are presented below.

TABLE 10.1 The Mean Adult House Martin

Mortality from October year 1 to October in year 2.

	1968/1969	1969/1970	Mean
Adult Mortality	12%	52.5%	32%
Young Mortality (over 1st year)	88%	78.5%	83%

These values for adult mortality can be compared with 18% for the Common Swift A. apus (Wietnauer, 1954), 63% and 54% for the Barn Swallow (Hirundo rustica) (Lack, 1949; Uchida, 1932) and 52% for the Cliff Swallow (Petrochelidon pyrrhonota) (Mayhew, 1958); the ecological counterpart of the House Martin in North America.) Mayhew also gives a figure of 81% annual mortality for the young over the first year, which closely

resembles the figures obtained in this study. Separation of real mortality from dispersal presents difficulties, though as Rheinwald and Gutschon (1969) record a high tenacity to the home site in the House Martin in Germany, it seems likely that these figures are a true reflection of mortality rates rather than the extent of dispersion in each year.

Movements

No recoveries have been reported up to the present time outside the immediate area of the colonies.

Two individuals were recorded at both colonies. Both were ringed as post juveniles (either adults or 1st brood young) on August 27th 1968 at the Farm colony. One was controlled on October 3 1968 at the Kennels colony, while the other was recorded breeding at the Kennels in the following year, 1969.

Survival of Adults and Young over periods of one year and relationships with brood size.

An examination of 15 adult controls and 8 first year controls enabled mortality rates for adults rearing different brood

sizes to be estimated over periods of one year. It was found that only adults rearing first broods of three, survived significantly worse than if survival was independent of brood size. These results are discussed further in section 12. (See Table 12.1).

SECTION 11

THE COMPOSITION OF THE AERIAL FAUNA AND ITS RELEVANCE TO ECOLOGICAL ISOLATION BETWEEN AERIAL FEEDING BIRDS.

Birds may be ecologically segregated in three principal ways. Firstly in space, which may be subdivided into segregation by habitat and by geographical range. Secondly in time, where different birds may exploit the same food supply but at different seasons or at different times of day. Thirdly separation by differences in the food taken even though they occupy the same habitat.

It was postulated by Steere (1894), as quoted in Lack (1971), that 'no two species structurally adapted to the same conditions will occupy the same area'. This principle has subsequently been developed by Gause (1934), Lack (1947) and Hardin (1960). It is implicit in Steere's statement and has been widely accepted recently (Lack, 1971) that through the process of competitive exclusion only one species can utilise a particular ecological niche and persist in that niche. At first sight therefore it appears anomalous that four species of aerial feeding birds namely the Swift (A. apus), Swallow (H. rustica), House Martin (D. urbica) and Sand Martin (R. riparia)

coexist in Britain, and more in other geographical areas, and apparently utilise the same food supply and are not separated necessarily on space nor time. Other aerial feeding birds in Britain are more obviously segregated in a variety of ways. For example the Nightjar (Caprimulgus europaeus) is a crepuscular feeder and also probably differs in the food taken. The Spotted Flycatcher (Muscicapa striata) differs principally in feeding station and habitat while the Hobby (Falco subbuteo) obviously differs in the food taken.

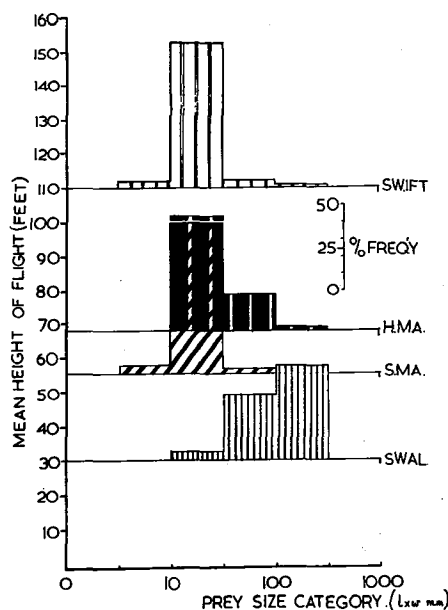
In order therefore to see if the potentially coexisting aerial feeding birds in Britain did utilise the same resource or whether there was ecological isolation through differences in the food taken, an investigation of the food of the four named species was undertaken. Lack (1971) suggested that these might be differences in the food taken by various European Swifts and that ecological isolation in the breeding season in the Hirundinidae was the result of separation in nesting sites, and therefore in effect by habitat.

The size frequency distribution of the insects preyed upon by House Martins, Swallows, Sand Martins and Swifts was determined by examination of faecal samples taken during June and July 1968 and 1969. Details are given of the method in an

earlier section.(4) For comparative purposes there were allotted to various size categories after Taylor (1962a) as portrayed in Johnson (1969). These categories were expressed as the product of the 'wingspan x body length' on a logarithmic scale. The precise dimensions of the wingspan were estimated from faecal remains and a knowledge of the taxa involved enabled the corresponding body length to be derived and hence the size calculated in $(\text{mm})^2$. Although, what is in effect a unit of area may seem inappropriate, I adopted it principally for comparative purposes with Taylor's data, and also because he had demonstrated it to be a satisfactory indication of size (Lewis and Taylor, 1967). The prey size distributions for each species is presented in Fig.11.1. It can be seen that prey is selected from a wide size range and is neither normally nor lognormally distributed with regard to size frequency. Within each species there is usually a clear dominance of one size category over the others. Thus the two Martins and the Swift mainly utilise the same sized prey while the Swallow takes larger prey items, at least in the months examined. Therefore it appears that the Swift and the two Martins are not ecologically separated by food and therefore the possibility of isolation by alternative mechanisms arises. It is therefore

FIG.11.1

The frequency distribution of prey size in the diet of nestling Sand Martins, House Martins, Swallows and Swifts. The vertical axis refers to both the percentage frequency in each sample



and to the mean observed height of feeding. Refer to text for methods. The size of prey items is presented on a logarithmic scale.

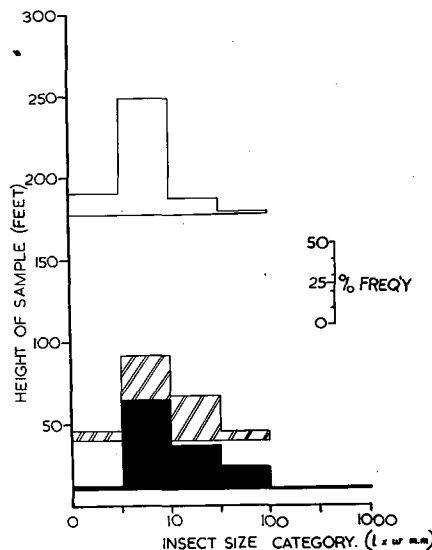


FIG.11.2

The frequency distribution of the size of aerial insects at different heights above ground level. The size of the constituent insects is presented on a logarithmic scale. Data from Taylor (1962), Hardy and Milne (1938) and Bryant (unpublished).

of interest to examine the feeding stations of each species and observe if differences are apparent, and further to examine the broad characteristics of the available prey in each of these stations for reasons explained below. The feeding stations may be described in terms of both the mean height of feeding flight and the distance from the nearest vegetation. The estimates of the mean height of flight were obtained by a visual estimate of the observed flying height of Hirundinas and Swifts by reference to adjacent structures of known height. The results for both 1969 and 1970 (June to August) are shown in table 11.1. There is no significant difference within species between years ('t' test) and so the data is also presented as a mean figure. The frequency distribution of feeding heights is not normal. The observations were made on a daily basis throughout the breeding season for the House Martin, readings being made at 9.00, 13.00 and 17.00 hours on each observation day. A similar programme was carried out for the Swift and Swallow, but the Sand Martin figure is based on considerably fewer observations.

Table 11.1

Mean height of Flight of Aerial Feeding Birds.(Feet)

(where these were judged to be feeding)

	Swift	House Martin	Sand Martin	Swallow
1969	125	64	68	25
1970	105	70	45	31
Mean	110	68	55	30
No observations (n)	(120)	(306)	(68)	(152)

Considerable data have been collected on the distance between the feeding birds and vegetation or buildings but this has not yet been critically analysed. However it is possible to subjectively rank their degree of association with vegetation as follows. The Swallow invariably feeds in close proximity to vegetation, often low over the ground or among the peripheral branches of trees. The House Martin and Sand Martin are generally less closely associated with vegetation, with the House Martin probably even less so than the Sand Martin. The Swift is the least frequently observed feeding close to vegetation. As the mean heights of flight are often distinct, it is interesting to observe if the size frequency distribution of the prey corresponds either more closely with the character of the available prey at different heights, or with certain

characters of the bird. If the size frequency distribution of the available prey is similar at each of the observed feeding heights, then the observed heights of feeding are not likely to be directly related to the feeding strategies of the birds. However if the size of available prey changes with height then it is likely that these differences in feeding height are functional, and that species is selecting that aerial zone that provides a relatively greater abundance of preferred food./ or reduces competition with other species Accordingly data published on the composition of the aerial fauna at heights greater or less than the forty foot sample, was examined and a size frequency distribution derived. The results for these and for the forty foot trap are shown in Fig 11.2 .

The data was taken from Johnson (1969) (after Taylor, M.S) for 10 foot above ground level, and from Hardy and Milne (1938a) for 177 feet above ground level. Incidentally the latter workers used a suspended aerial plankton net rather than a suction trap, though this is not thought to seriously bias the sample because of the generally small size and correspondingly low mobility of the insects at that height (Lewis and Taylor, 1967). These data do not correspond absolutely with the

calculated mean heights of flight, however they do provide an indication of the change in the quality of the available prey the greater the height above the ground. The mean size of the insects involved in Hardy and Milnes' data were assumed to be similar within each family unit as the sizes of the respective taxa in the forty foot suction sample. The frequency distributions have been calculated on this assumption. In practice however they are likely to be smaller and I emphasise that these distributions can probably be considerably improved.

It is evident that the observed prey spectra correspond to a certain degree with that available at or near their mean height of flight. The Swift, feeding highest, takes correspondingly more of the smaller items available at such heights, while at the other extreme, correspondingly more larger items are present in the lower strata (10 feet) and this is reflected in the prey of the Swallow which generally feeds at these lower levels. The House Martin occupies in both respects an intermediate position. Anomalously the Sand Martin most closely resembles the Swift in its prey spectrum indicating a potential overlap in feeding niche. However they are separated in feeding station and the Sand Martin.

ancestrally is separated in habitat from the Swift, being associated with soft cliffs for nesting which are usually close to water, while the Swift and House Martin are associated with rocky cliffs (or later, houses) which rarely occurred near the typical Sand Martin habitat. Therefore competition between the Swift and the Sand Martin was unlikely because of this separation in habitat. They were therefore able to both exploit a similar size range of prey.

In several species of bird that are known to take different foods, (where this may be a difference in both size and/or quality) structural adaptations are apparent that apparently facilitate exploitation of their specific resource. For example the Galapagos Finches (Lack, 1947, 1971) and the British Fringillidae (Newton, 1967a). The principal structural differences between the aerial feeders are differences in weight, wing length, tail length and possibly gape size and the extent of the associated rectal bristles. However the last two aspects have not been investigated. The wing lengths and weights follow the same sequence with the longest wings being associated with the heaviest birds (Table 11.2). The sequence goes from the lightest , the Sand Martin, through the House Martin and Swallow, to the heaviest, the Swift. Within the

Table 11.2.

Statistics of Aerial Feeding Birds.

	Weight (gms)	Wing length (mm)	Tail length (mm) (Outer Feathers)
Swift	42.7	164 - 179	72 - 81
Swallow	23.4	116 - 129	76 - 122
House Martin	19.4	104 - 113	57 - 63
Sand Martin	14.2	101 - 110	49 - 57

Hirundinidae there is an increase in weight which is associated with an increase in preferred prey size. The adaptive function of this is possibly that this increase in size of prey involves an associated increase in the mobility of those items (Lewis and Taylor, 1967) while an increase in the size of the predator also involves an increase in the economic (in terms of energy expenditure) cruising speed of that bird (Pennycuik, 1969) and hence their ability to secure such prey is probably increased. The fact that the larger items taken by the Swallow have flight speeds of up to 40% of that of the Swallow emphasises the point. The flight speed of such insects is up to 320.0 cm/sec and the economic cruising speed of the Swallow, which would be the most economic method to use during hunting is 800.0 cm/sec (Pennycuik, 1969). However the corresponding increase in energy requirements with size increase would reduce the potential advantage of such an increase in flight velocity. In fact the rate of increase in energy requirements with weight^(w) increases proceeds at a greater rate than the increase in flight velocity^(v) where $R \propto W^{0.74}$ while $v \propto W^{0.16}$. Hence selective forces, rather than favouring a continuing increase in body size have favoured stabilisation within a presumably optimal range. This optimal range is such

that for each species, both competition for prey of a particular size and at a particular feeding station and the energy costs of hunting are minimised.

The Swift represents a different situation. The large body size and long wings ensure a high flight performance and it seems to adopt a distinct feeding strategy. Instead of picking items out of the air as do the Hirundines, where mobility (as indicated by tail length) and flight speed is related to that of their prey, the Swift sweeps through the air acting more in the fashion of a directed 'scoop' and feeds on less mobile prey which do not actively avoid the predator. Hunting will also be directed towards regions of insect aggregation. Johnson (1957) has derived an empirical relationship describing the decline in Aphid abundance with increase in height above the ground. This appears also to be a valid generalisation when applied to the entire aerial fauna (Glick, 1939). Hence in order to obtain a yield per unit time similar to or in excess of that of the Hirundinidae, it would be advantageous for the Swift to fly faster. However an increase in flight performance as a result of increase in body size would involve a correspondingly greater increase in energy

requirements, and the advantage would appear to be nullified. It seems probable that the Swift minimises this disadvantage by changing its flight behaviour. The Swift probably has a higher Gliding Flight./ Active Flight ratio than do the Hirundines (though I have no quantitative information on this point), which is made possible and successful because of the relative immobility of their prey. The energy expenditure per unit time of hunting flight is therefore reduced.

Thus the differences in size and form of the aerial feeding birds are primarily adaptations allowing co-existence within the same broad habitat, and have come about through the process of competitive exclusion and subsequent adaptation in form and habits.

These adaptations facilitate the exploitation of certain sized prey which have partially distinct aerial distributions and the birds that feed on them therefore also have distinct aerial distributions. The ecological differences in feeding strategies between the species are probably reinforced in certain weather conditions. High winds or atmospheric stability (i.e. during temperature inversions) cause the dispersed aerial population to become aggregated. (Johnson 1969, Lewis 1965a, 1970). Then in the absence of alternative

food or because of a local superabundance of food, all the aerial feeding birds concentrate in such areas to feed. The feeding groups may consist of all the four species (personal observation) or of less diverse groups, depending on the availability of alternative food supplies. Then without segregation in space there is presumably segregation by food, though this has not been critically examined.

Summarizing therefore it seems probable that the four aerial feeding birds in Britain are ecologically isolated primarily in terms of differences in food, which in turn often leads to isolation in terms of space. The Swallow is more distinctly isolated than the others. The Sand Martin, House Martin and Swift although to a certain extent isolated by differences in prey size and more importantly isolated in terms of feeding station and/or habitat.

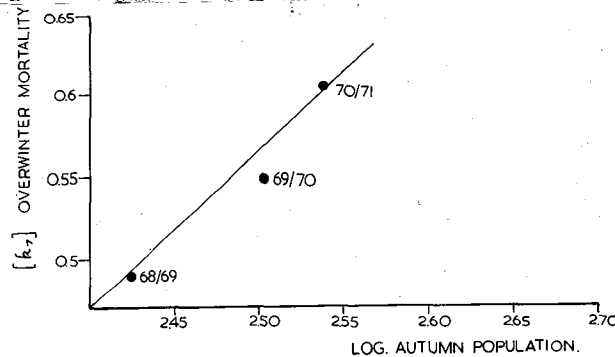
SECTION 12

DISCUSSION

The important points arising from each section of the thesis have been discussed in association with the appropriate section. It is now necessary to collate those conclusions and assess the important relationships between the breeding House Martin and its food and their relevance to population processes. It must initially be suggested that the principal process regulating the House Martin population, lies outside the scope of this study. This was demonstrated by employing the key factor analysis of Varley and Gradwell (1960). It involved assuming that the colony size in 1971 (for which no actual figures were available) remained at roughly the same level as in earlier years. Its precise value was assumed to be the mean of the other three years, though it would make little difference to the results if the change in colony size was of the order of $\pm 50\%$. The total post fledging mortality of the young plus the overwinter adult mortality was then examined in relation to the total population at the beginning of this period (assuming net dispersal to other colonies is nil) Fig 12.1. It can be seen that the overwinter mortality is almost perfectly density dependent ($b = 0.95$) where $r^2 \times 100 = 94\%$.

FIG.12.1

The overwinter mortality of adult and juvenile House Martins in relation to the size of the autumn population. The overwinter mortality includes all mortality after the nestlings fledge. The autumn population is the total adult population of the two main colonies plus the



total young fledged from first and second broods, less any recorded post fledging breeding season mortality.

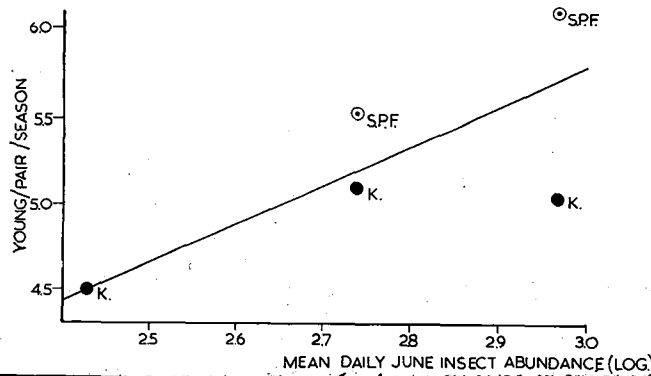


FIG.12.2

Annual production of young by breeding House Martins in relation to the Geometric Mean of the daily June aerial insect abundance.

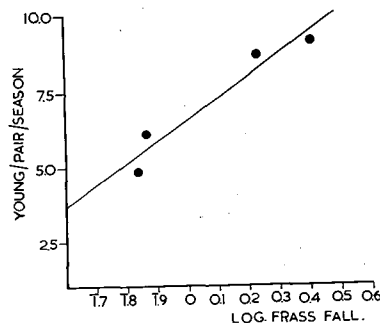


FIG.12.3

Annual production of young by breeding Great Tits (Parus major) in relation to the abundance of Lepidopterous larvae (estimated from Frass fall on a logarithmic scale). See text for details.

However the correlation is not significant ($r = 0.97$) because of the shortage of data, and a certain amount of residual variation (6%). The nature of this almost 'perfect' density dependence, suggests that it is regulatory and probably results from food shortage in the overwintering area or on migration, and these aspects lie outside the scope of the present study. However given the observed stable breeding population, then the intensity of the density dependent mortality is a direct product of the total production of young over each breeding season. The greater the number of young produced the greater the subsequent mortality. The ultimate cause of this variation in overwinter mortality will be those factors that precipitate a successful breeding season and it is these that have the centre of interest in this study. It was first essential to establish the validity of the sampling system. Taylor (1962) has discussed the absolute efficiency of suction traps, in sampling the aerial insect population, though there is no reason to believe a trap of even 100% efficiency would assess the insects actually available to the House Martin. However the qualitative results suggested that the food taken by the Martin in terms of size and species was a close reflection of the suction trap catch, though they both varied in a predictable

way with the actual insects available. Additional proof that the suction trap sampled the available food was the close correlation between growth rates and food abundance. Nestling Martins' weight increments over a standardised growth stage are a positive linear function of the logarithm of food abundance (= total catch/day), and this supports the well recognised fact that the amount of food and its quality are important factors determining rates of growth.

With this validification of the food sampling method it was of interest to examine the effects of variation in food abundance on the breeding cycle. Most obviously there is a striking difference in food abundance between the summer and winter levels. This disposes the House Martin to overwinter in the tropics where food is presumably more abundant at this time, and to migrate to the Temperate (N) region in summer to harvest the great abundance of food. It would be interesting to have comparable data on insect abundance from the Tropics so that this summer abundance could be quantitatively compared with the alternatives available in Africa. To date no systematic aerial sampling has been undertaken; nor is there much information on the winter distribution of the House Martin (Moreau, 1966). It is unusual for an abundant and conspicuous

(in summer) palaeartic migrant to be so poorly known in winter quarters and it deserves comment. I propose two possibilities which may render the House Martin relatively inconspicuous. It is obvious that the birds do not frequently form dense aggregations in winter quarters over water as does the Sand Martin (R. riparia) in the region of Lake Chad or is as conspicuous as the Swallow (H. rustica). I suggest therefore that either the House Martin feeds in a highly dispersed manner just above the forest canopy, in forest clearings or at the forest edge, or else they feed at considerable heights on insects aggregated by atmospheric instability in their usual feeding groups. Both these mechanisms would make individuals inconspicuous and account for the paucity of observations. Such a difference in conspicuousness from the Sand Martin and Swallow could be expected from comparative observations in Britain, where of all the three Hirundines only the House Martin is regularly observed exploiting aggregations of insects in front of Cold Fronts along with Swifts (A. apus) (Pers.obs. and Voipio, 1970).

It is subjectively evident that the arrival of the aerial feeding birds in Britain coincides with the development of the aerial phase of several insect populations. The sequence of

arrival of the four species Sand Martin, Swallow, House Martin, Swift is the same sequence as the ascending sequence of mean heights of flight. It seems probable therefore that the mean arrival time of each species corresponds with the adequate development of aerial populations of the type exploited by that species. The Swift is the last to arrive because the migratory phase of, and conditions suitable for, Aphid flight have not usually developed before the end of April. The earlier arrivals of all species frequently utilise the insects available over water which are apparently present largely irrespective of inclement weather, whereas the aerial fauna at this time is highly dependant on weather, especially temperature changes. For example the regression coefficient for a regression of Logarithm Insect Catch/Day on mean temperature for that day is $b = 0.15$ and $r = 0.88$ ($p = < 0.01$) in May (1968) which strongly contrasts with the more stable conditions evident even one month later in June where $b = 0.08$ and $r = 0.37$ (N.S) (June 1968). The aerial feeders also resort to this food supply later in the season whenever the weather is so bad that the total aerial population falls. The most significant inclement conditions are associated with low temperatures and high winds, though in fact aerial insect abundance over the

summer of 1969 was also significantly correlated with Rainfall and Radiation (Hours of Sunshine). Detrimental extremes of any of these factors could therefore result in a movement of feeding birds to the proximity of water. The fact that Martins occur more commonly near water early in the season is a function of both the greater incidence of inclement weather and the low developmental state of many insect populations, which is in part a function of preceeding weather conditions. (Williams, 1961). The instability of the aerial food supply means that aerial feeding birds have not only to contend with seasonal changes in food abundance, but also daily changes in abundance and availability largely precipitated by weather. In the Swift (Apus apus) the effects of food shortage on nestling survival are minimised by the young becoming hypothermic in extreme food shortages, evidently in an effort to conserve energy (Lack, 1951). The Nightjar (Caprimulgus europeas) has recently been shown (Peiponen, 1970) to do the same. The young of House Martins evidently have a similar ability. In several broods where one of the parents disappeared (presumed dead) the nestling assumed a torpid state for several days before death. They felt cold to touch, and this was probably

induced directly by malnutrition. One nestling was transferred into a brood at a similar stage of development, while in a torpid state, but subsequently died. This suggests that in the House Martin hypothermia necessarily precedes death, rather than being a facultative mechanism to survive periods of food shortage. Therefore in an attempt to determine whether lowered body temperature was induced by, or associated with adverse conditions and whether recovery was possible, nestling rectal temperatures were recorded for a sample of broods throughout the latter half of the 1969 season. It was found that the mean nestling temperature was $37.9^{\circ}\text{C} \pm 2.3^{\circ}\text{C}$, which is close to the normal range of adult birds, which are known to be able to assume torpor (Dawson and Hudson, 1970). On several occasions markedly lower rectal temperatures were recorded. In the first case it involved a 2 day nestling, probably unable to control its body temperature during the period of examination (Seel, 1968). However on July 29th at 18.00 hrs when the day's catch was $\text{Log } I = 1.47$, the lowest food abundance in the study period, very low rectal temperatures were recorded in two broods of the three examined. A brood of four had normal temperatures, illustrating the insulative effects of

the larger broods, while two broods of two had mean temperatures of 31.0°C and 32.3°C . Both these latter broods lost considerable weight over the day, though they had regained their former weight by the following day when food was abundant again, and fledged normally. It was unfortunately not recorded whether these birds felt cold to the touch, though it is probable that they did. By this means they deprive their peripheral tissues of the usual copious blood supply and hence reduce heat loss. It is apparent then, that there are various degrees of hypothermia in House Martin nestlings closely allied with food shortage. It is rapidly induced, as food abundance on the 28th, the day before these observations, was well above average. It probably serves to extend energy reserves in times of food shortage over the maximum period of time, because of the high probability that adequate food conditions will eventually be restored. In the situation where food is not restored, as when one of the pair disappeared, then it merely prolongs the period before death. However this latter state does illustrate that the mechanism is a direct product of undernourishment. The House Martin nestlings therefore resemble many other Adult Apodiformes and Caprimulgiformes which feed on aerial insects or in some cases nectar

(Bartholomew et al, 1957 & Pearson, 1950, 1954).

The ability of nestling House Martins to become torpid, illustrates the potential severity of food shortages. It is therefore not surprising that seasonal, daily and annual differences in food abundance together precipitate most of the breeding season mortality, where this includes both death and failure to achieve maximum fecundity. The latter is usually induced by broad annual differences, which are ultimately due to factors outside the scope of this study, namely those factors that determine the size of insect populations, their rates of development and the proportion that partake in the aerial phase. The results of these influences are illustrated in fig 12.2 where the total seasonal production of young is plotted as a function of food abundance in June. It can be seen that the total annual production of young is closely associated with food abundance in June. This involves both the direct effect of a plentiful food supply on nestling survival and a close correlation with other seasons which themselves directly affect some factor (i.e. clutch size and May food abundance). In the knowledge that similar relationships can be established whatever the particular habitat (refer to Southwood and Cross, 1968 and Perdix perdix) it would be

interesting to extend this study of the cause of increased productivity, to other species in all habitats. As an illustration I plotted data in Lack (1966) for the Great Tit (P. major) as a function of (Log.) Frass Fall (itself an index of caterpillar abundance, the principal food of nestling tits). A similar result was obtained. Fig 12.3 where $r = 0.97$ (N.S)

Breeding success is influenced by increases in fecundity as well as by reductions in mortality. Such increases in fecundity are partly dependent on the timing of the breeding season and partly on additional annual variations. The two processes are linked in a complex interdependent way, though both are ultimately dependent on food abundance. Thus differences in the time of appearance and the aerial abundance of Aphids and other insects in spring can both influence clutch size and the time of breeding. Both these responses appear to have an adaptive function, in that they adjust the mean brood size in each year to, or parallel to, the probable subsequent conditions of food abundance. Cohen (1967) argues that optimising yield in relation to probable/future environmental conditions, maximises the long term growth rate of the population, which, other things being equal, should then eventually replace less efficient genotypes. The seasonal

adjustments of spring clutch size in relation to food abundance appears to be a natural example of Cohen's theoretical model. It might be expected that the magnitude of the adjustment would be depressed at high densities because of the probability of competition for food being more intense. This was not observed in the House Martin, probably because the population is not limited by food at this time but rather by the inability to increase at a greater rate. The distribution of clutch sizes over a range from three to five eggs may reflect the inherent imprecision of the prediction. Genotypes with the smaller clutches may prevail, because in some years they produce more young that survive to breed, than the larger clutches. The timing of the breeding season, and in particular egg laying, is of interest because the results of many studies indicate that nestling survival from the earliest broods is better than from later broods (Perrins, 1965, Harris, 1967, Perrins, 1966, von Haartman, 1967a, Klomp, 1970). It is of potential advantage then for each pair to breed as early as possible and so maximise production of young within each year. The overriding importance of daylength in regulating laying is well known (Farner, 1964) and is a long term evolutionary adaptation to

prevent breeding when the probability of food shortage and nesting failure is high. However because in different years the actual suitability of conditions on any particular date may vary, it is of obvious advantage to have some means of secondary or "fine" adjustment. These secondary releasers or post regeneration accelerators may take the form of temperature thresholds (Snow, 1955; Delius, 1965) or as suggested here and elsewhere (Davis, 1955; Lack 1950b) food availability. However I suggest that many apparent correlations of spring temperature with mean dates of laying (Perrins, 1965; Kluijver, 1951) are in fact a reflection of the influence of temperature or the development of food supplies. A model is presented that shows a reasonable correspondence with field observations, which proposes that the emergence of aerial insects and in particular Aphids, is the direct secondary releaser of laying. The distribution of laying dates after the appearance of the first individual clutch is influenced partly by food abundance, such that severe food shortages are followed several days later by suspension of laying. However quite apart from this, laying is spread over several weeks in the first clutch and it is suggested that this is a reflection of structural differences in the laying females, that determine the efficiency with which

different individuals can exploit the aeroplankton, and are thus able to accumulate sufficient food to form eggs. An alternative formulation of this same hypothesis is that these structurally different females respond to different thresholds of food abundance, which are ultimately associated with average levels of food abundance at which females of that form are able to breed successfully. This threshold is probably influenced by age, though usually being stable by the second season of breeding. The timing of the second clutch is largely a reflection of the timing of the first, and the period spent rearing the first brood. The first egg of the second clutch is usually laid $7.9 \text{ days} \pm 3.1 \text{ days}$ after the last young has fledged and because food is rarely short in the middle of the breeding season, is not often delayed by bad weather or food shortage. On one occasion eggs were laid four days before the young fledged. However after the third egg was laid, the eggs were ejected and relaying recommenced five days after the young fledged.

The mechanisms by which nestling mortality is induced appears to be largely a function of the immediate effects of poor environmental conditions, which subordinate the effects of

prehatching influences, such as differences in egg weight and hatching order. Asynchronous hatching was only briefly discussed in section 5. Lack (1947, 54, 66, 68) proposes that it facilitates brood size reduction in times of food shortage, to that size for which the parents can find sufficient food, by causing young that would die anyway to succumb as quickly as possible. However Lack and other authors (Ricklefs, 1965) do not discuss the degree of asynchrony that is most efficient in bringing about this brood reduction. It appears from this study that the size difference associated with eggs hatching on the same day are such to give all nestlings a reasonable survival probability, while not removing the possibility of brood reduction if food is very short. However it seems that asynchrony of one or two or more days between the hatching of the first and last eggs commits the smaller nestlings to a low survival probability in certain cases, and because these differences are forcibly imposed on the laying bird by severe food shortages during laying rather than being the usual strategy, it is evident that not all asynchronous hatching is a mechanism to enhance nestling production. This degree of asynchrony in hatching

seems to be more likely to reduce the number of young raised or at least surviving until breeding, rather than increase it. For example of several first broods of 5 young in 1969, only one fledg¹ing left the nest with a winglength significantly less than the other members of the brood. This was a nestling that hatched two days after the other four synchronously hatching young, which had winglengths of 100 + mm by the 29th day, whereas the fifth nestling had a winglength of only 96 mm when it became fully independ^ent on the 32nd day. All the other broods of five at this time hatched synchronously. Also, in a 2nd brood of two, where food shortage would not be expected to be severe, one nestling hatching a day later than the other, by the ninth nestling day (9 days in nest for 1st hatched and 8 days for 2nd hatched) was only 36% of the heavier nestling's weight. Nestling 1. = 16.4 gms and Nestling 2. = 6.0 gms. This weight difference was continuously sustained throughout the whole nestling period and didn't resemble the sudden differences in weight that came about through food shortage. Food was known to be of average abundance through the whole period. It seems therefore that under certain conditions asynchronous hatching may disproportionately affect the last nestling to hatch, and the magnitude of this effect . . .

is probably most extreme in the smallest and largest brood sizes. However in normal conditions it probably serves the function proposed by Lack. The situation needs further study.

The determination of clutch size is a subject area extensively discussed by Lack (1954, 1966) in an attempt to explain the observed frequency of occurrence of different clutch sizes in the field. The problem has been investigated by many workers, some providing supporting evidence and others not. Many authors have concentrated their efforts in demonstrating that clutch size has evolved through differences in the productivities of different brood sizes, and have not favoured the approach which accepts that selection acts on the whole animal, where adult survival associated with different brood sizes may be of similar importance as the survival of nestlings. Lack argues that maximisation of the rate of production of the viable young is/most important factor in establishing a genotype in the population. However in certain species it is clear that maximisation of the annual production of young is not taking place, as in the Gannet (Sula bassana) (Nelson, 1964). However what appear to be breeding restraints could become established in a population by natural selection if

instead of a maximisation of yearly production, there was a
 the of individuals.
 maximisation of/lifetime production/ The disadvantage of
 jeopardizing reproductive potential in the short term, might
 be then compensated by increased long term reproductive
 potential by extended adult longevity. However the validity
 of this suggestion needs much more rigorous examination than
 I have been able to give it. Meanwhile evidence is presented
 (Section 9) which indicates that broods of the most frequently
 observed size are the least influenced by environmental
 disturbances and it is suggested that over a long period this
 will tend to minimise both nestling mortality and strains on
 the breeding adult, which will encourage longevity. I
 investigated survival of adults and fledged young over the
 year following ringing to see if adult or fledgling survival
 was influenced by the size of brood reared or the brood size
 If they were independent,
 of which they were a part./then the number of adults controlled
 alive in the following breeding season, rearing broods of
 known sizes in the first year, would be relatively represented
 in the same proportions as they were ringed. (The ringing
 totals and controls are presented in table 12.1). The
 percentages controlled from each brood size did not differ
 significantly from the proportional numbers of each category

Table 12.1.

The number of adults ringed known to be associated with different clutch sizes and the percentages of these recaptured in the following breeding season.

Clutch Size	No. Ringed	% Associated with Each Clutch Size	No. Ringed	% Associated with Each Clutch Size
1st Brood			2nd Brood	
2	5	9.4	9	20.0
3	4	7.5	31	66.6
4	34	64.1	5	11.1
5	<u>10</u>	18.8	<u>0</u>	0
Total	53		45	

Clutch Size	No. Recaptured in following breeding season	% Recaptures associated with each clutch size in first year	No. Recaptured in following breeding season	% Recaptures associated with each clutch size in first year
1st Brood			2nd Brood	
2	1	14.0	2	25.0
3	0	0.0	5	62.0
4	5	71.0	1	13.0
5	<u>1</u>	14.0	<u>0</u>	0.0
Total	7		8	

Table 12.1 (cont.)

The percentages of adults ringed, and recaptured in the following year, in relation to the clutch size with which they were associated. The data for first and second broods is combined.

Clutch Size	No. Ringed	% Associated with each clutch size
2	14	14.7
3	35	37.0
4	39	37.6
5	<u>10</u>	9.4
Total	98	

Clutch Size	No. Recaptured in following breeding season	% Recaptures associated with each clutch size in first year
2	3	20.0
3	5	33.0
4	6	40.0
5	<u>1</u>	7.0
Total	15	

Table 12.1 (cont.)

Retraps of House Martins (ringed as nestlings) in the breeding season following ringing, in relation to the size of brood in which they were reared.

<u>Clutch Size</u>	<u>No. Ringed</u>	<u>% Ringed</u>	<u>No. Ringed</u>	<u>% Ringed</u>
	<u>First Brood</u>		<u>Second Brood</u>	
2	14	3.6	25	8.3
3	63	16.4	221	73.2
4	209	54.4	56	18.5
5	98	25.5	0	0.0
Total	384		302	

<u>Clutch Size</u>	<u>No. Retrapped</u>	<u>% Retrapped</u>	<u>No. Retrapped</u>	<u>% Retrapped</u>
	<u>First Brood</u>		<u>Second Brood</u>	
2	0	0.0	0	0.0
3	1	25.0	1	50.0
4	1	25.0	1	50.0
5	2	50.0	0	0.0
Total	4		2	

The results for both first and second broods combined.

<u>Clutch Size</u>	<u>No. Ringed</u>	<u>% Ringed</u>
2	39	5.6
3	284	41.4
4	265	38.6
5	98	14.2
Total	586	

<u>Clutch Size</u>	<u>No. Retrapped</u>	<u>% Retrapped</u>
2	0	0
3	2	33.3
4	2	33.3
5	2	33.3
Total	6	

Retraps from first and second broods in relation to the proportion of nestlings ringed in each brood.

	<u>Total Ringed</u>	<u>% of Total Nestlings Ringed</u>	<u>% of Total Retrapped in following year</u>
First Brood	384	55.9	66.7
Second Brood	302	44.1	33.3

that were ringed, except for 1st broods of 3 ($d = 28.3$
 $p = < 0.001$). The small size of the samples makes positive
conclusions impossible. There is no significant indication of
lowered adult survival associated with rearing different sized
first or second broods though it may be noted that adults
laying large first broods of 5 were recovered at a rate below
expectations and ^othese rearing broods of two survived better
than expected. Adults rearing the most frequent first brood
size, of four young, survived proportionately better than any
of the others. Similarly when the survival of young in
their first year was examined, there was no significant
indication of a reduced survival after fledging from any
brood size. However relatively more young were controlled
alive from the largest broods in both the first and second
broods. There are indications therefore that determination
of brood sizes, and hence clutch sizes in birds is likely to be
partly
/ a product of mortality acting on the adults which varies in
intensity according to the brood size (particularly first brood
size) that they rear. The ^{mor} ~~nat~~ality acting on the young
either within the nest or outside the nest gives no indication
that different intensities of mortality are associated with
different brood sizes that could give rise to different survival

rates of young emerging from different brood sizes. It must be emphasised however that these results are at a very low level of significance.

Ecological Isolation in aerial feeding birds has been discussed in relation to the size of prey available, and the structural characteristics of each species. However these differences in precise feeding niche have implications for other aspects of the breeding biology. They determine the broad timing of the season, the number of broods that can be raised in each year, the growth rates of the young and undoubtedly many other aspects.

Certain other topics of general interest are illustrated well by the House Martin. Firstly the subject of co-operative feeding of young, illustrated by the first brood nestlings of the House Martin feeding the second brood young in the nest. Skutch (1961a), White (1941) and Williamson (1941) have discussed its occurrence in the Hirundines. Lack (1968) discusses a few species in which the practice enables the adults to rear more young than they otherwise could. In this respect the adaptive significance is clear. It implies that co-operative feeding should occur in the largest broods if it is

to occur at all. However in 5 second broods, of one to five young each, observed in 1969, only the brood of three was helped in feeding by the first brood young. It must be noted though that the broods of 4 and 5 were artificially enlarged. There was no difference in fledging weight or wing lengths between the brood of three and the broods of four and five. Possibly therefore the advantage accrues to the first brood young involved in terms of "experience", which then fits them better for breeding in the following year. The other possibilities are for increased adult survival or survival of the young after fledging.

Nesting dispersion in the House Martin can be presumed to be both a reflection of the quality of the available food and the suitability of the nest site. Precisely how this is related to the size of each colony is less clear. Assuming population that the overwinter mortality is regulating the population, the/ is not ceiling/set by shortage of food in the early part of the breeding season. In fact there is no significant indication of density components in any of the mortalities examined. In this situation most colony sizes will not be limited, or only very imprecisely limited, by food shortage. However while there

may not be an absolute shortage of food, it may at times be sufficiently difficult to obtain and bring back to the nest, thus making it profitable for individual Martins to leave a colony, Martins feed in flocks, probably because they feed more efficiently in this way and also obtain protection from predators. They are brought together initially by aggregations of food, possibly through the process of local enhancement, and in this way optimise the efficiency of food location as well as rate of food collection. There is probably a level at which mutual interference in the feeding flock tends to reduce feeding efficiency. Certain members of these flocks may then disperse to other areas where the process could repeat itself. So ultimately there is a limit to the number of sites, especially during bad weather, where food can be exploited efficiently. In such a situation it may be necessary for the least efficient members of the colony to feed so far away from the nest sites that delivery of food to the colony becomes excessively energy consumptive. This process could provide the selection pressure to limit individual colony size through a consequent increase in adult or nestling mortality. Colony size may also be limited by the safety and number of the nest sites (though this is extremely unlikely as there were many

untenanted sites available in each colony that were identical to occupied sites) and parasite infestations. A recent study of the Purple Martin Progne subis (Wayne and Moss and Camin, 1970) has demonstrated how large parasite loads are usually associated with the least productive broods, and suggest that this might influence survival of the nestlings. It would thus be advantageous to shift colony sites away from areas of high parasite infestation if a similar situation pertained in the House Martin. However this is not thought to occur as discussed in Section 3.

Finally therefore, use of the aerial insect suction trap as a means of estimating the aerial abundance of insects has demonstrated the dependence of the biology of the House Martin upon the quantity and quality of the food available. This dependence however must go further than that dependence demonstrated here where the predator is influenced by the vagaries of its prey. Because the abundance of prey is determined by factors outside the immediate arena of the predator and most probably by weather factors though also by interactions within the insect populations. The outcome of these density independent mechanisms on the breeding strategy of

the House Martin has been demonstrated. It emphasises a need for density independent population processes acting on both prey and predator to be discussed, particularly in species exploiting food supplies with weather influenced abundance or availability, such as aerial feeding birds, Vespertilionid bats and seabirds. It is possible that such density independent effects determine the abundance of some species over considerable periods, though it appears that in the House Martin density dependent mortality outside the breeding season is the principal mechanism regulating the breeding population in spring. The intensity of this overwinter mortality however is largely related to the outcome of density independent responses by the House Martin to breeding season food abundance.

SECTION 13

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SECTION 14

APPENDIX

APPENDIX I

Specific Identity of House Martin Prey Items.

Dipteran Species

Bibionidae:- Dilophus febrilis

Empididae:- Hilaria sp.

Syrphid Syrphus ribesii

Anisopodidae:- Anisopus fenestralis

Stratiomyidae:- Beris vallata or chalybeata
Microchrysa polita

Rhagionidae:- Rhagio lineola

Tabanidae:- Haemotopsta pluvialis

Phoridae:- Megaselia halterata

Sepsidae:- Sepsis fulgens

Chloropidae:- Oscinella frit

Calliphoridae:- Lucilia caesar

APPENDIX II.

Breeding Season Census data 1968 to 1970 at the two main colonies. 1. Kennels. 2. Sunninghill Park Farm (Home Farm).

Year	1968	1969	1969	1970	1970
Site	Kennels	Kennels	Farm	Kennels	Farm
No. of pairs in boxes	14	14	11	17	12
Mean Clutch Size (1st)	3.50	4.71	4.27	4.00	4.00
Natality (1st clutch)	49	66	47	68	48
Total Young Hatching	43	49	42	52	46
Total Young Flying	38	44	41	51	45
No. of pairs laying 2nd clutch	10	11	9	14	11
% pairs laying 2nd clutch	71.4	78.5	81.8	82.3	91.7
Mean Clutch Size (2nd)	3.10	2.82	3.00	2.78	3.09
Natality (2nd clutch)	31	31	27	39	34
Total Young Hatching	27	30	24	36	29
Total Young Flying	25	29	20	35	28

APPENDIX III.

Data for (K)-factor analysis.

Log 10 of population data	1968 Kennels	1969 Kennels	1969 Farm	1970 Kennels	1970 Farm
Maximum potential first clutch natality	1.8192	1.8195	1.7144	1.9031	1.7522
k_1	0.1290	0.0000	0.0423	0.0706	0.0710
Actual first clutch natality	1.6902	1.8195	1.6721	1.8325	1.6812
k_2	0.0567	0.1293	0.0489	0.1165	0.0184
Total young hatching	1.6335	1.6902	1.6232	1.7160	1.6628
k_3	0.0537	0.0467	0.0104	0.0084	0.0096
Total young flying	1.5798	1.6435	1.6128	1.7076	1.6532
Maximum potential second clutch natality	1.5996	1.5996	1.4949	1.6842	1.5328
k_4	0.1082	0.0668	0.0493	0.0467	0.0000
Potential second clutch natality	1.4914	1.5328	1.4456	1.6375	1.5328
k_5	0.0000	0.0414	0.0142	0.0464	0.0013
Actual second clutch natality	1.4914	1.4914	1.4314	1.5911	1.5315
k_6	0.0600	0.0143	0.0512	0.0348	0.0691
Total young hatching	1.4314	1.4771	1.3802	1.5563	1.4624
k_7	0.0335	0.0147	0.0792	0.0122	0.0152
Total young flying	1.3979	1.4624	1.3010	1.5441	1.4472
(K_B) Total Breeding Season Mortality	0.4411	0.3132	0.2955	0.3356	0.1846

APPENDIX IV.

Multiple Regression Analysis to examine the influence of named variables on nestling growth rates.

Brood Size	F	$(\beta Wts)^2$						Correlation Coefficients (r)						r^2	N
		1	2	3	4	5	6	1	2	3	4	5	6		
2	0.6 N.S	0.8	0.0	0.4	0.0	0.4	0.3	0.36	0.50	-0.22	-0.35	0.49	0.25	33%	14
3	6.7 15%	1.6	0.4	0.2	0.0	0.2	0.2	0.72 3%	0.50	-0.77 2%	-0.46	0.22	-0.18	95%	9
4	6.2 1%	0.7	0.1	0.0	0.5	0.1	0.0	0.52 1%	0.13	0.01	-0.29	-0.03	-0.09	66%	26
5	1.8 20%	1.3	1.0	0.2	0.0	0.0	0.0	0.59 3%	0.21	-0.04	0.22	0.39	-0.22	53%	17
1	65.3 10%	3.9	0.4	1.0	0.0	1.9	0.3	0.35	-0.15	-0.10	0.39	0.30	-0.28	99%	9
2	6.2 1%	0.0	0.0	0.4	0.1	0.2	0.0	0.47 5%	0.10	-0.81 1%	0.60 1%	-0.72 1%	0.20	79%	17
3	1.2 30%	0.0	0.0	0.1	0.0	0.0	0.2	0.01	0.03	-0.24	0.22	-0.16	-0.36 5%	21%	33
4/5	2.4 10%	0.3	0.1	0.2	0.5	0.2	0.3	0.53 5%	0.47	-0.49	0.73 1%	-0.55 5%	-0.02	67%	14

(Second Broods of 4 and 5 were combined to increase the significance of F).

Appendix IV (cont.)

Multiple Regression Equations for first and second broods of named size.

Brood
Size

Multiple Regression Equations

$$\begin{aligned}
 2 \quad Y &= 1191.7 + 157.2X_1 - 8.7X_2 - 1.9X_3 - 6.4X_4 + 9.6X_5 - 12.3X_6 \\
 3 \quad Y &= -501.4 + 107.5X_1 - 7.7X_2 - 0.4X_3 + 1.7X_4 + 3.16X_5 + 2.9X_6 \\
 4 \quad Y &= +1796 + 50.9X_1 + 3.0X_2 + 0.2X_3 - 10.5X_4 + 2.7X_5 - 1.2X_6 \\
 5 \quad Y &= -734 + 119.7X_1 - 25.5X_2 - 1.3X_3 - 5.7X_4 + 0.1X_5 - 2.8X_6 \\
 \\
 1 \quad Y &= -364 + 174.7X_1 + 15.8X_2 + 1.2X_3 - 2.8X_4 + 20.4X_5 - 2.2X_6 \\
 2 \quad Y &= +225.1 + 22.7X_1 - 1.0X_2 - 0.6X_3 - 0.7X_4 - 3.2X_5 - 0.4X_6 \\
 3 \quad Y &= +295 - 5.1X_1 + 0.8X_2 - 0.6X_3 - 0.8X_4 + 0.6X_5 - 1.4X_6 \\
 4/5 \quad Y &= -479.0 + 25.3X_1 - 2.4X_2 - 1.3X_3 + 3.1X_4 + 2.3X_5 + 0.7X_6
 \end{aligned}$$

X_1 Insect Abundance. Total Catch (Log Transformation)
 X_2 Mean Day Temperature $^{\circ}\text{C}$
 X_3 Rainfall - Duration (Hours)
 X_4 Daylength
 X_5 Wind Index. (Speed x Duration of Wind over daylight period). (Knots x Hours 08.00 - 16.00)
 X_6 Mean Calorific Value of available prey.
 Y Growth Index.

APPENDIX V.

Multiple Regression Equations describing the relationship between Nestling Weight and Winglength on Day 25 and named environmental variables.

Nestling Weight on Day 25.

$$y = 13.4 - 1.35X_1 - 0.52X_2 - 0.63X_3 + 5.02X_4$$

Nestling Wing length on Day 25.

$$y = 83.5 - 0.98X_1 - 2.07X_2 - 1.59X_3 + 6.93X_4$$

X_1 = Weight on third day

X_2 = Hatching Order

X_3 = Brood Size

X_4 = Insect Abundance