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THE USE OF TIME AND ENERGY BY AERIAL FEEDING BIRDS

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ABSTRACT

The breeding and feeding ecology of the Swallow, Hirundo rustica, and the Sand Martin, R. riparia, in Central Scotland is described, with particular reference to the constraints imposed by environmental conditions. The time and energy investment in reproduction was examined for all stages of the breeding season in a wide variety of environmental conditions. Brood sizes were manipulated to change the investment of each parent in the brood. The D_2O^{18} technique was used to measure flight costs (0.0848 kcal $g^{-1}h^{-1}$ for the Swallow, 0.1288 kcal $g^{-1}h^{-1}$ for the Sand Martin) and the rate at which each species collected food under a variety of conditions was examined (mean values were 0.14 assimilable kcal min^{-1} for the Swallow, 0.05 assimilable kcal min^{-1} for the Sand Martin). These data, along with measurements of the nestlings' daily energy requirements, were used to investigate energy balance and the consequences for the timing and level of each breeding attempt.

It is suggested that the Swallow lays later than the Sand Martin because (a) it takes larger insects and does not lay until these become abundant and (b) the female Swallow incubates alone whereas both Sand Martin sexes incubate, hence the Swallow defers laying until the risk of encountering bad weather during incubation is low.

On 65% of the days on which measurements were made Sand Martins were unable to feed adequately a brood of five or more nestlings (31% of days for the Swallow) because foraging rates were depressed by bad weather. The risk of encountering bad weather is thus likely to limit the upper level of brood size.

Energetics data are used to show that parents feeding nestlings maximise the net intake rate of energy rather than that of nutrients (protein, sulphur or calcium). The Swallow's diet includes non-preferred small items, especially when these are relatively abundant, even when the preferred large items are available - contrary to predictions of optimal foraging models. It is shown, however, that foraging effiency is high when small items are taken.

In agreement with central place foraging theory the bolus size of Sand Martins is mainly determined by the distance travelled to the feeding site. This is not always the case, however, since patch and prey quality and the search methods employed have a greater influence on the bolus size of the Swallow.

Overall, the study allowed the scope for breeding activity for hirundines under different conditions to be defined and showed the importance of each species' reproductive and foraging strategies in optimising the number of offspring produced.

CHAPTER 1

1. INTRODUCTION

1.1

The allocation of time and energy to different often conflicting activities concerned with self-maintenance and reproduction is clearly important for any animal. During the breeding season in particular demands on a parent's time and energy will be high; hence individuals which optimise choices between various activities will be favoured by natural selection.

The question of how animals partition their available time and energy between behaviours has been studied using time budgets. These have progressed over the last few decades from the basically descriptive work of Verbeek (1964) on the Brewer's Blackbird, _Euphagus cyanocephalus_ and Verner (1965) on the Long-billed Marsh Wren, _Telmatodytes (Cistothorus) palustris_, to their use in studying foraging strategies (Wolf and Hainsworth 1977) and the costs and benefits of territoriality (Pyke 1979a). Comparatively few studies have considered the sensitivity of the time budget to environmental influences and constraints, although activity may be greatly affected in this way. The Verdin, _Auriparus flaviceps_, for example, reduces its foraging time considerably when environmental heat gain is high (Austin 1978).

The investigation of time budgets alone, without a knowledge of the animal's energy requirements, is of limited value; hence time budgets are usually converted to energy budgets (for example Wolf 1975, Wolf and Hainsworth 1971, 1975, 1977 on sunbirds and hummingbirds). However, this ideal is hard to meet since the energetic cost assigned to each behaviour has not usually been measured for the species concerned. Instead metabolic rates are often calculated from equations obtained for broad taxonomic groups or even less satisfactory approximations may be used. Flight metabolism, however, has been measured directly by O_2 consumption in the hummingbird studies mentioned above, by telemetry of heart rates in the Black Duck, Anas rubripes, (Wooley and Owen 1978), and by the D_2O^{18} technique for a few species including the Purple Martin, Progne subis, (Utter and Lefebvre 1970) and the House Martin, Delichon urbica, (Hails 1977, Hails and Bryant 1979, Bryant and Westerterp in press). The latter technique is especially useful as it can accurately measure the metabolic rate of free living, rather than captive, animals.

Energetics models have often been concerned with non-breeding animals (e.g. Gill and Wolf 1979a, b; Morrison 1978; Powell 1979) but they are also of considerable use in understanding how the foraging and reproductive strategies of animals might maximise fitness (e.g. Siegfried, Burger and Frost 1976, Yom-Tov and Hillborn 1979, Bryant and Westerterp in press). Of particular interest is the effect of constraints on the timing and level of the breeding effort, a clearly important fitness parameter. Food supply is usually considered important in this respect: a seasonal abundance of food is commonly exploited by species for a period of growth and/or reproduction. It has been argued by Gibb (1950), Lack (1954) and Perrins (1970) that the presence of young birds in the nest often coincides with the time of greatest food abundance. Perrins (1970) further suggested that food shortage before egg laying could delay the onset of breeding and Lack (1947) put forward the view that brood size in birds depends on the ability of the parents to feed the nestlings. Large broods or those outside the main breeding period might thus be subjected to a food shortage.

An efficient use of this food supply is obviously important to any animal, especially if energy demands are high, food is scarce or feeding time is limited. The predator is therefore likely to maximise its net intake rate of energy or of some other "currency". This idea forms the basis of optimal foraging theory. Although early work on predation was concerned with the functional response (Holling 1959a, b), hunting by expectation (Gibb 1958, 1962), searching images (Tinbergen 1960) and hunting in profitable areas (Royama 1970), recently emphasis has been placed on optimal foraging behaviour. Much of the work has been theoretical in nature (Schoener 1969, 1971, Rapport 1971, Charnov 1973, Pulliam 1974, Werner and Hall 1974). Evidence supporting the predictions of optimal foraging theory has come from a number of experimental studies on birds (Krebs, Ryan and Charnov 1974, Krebs, Erichsen, Webber and Charnov 1977, Cowie 1977), mammals (Emlen and Emlen 1975, Dunstone and O'Connor 1979a, b), fish (Werner and Hall 1974, Werner 1977) and arthropods (Charnov 1976, Elner and Hughes 1978, Hubbard and Cook 1978, Pyke 1979b, Waage 1979), but few field studies have been made (Davies 1977a, b, Goss-Custard 1977a, b, c). A recent development has been the study of central place foraging (Orians and Pearson 1979). Feeding behaviour, in this case, is restricted because the predator has to bring food back to a fixed point such as a nest or a food cache. As yet, however, little work has been done on this topic.

Besides having a foraging strategy based on optimality principles an animal will have an optimal reproductive strategy, i.e. one which will maximise its contribution to the gene pool. However, the investment of time and energy in reproduction during any one breeding season entails costs to the parent which may affect its future reproductive output. A possible link between reproductive output and parental mortality has been explored by several authors (Emlen 1970, Gadgil and Bossert 1970, Goodman 1974, Schaffer 1974, Stearns 1976). There is indirect evidence for increased mortality or weight loss for birds feeding large broods (Klujver 1952, 1970, Snow 1958, Campbell in Lack 1966, Newton 1966b and Hussell 1972) and confirmation of such a link has been shown for the female House Martin (Bryant 1979) and the male Pied Flycatcher, Ficedula hypoleuca, (Askenmo 1979). Hence each parent will balance current reproductive investment against its need to maximise its lifetime contribution to the gene pool.

The theories of optimal reproductive tactics, the optimal allocation of time and of optimal foraging behaviour are closely linked (Pianka 1976). In addition, the overall breeding system of a species may be closely associated with the nature of its food supply. For example, Crook (1964) compared the social organisation (coloniality, territoriality and mating system) of weaver birds, the Ploceidae, in relation to the distribution in time and space of food and nest sites and to the effects of predation. Forest species, for instance, space out their nests in response to a dispersed food supply and predator pressure; savannah species nest colonially feeding on clumped but temporary food sources. This analysis of breeding biology in relation to environment has been extended to other bird species by Crook (1965) and Lack (1968) and to primates (Clutton-Brock and Harvey 1977).

The aim of this thesis has been to define the scope for breeding activity of two hirundines, the Swallow, Hirundo rustica, and the Sand Martin, R. riparia, under different conditions; in particular to investigate limitations on (a) the timing of laying and (b) the upper brood size. Accordingly the foraging ecology of these hirundines has been investigated, an energetics model has been constructed from time budgets and flight costs have been measured by the D_2O^{18} technique. Predictions of optimal foraging and central place foraging models were tested in this field study. The investment in reproduction of these hirundines has been examined under normal and experimental conditions.

1.2 Description of the Study Area

This study was made in the vicinity of the University of Stirling (O.S. 1:63,360 reference NS 808 965). The Swallow nest sites were on low lying, rather evenly spaced farms. The surrounding fields were mixed arable and pasture land. The Sand Martin colony (250-300 pairs) was situated in a sand quarry near Dunblane 8 km from the University. Other, smaller colonies in the area were present along river banks.

1.3 Description of the Study Species

This study was made on the Swallow, *Hirundo r. rustica*, and the Sand Martin, *R. riparia*. Reference is also made to the third British hirundine, the House Martin, *Delichon urbica*, and to the common Swift *A. apus*. The Sand Martin, the smallest of these birds, the House Martin and the Swift are colonial species. The Swallow may nest alone or in small groups. In North America the Sand Martin is called the Bank Swallow, and the Swallow, a different subspecies, *H. r. erythrogaster*, is called the Barn Swallow. Details of the measurements and breeding biology of the Swallow and Sand Martin are given in the text. All species are summer migrants to their breeding ground.

CHAPTER 2

2. FOOD AVAILABILITY AND DIETARY REQUIREMENTS

2.1 Introduction

Hirundines and Swifts, with one exception, feed solely on insects, usually catching them in flight, but occasionally picking them from leaves and flowers. The exception is the Tree Swallow, Tachycineta bicolor, which will take berries, especially the Bayberry, Myrica carolinensis, mainly in bad weather conditions when insects are scarce (Beal 1918).

Insects form a balanced, nutritious diet but their absolute abundance and the relative abundance of particular types can vary considerably seasonally and from day to day, since they are greatly influenced by prevailing weather conditions (Williams 1961). Hence their predators are faced with a varying, unpredictable food supply.

In Britain insects are always scarce over winter and aerial feeding insectivores either migrate (birds) or hibernate (bats). In summer, insect abundance is usually high but is still unpredictable since some days may be cold and wet even in midsummer. Thus the production of offspring by an individual, and by the population as a whole, will be very much influenced by the availability of insects in any one year.

The period of greatest energy demand for a hirundine in Britain is during nestling rearing (Bryant and Westerterp in press). This stage coincides with generally high insect numbers (Bryant 1972) but there may be other constraints on the adult bird: specific nutrients may be required (Jones 1976, Dolnik and Gavrilov 1979), and the time available for feeding may be limited.

Bryant (1972) investigated reproduction in the House Martin in relation to the food supply. In the present study the effects of a varying food supply on the behaviour and reproductive output of Swallows and Sand Martins were considered.

This section examines the availability and nutritional value of the insect prey during the breeding season and the energetic and nutritional demands of the nestlings.

METHODS

2.2.1 The Food Supply: the Measurement of Food Availability

The food available to the birds was monitored in two ways: with a 12.2m high suction trap (Johnson 1950a, b, Taylor 1962, Taylor and Palmer 1972, Bryant 1973) and with a fine mesh butterfly net (Parker 1949, Linsley, Macswain and Smith 1952, Nielson 1963).

The aerofoil trap was sited in the University campus 2-5 km from the Swallow nest sites and 8 km from the Sand Martin colony. This trap draws air vertically downwards (to avoid directional effects) through 1mm mesh gauge and all trapped insects are collected in plastic bottles at the base of the conical filter. It samples air at a constant rate throughout the day, it is non-selective with respect to insect size and it is neutral in attraction. The centrifugal fan in this trap ensures a constant air intake ($2.86 \times 10^3 m^3 h^{-1}$) in almost all wind speeds (Taylor and Palmer 1972). It is designed to sample a randomly dispersed insect population and is high enough to exclude local insect populations, which are most common near to the ground (Waugh 1978). The insect samples were considered to adequately reflect the availability of taxa to birds feeding on aerial 'plankton', especially the House Martin and Swift.

The growth of nestling House Martins, for instance, correlates well with aerial insect abundance measured in this way (Bryant 1973).

The Swallow and, to a lesser extent, the Sand Martin, however, feed closer to the ground and exploit local concentrations of insects not represented in the suction trap catch. They also take large insects which are more abundant lower down than at the height of the suction trap (Waugh 1978). Another disadvantage of the suction trap in this study was that the catch was not segregated into the short time periods (1 - 3h) required for time budget and feeding rate studies.

To overcome these problems a fine mesh net (< 1mm) was used to sample the prey available at the sites where the Swallows were feeding. At each site insects were collected by sweeping the net back and forth for 50 to 150 strokes between 0.3 and 2m above the ground: the most frequent feeding station of Swallows (Waugh 1978). The suction trap was used to obtain a measure of overall insect activity.

It was not usually feasible to sample the sites used by foraging Sand Martins with a net because of the distance of the feeding site from the nest site, the greater height of the birds when feeding and the inaccessibility of some feeding sites. For these reasons the suction trap catch alone was used as an estimate of prey availability.

The suction trap was emptied daily at 1000h BST; the volume of the catch was measured and the sample stored in methanol/glycerol (10:1) solution. For those days when a measure of food availability was required the catch, or 13% sub-samples of large catches, was counted and sorted into readily identifiable taxa on the basis of the wing venation (Chinery 1976).

Bryant (1973), in his study of House Martins, excluded the very small, numerous Thysanoptera, but they were never abundant (in terms of numbers or biomass) in this study and they were included in all calculations. Large Hymenoptera were included, although not often eaten by aerial feeders, since they formed an insignificant part of the numbers in the samples. Some taxa have more than 50% of their flight periods after dusk and before dawn (for example Psychodids and Chironomids, Lewis and Taylor 1965) but Swallows and Sand Martins will take individuals of mainly crepuscular orders so these were included unless otherwise stated.

Immediately following collection of a net sample, the insects were killed by placing the end of the net in a vapour jar (chloroform). The samples were deep frozen until the insects could be counted and sorted into taxa on the basis of the wing venation (Chinery 1976). All the insects in a sample were counted and used in subsequent calculations.

Individuals of each taxon in the net samples, and in the suction trap samples or sub-samples, were measured in wing length to the nearest millimetre.

For further calculations the number of items in, and the volume or dry weight of, the insect samples were transformed logarithmically since House Martin breeding biology is most closely related to the logarithm of insect abundance (Bryant 1973).

The net sample is greatly affected by the behaviour of the insects which may depend on the stage of the life cycle, weather and diurnal cycles (Romney 1945 , Hughes 1955, Saugstad, Bram and Nyquist 1967) but it should provide a good estimate of those insects which are flying and are thus available to hirundines. The efficiency of sampling varies with the collector; a rapid sweeping will provide a larger catch (Balogh and Loksa 1956) and be more likely to catch fast flying insects.

In this study the effects of diurnal changes, site, weather and season on the net sample were investigated; an estimate was made of the effect on the catch of increasing the number of sweeps per sample; and the size of the net sample was compared to the size of the suction trap catch on different days.

During the study standard meteorological measurements were obtained from the meteorological station at the University of Stirling. In addition, weather variables were noted when net samples were taken. These variables included ambient temperature, rainfall, wind strength and cloud cover. The weather was classed as follows:

Good

when (a) Temperature > 15°C, no rain, little or no wind,

or (b) Temperature > 17°C, some rain and/or wind,

Intermediate

when (a) Temperature > 15°C ≤ 17°C, some rain and/or wind,

or (b) Temperature > 17°C, very heavy rain and/or strong wind,

or (c) Temperature ≥ 13°C ≤ 15°C, dry, little or no wind,

Bad

when (a) Temperature < 13°C, wet or dry, windy or calm,

or (b) Temperature ≥ 13°C ≤ 15°C, wet and/or windy.

2.2.2 The Food Supply: Size

The size of an insect is important to a predator in two ways: large insects provide more calories per prey item than small insects yet the capture of large, fast items may also involve a longer pursuit and handling time. The energy cost of capture would thus be increased. Lewis and Taylor (1967) loosely correlated increasing flight speed with increasing size in insects. Flight speed, however, varies with the type of insect and is more dependent on the ratio of body length to wing length than on wing length alone (Lewis and Taylor 1967).

In this study insect dry weight was used as a measurement of size. The weight of a prey item is a direct measure of the calories it provides and is also a better indicator of the speed of the insect than wing length alone.

A formula relating wing length and dry weight was obtained for freeze-dried insect specimens.

2.2.3 The Food Supply: Body Composition

The body composition of insects was examined to determine their nutritional value. Insects collected in a 1.8m suction trap were sorted into separate taxa and freeze-dried. Determinations were made of calcium, sulphur, chitin, lipid, nitrogen and ash content and of the calorific value on a number of insects collectively.

Calcium determination

A number of insects of each taxon were weighed collectively and digested in concentrated nitric acid on a hot-plate at 50°C. The solutions were analysed for calcium ions with a Perkin-Elmer atomic absorption spectrophotometer. Standards of 1ppm and 2ppm were run at the beginning, end and at intervals during, a sequence of analyses. Each solution was sampled twice. Deionised water was used for making up solutions and washing equipment. The solutions were kept in plastic bottles, since ions can be transferred from glass into solution.

Because of the high level of phosphorus in animal tissues which depresses the sensitivity of the spectrophotometer for calcium, lanthanum chloride was added to both samples and standards bringing the final solution to a concentration of 1% lanthanum.

Sulphur determination

The turbidimetric method was used to test for sulphate (Allen, Grimshaw, Parkinson and Quamby 1974). A number of insects were digested in warm, concentrated nitric acid and the solutions made up to 25 ml. An aliquot of the sample was pipetted into a 25 ml volumetric flask and 2.5 ml of 50% acetic acid and 0.5 ml of orthophosphoric acid were added and mixed. 1g of barium chloride crystals was added and the solution was left for 10 minutes. The solution was then made up to 25 ml (solution b), the flask inverted several times and left to stand for 1.5 hours. A blank was similarly prepared with deionised water and standards of 1, 5, 10, 25 and 50µg SO_4-/ml were made up.

The turbidity was measured with reference to the blank with an absorption spectrophotometer at a wave length of 470nm.

The percentage of sulphur in the insect material equals

$$\frac{\text{concentration sol't} \times \text{volume sol't a} \times \text{volume sol't b}}{10 \times \text{aliquot volume} \times \text{weight of original material}}$$

Solution a = original solution.

Three determinations were made for each taxon.

Chitin determination

A known weight of insects was digested in sodium hydroxide solution to remove the soft tissue, the solution was filtered and the chitin residue weighed.

Lipid determination

Lipid was removed from a number of insects in a soxhlet apparatus using a diethyl ether : chloroform solvent (80 : 20 parts by volume).

Nitrogen determination

Homogenised insects were examined for nitrogen in a Perkin-Elmer nitrogen-carbon gas analyser.

Ash determination

A number of insects were ashed at 450°C. The temperature was increased from 250°C in steps of 50°C, every 4h to avoid splatter. Volatilization of potassium may occur at temperatures above 450°C. Samples remained in the furnace for 16h.

Calorific value

This was determined by bomb calorimetry (microbomb calorimeter, Phillipson 1964).

Water content

The wet/dry weight ratio was determined from insects freshly caught and anaesthetised with chloroform. The insects were weighed, freeze-dried and reweighed.

2.3 Techniques of Dietary Analysis

The diet was examined both directly from choker samples and indirectly by faecal analysis.

2.3.1 Choker Experiments

This method has been used successfully in other studies, especially on aerial feeding birds (Lack & Owen 1955, von Gunten & Schwarzenbach 1962, Waugh 1978).

Throughout the season food boluses were obtained by tying knitting cotton round the necks of the nestlings, aged 8-17 days, to prevent swallowing. The collars were kept in place for two hours at a time. The food was then removed from the throat of the nestling and from the nest and floor where boluses had fallen after ejection by the nestling. A time period of two hours was chosen to give the parents sufficient time to become accustomed to the collared nestlings because after a lot of disturbance some birds would take an hour before bringing food back to the nest. The collars were not left on for longer so that begging rate and external weather conditions remained effectively constant. The nestlings were fed artifically after the collars were removed or between consecutive sampling periods, to guard against brood undernourishment.

It was assumed that each bolus represented one feeding trip by the parent. If one or two boluses were obviously small they were excluded from that period's sample. The parent will split boluses for small nestlings but rarely does so at least for older nestlings of House Martins (D.M. Bryant pers. comm.). It was not possible to see how often this occurred with Sand Martins as the nests were not easily observed. Feeding was closely observed at five nests of Swallows but bolus splitting was not seen.

As the parents were disturbed while boluses were being collected the birds were observed feeding the nestlings for an hour before collars were put on to determine the prevailing feeding rate and the time taken to collect a bolus. Disturbance by the experimenter reduces the number of feeding visits but not the prey selected nor the time taken to collect a bolus (Waugh 1978) so the boluses can be assumed to represent those normally brought to the nest in those conditions.

The food boluses were frozen and later dissected. The prey items were identified (to family) and the wing length was measured. The bolus was washed, freeze-dried and weighed. Any grit in the boluses was weighed separately.

2.3.2 Faecal Analysis

This method was used for investigating the diet of adults and also nestling diet when disturbance was undesirable (in brood size manipulation experiments for example). The diet was determined from the prey remains (wings) in the faeces collected from under the nest. In the case of Sand Martins faeces were sometimes obtained direct from the nestlings or adults when they were handled, sometimes from the floor of the quarry where they are dropped by the parents. In the latter case the faecal sample represents the colony's diet rather than a brood's diet.

Hartley (1948) discussed possible errors in this technique but Bryant (1973) and Waugh (1978) have satisfactorily used it to sample the diet of House Martins, Sand Martins and Swallows. Davies (1976a, 1977a) has shown that insect remains in the faeces of Pied Wagtails, Motacilla alba, correlate well with emetic samples and diets of known composition fed to captive birds. Similarly, Waugh (1978) has shown that the proportions of different prey types ingested and the proportions recovered for the Swallow nestling are in close agreement. The proportion of all prey recovered was found to be 34.2% for the Swallow (Waugh 1978) and 31.9% for a Pied Wagtail (Davies 1976b), but was 92.5% for a nestling Spotted Flycatcher, Musicapa striata (Davies 1977a). The amount of fragmentation and the conspicuousness of the remains may thus vary with the predator species.

These two methods of diet analysis were compared in the field by simultaneously collecting faecal samples and boluses from Swallow and Sand Martin broods. The faeces would have included items taken shortly before the nestlings were collared so were expected to be of a similar composition to the boluses.

2.4 Body Composition and Growth of Nestlings

Nestlings were weighed (to the nearest 0.1g, NW) and wing length measured (maximum chord, mm, NWL) in experimental and control broods throughout the breeding season. Some broods were measured regularly, others only occasionally. Pits were dug at the back of Sand Martin nests to allow access for examination of the broods. Eleven swallow and twenty one Sand Martin nestlings were taken for carcass analysis to determine their composition and energy content at different ages. They were weighed, sacrificed and frozen. Freeze-drying, lipid extraction (soxhlet 20% chloroform : 80% petroleum ether) and combustion for 16h at 450°C in a muffle furnace allowed calculation of the following weights: water content (W), dry weight (DW), lean dry weight (LDW), lipid weight (L), ash free lean dry weight (ALDW) and ash weight (Ah). The following indices were derived:

lipid index = L/LDW, water index = W/LDW, ash index = Ah/LDW.

The energy content was calculated by multiplication of the ALDW × 5.65 and L × 9.5 to yield energy content in kilocalories. A relationship between 'dry' energy density (DED kcal g^{-1} dry weight) and 'wet' energy density (WED kcal g^{-1} wet weight) and nestling age was derived. The product of average daily dry weight changes (Δ DW) and DED yielded daily growth increments (Pi).

The metabolic rates of nestlings were calculated from the metabolic intensities of nestling House Martins for different ages and brood sizes (given in Bryant and Gardiner 1979). Age-specific weights corrected for brood size were obtained from multiple regression equations.

Assimilation was calculated as the production (DED × Δ DW kcal dy^{-1}) plus respiration (R : kcal dy^{-1}) of the brood.

Faecal output of Swallow broods was measured over 22 nest-days for nestlings aged 8 to 17 days.

Asimilation efficiency was obtained for eight captive Swallow and Sand Martin nestlings of different ages on a mixed insect/meat diet.

The daily energy budgets (DEB) of Swallow and Sand Martin nestlings were obtained on 26 days from field data where feeding rates and food bolus sizes were known.

The nutritional demands of the nestlings and adults for protein, calcium and sulphur-containing amino-acids (SAA) were calculated from measured body composition and published data.

Nestlings were aged from the day the last egg in the brood hatched (= day 1). Statistics are given as the mean ± 1 s.d. Energy values are expressed in kilocalories (1 calorie ≡ 4.184 Joules).

RESULTS

2.5 The Food Supply

2.5.1 Seasonal Effects

Net samples from all sites are shown in Figure 2.1a, b, c. The numbers of large items and available prey sizes throughout the season are shown in Figure 2.1d, e. Details are given in Appendix 1.

Weather had the greatest influence on the numbers and biomass in the net catch, (Table 2.1). The season affected the catch at different times of the day, e.g. late in the season catches were still high early and late in the day. Available prey size (PS) and the number of large items (LI) were significantly higher after May ($t_{PS} = 7.13$, $p < 0.001$, $t_{LI} = 4.12$, $p < 0.001$).

The suction trap also showed clear seasonal effects (Figure 2.2) with an increase in abundance of insects during April to variable but sometimes very high values in May and June. There was a generally average to high catch in July and August although there can be marked differences between years. The catch decreased again towards the end of September when the birds start to migrate.

2.5.2 Diurnal Effects

Numbers and biomass in the net samples were highest at midday and early afternoon (Figure 2.1). Increases in numbers and biomass did not always coincide since items such as large Hymenoptera, Brachycera and Cyclorrapha reach peak numbers at this time (Lewis and Taylor 1965) so biomass may increase whether or not numbers do. Biomass remained high over most of the day especially in June and July.

Table 2.1

Analysis of variance of factors affecting the biomass of, and the number of items in, net samples for the months May to August in 1978 and 1979

1. Biomass

	Sum of Squares	Mean Square	F	d.f.	Significance
Weather[1]	5906.10	5906.10	8.67	1	$p < 0.05$
Month[2]	392.63	196.32	0.29	2	n.s.
Time of day	1247.92	178.27	0.26	7	n.s.
Time, Month	325.53	23.25	0.03	14	n.s.
Time, Weather	889.38	127.05	0.19	7	n.s.
Weather, Month	347.07	173.54	0.25	2	n.s
W, M, T	9537.74	681.27		14	

2. Numbers

	Sum of Squares	Mean Square	F	d.f.	Significance
Weather[1]	1074.56	1074.56	2.24	1	n.s.
Month[2]	30.86	15.43	0.03	2	n.s.
Time of day	467.32	66.76	0.14	7	n.s.
Time, Month	342.87	24.49	0.05	14	n.s.
Time, Weather	203.63	29.09	0.06	7	n.s.
Weather, Month	1380.43	690.22	1.44	2	n.s.
W, M, T	6716.04	479.72		14	

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[1] Weather was classed as good or bad, intermediate values were excluded.

[2] Month indicates May, June to mid July, mid July to August, representing the main periods of egg laying, 1st broods and 2nd broods respectively.

Figure 2.1

Diurnal variation in the abundance of prey items in the net catches.

Number of items in, and biomass of, the catch (50 sweeps) in May (a), June and early July (b), and late July and August (c).

squares = good weather catches,
circles = bad weather catches,
closed Symbols = biomass,
open symbols = numbers.

Means ± 1 s.d. are shown.

(d) Number of large items (≥ 1.5 mg dry weight) in the net.

squares = catches in May,
circles = catches in June and early July,
triangles = catches in late July and August.

Good weather catches only are shown.

(e) Mean prey dry weight (mg) in the catch. Symbols as in (d).

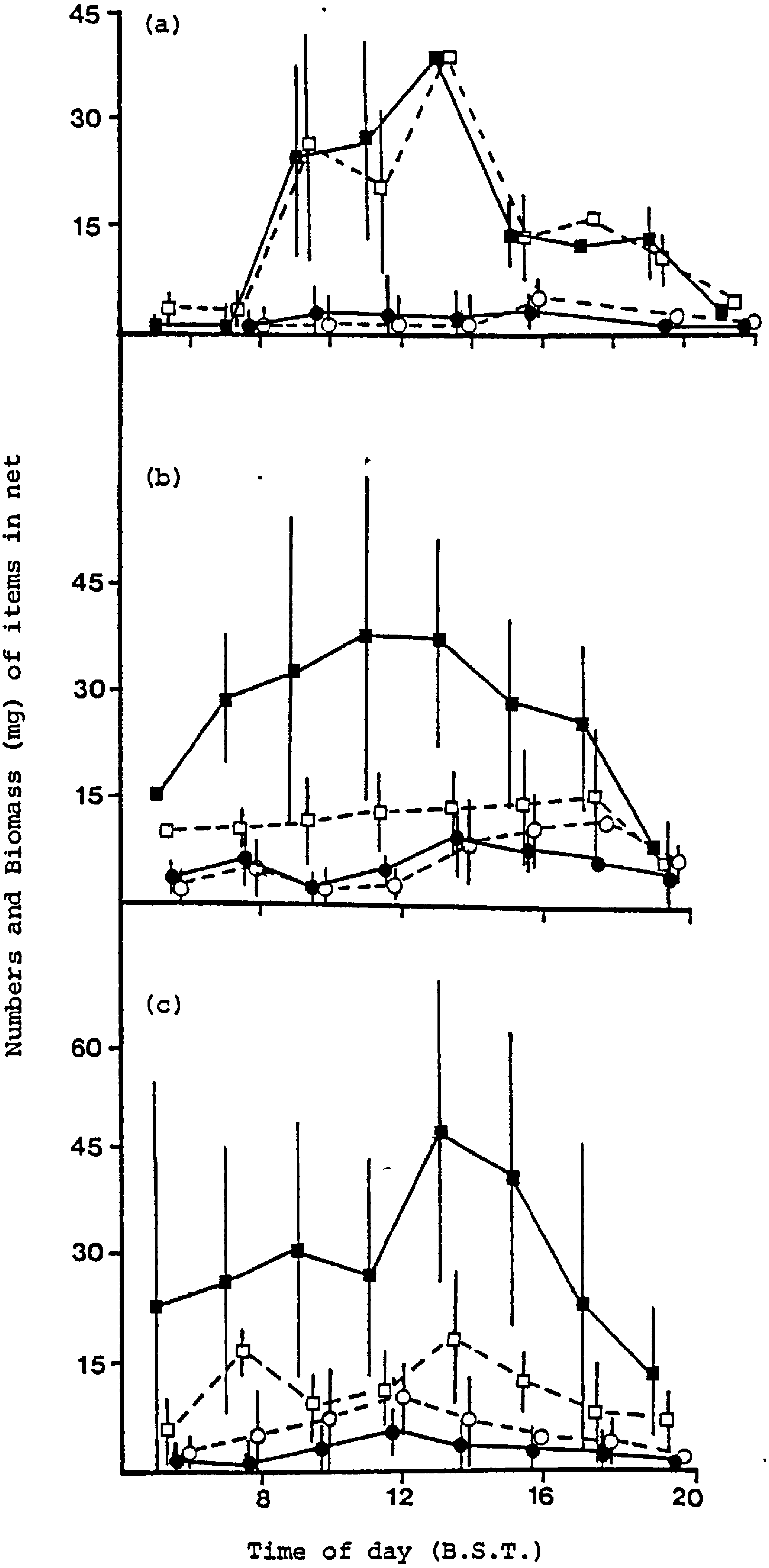


Figure 2.1 a, b, c.

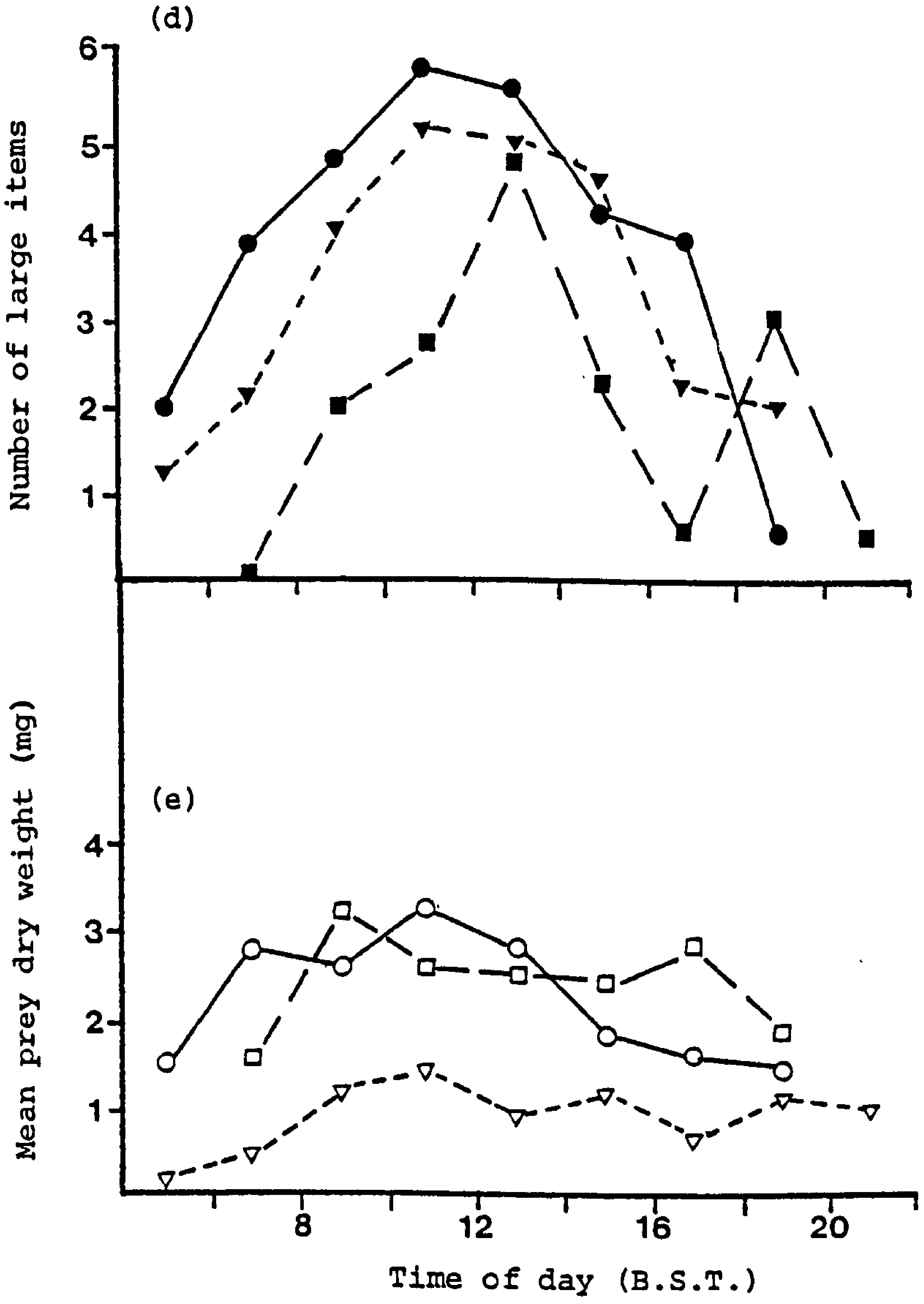
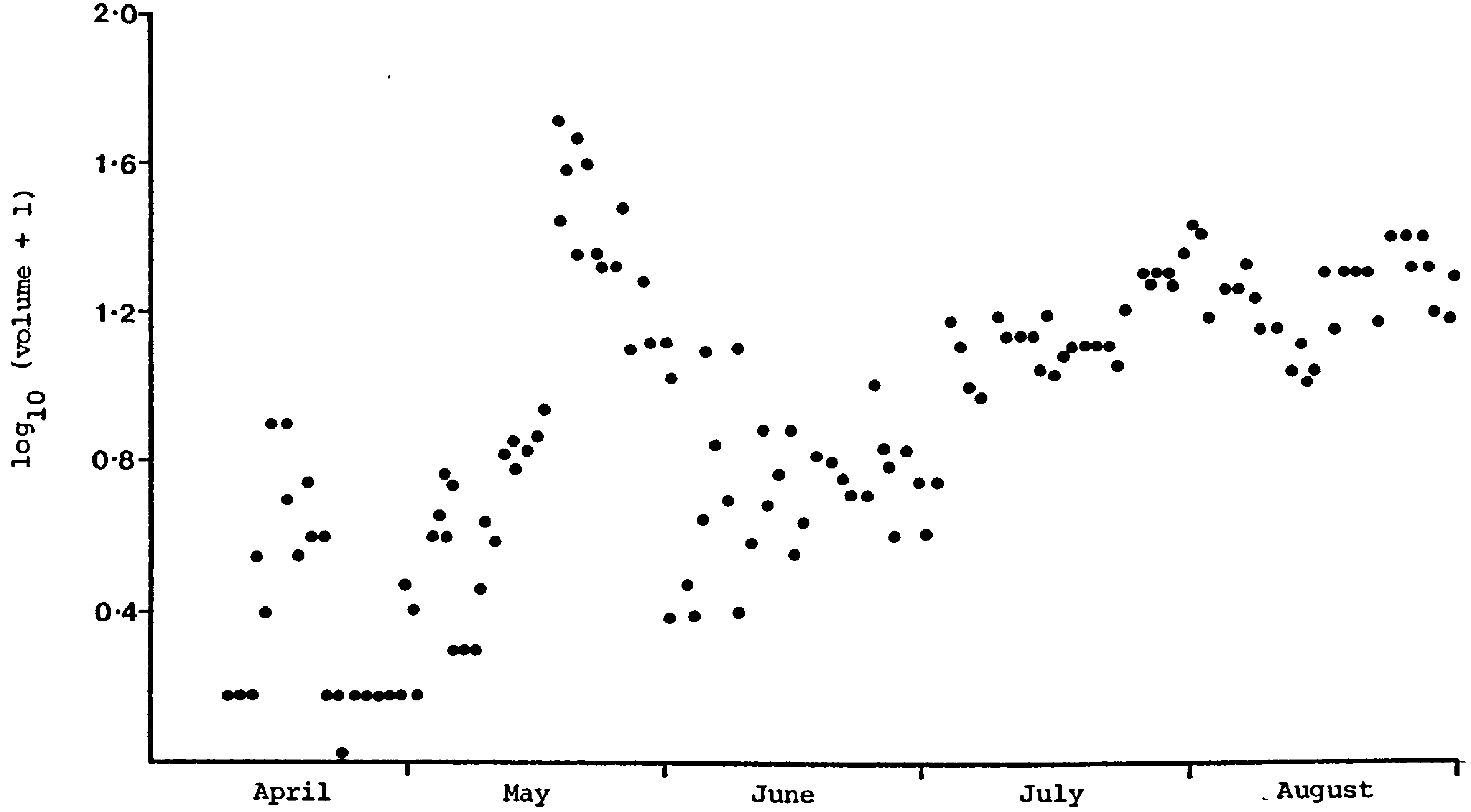

(d)
Number of large items
6
5
4
3
2
1
(e)
Mean prey dry weight (mg)
4
3
2
1
8
12
16
20
Time of day (B.S.T.)

Figure 2.1 d, e.

Figure 2.2

Seasonal variation in food abundance in 1978 as shown by the 12.2m suction trap.


2·0
1·6
1·2
0·8
0·4
log$_{10}$ (volume + 1)
April
May
June
July
August

2.5.3 Weather Conditions

Numbers and biomass of insects were kept low at any time of the season by cold, wet, windy weather. The effect sometimes lasted all day in which case the suction trap also showed a depressed catch, but sometimes only for a short period which depressed the net catch but had only a small effect on the suction trap sample. In windy conditions insects might still be abundant but they would be kept to shelter belts so would show more localised patches of abundance.

2.5.4 Site Differences

Three sites (pasture, lochside vegetation and arable/tall grass) were sampled on the campus at Stirling. Two hundred and fifty sweeps were taken at each site, three times a day (Figure 2.3). Catches at these sites were sometimes similar, sometimes very different; the best site on one day was not necessarily the best on another day. In particular the catch was greatly affected by the presence of fresh dung with the resulting attraction of Scatophagids, Borborids and Sepsids to the site. Slow flying or swarming insects such as these are over estimated by the net compared to strong flying items. This variability between sites is of particular importance to Swallows in their selection of a patch in which to feed.

These samples, however, still showed the trend of increased numbers and biomass during the season which was evident in the samples from the Swallows' nest sites.

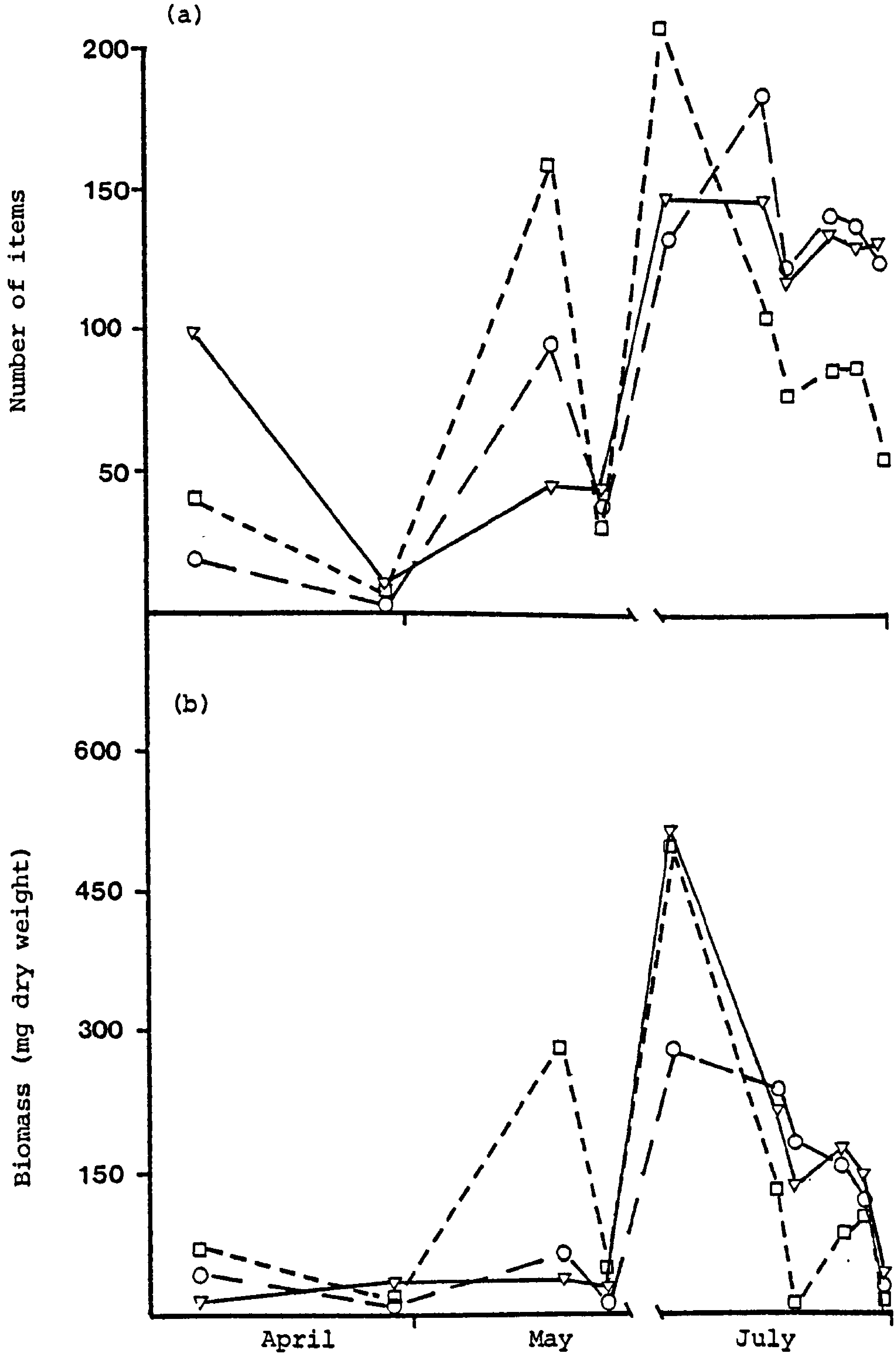
2.5.6 Sample Size

Samples of five sets of 50 sweeps were taken at each of the three sites on the campus to examine the effect of increased sample

Figure 2.3

Seasonal changes in insect abundance ((a) numbers, (b) biomass) in daily net samples at three sites on the campus at Stirling University:

triangles = arable site;
squares = pasture;
circles = lochside site.


(a)
200
150
100
50
Number of items
(b)
600
450
300
150
Biomass (mg dry weight)
April
May
July

size on the catch (Figure 2.4). The results are expressed as the ratio of $\log_{10}$ (Numbers +1) per 50 sweeps after 50, 100, 150 and 200 sweeps to the mean $\log_{10}$ (Number +1) per 50 sweeps in the full 250 sweeps. The variability decreased as the sample size increased from about 50% to about 25% for numbers of items. Biomass was more variable than numbers. The variability appeared more extreme in bad weather catches when one or more sets of 50 sweeps could contain nothing and others several small items. Hence, whereas 50 sweeps may be adequate in good conditions, 150 sweeps or more may be more appropriate in poor conditions. A 25% error in any conditions would still give an acceptable estimate of food availability.

2.5.7 Comparison of Suction Trap Catch with Net Sample

The above mentioned sites were sampled on 10 days from April to the end of July in 1979 three times a day and a site on arable land five km away was sampled during the afternoon on those days. The numbers of items in, and biomasses of, the catches are compared with those from the suction trap in Figure 2.5.

The correlations are close (r (numbers) = 0.82, $p < 0.01$, r (biomass) = 0.84, $p < 0.01$, $n = 10$) although there are several reasons for differences between the two. It took only a few minutes to obtain the net samples so the catch may not be representative of a longer time period especially when the weather is variable. The net will pick out some local concentrations not represented in the trap but equally other aggregations of insects not on the route taken may be missed. Temporary attractants such as fresh dung affected the net catch but not the suction trap catch; this occurred particularly at the site nearest to the suction trap. Winds also have a greater effect close to the ground than at 12.2m.

Figure 2.4

Variation in the net sample depending on the number of sweeps taken (see text for explanation).

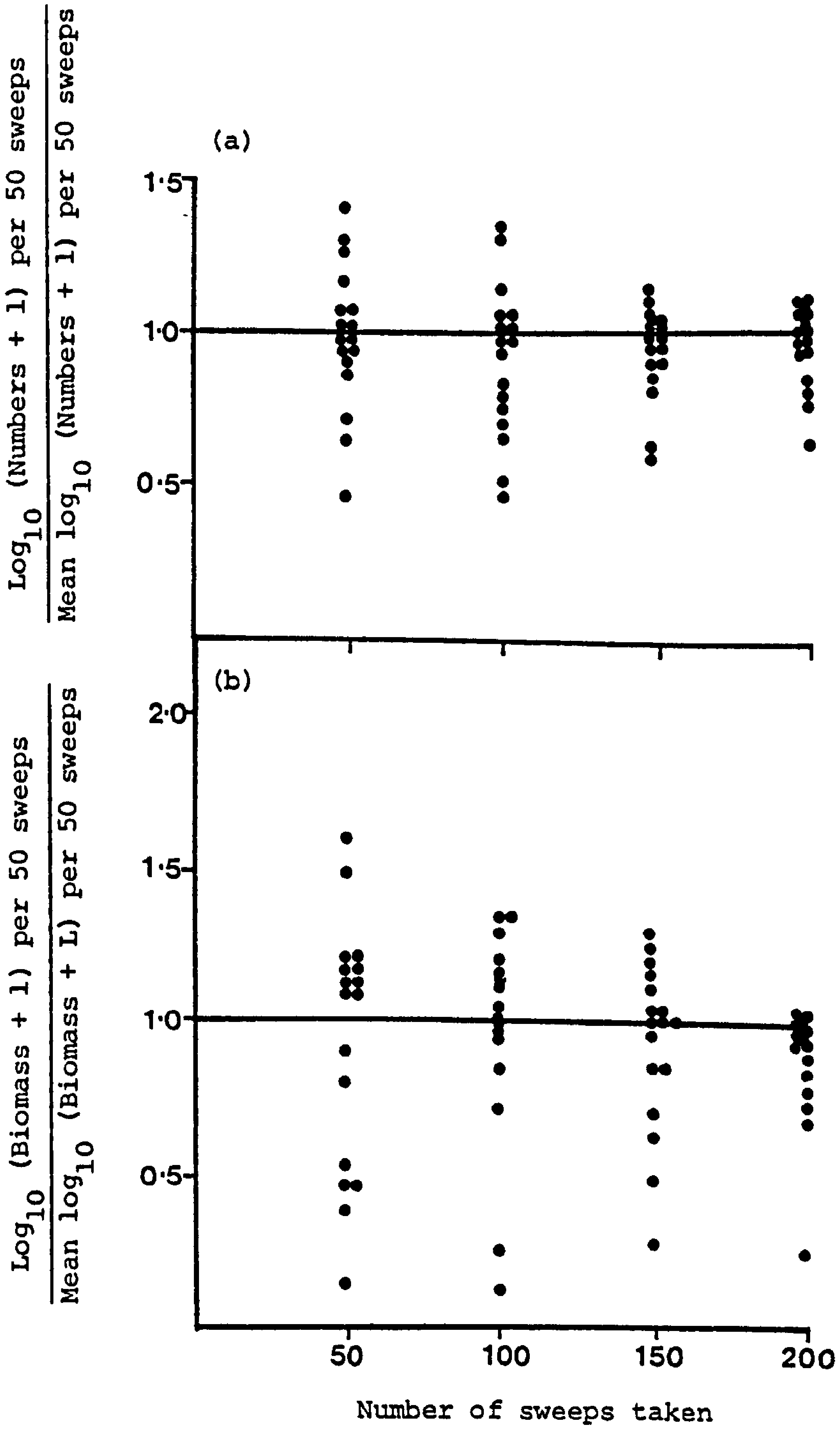

(a)
Log10 (Numbers + 1) per 50 sweeps / Mean log10 (Numbers + 1) per 50 sweeps
1·5
1·0
0·5
(b)
Log10 (Biomass + 1) per 50 sweeps / Mean log10 (Biomass + L) per 50 sweeps
2·0
1·5
1·0
0·5
50
100
150
200
Number of sweeps taken

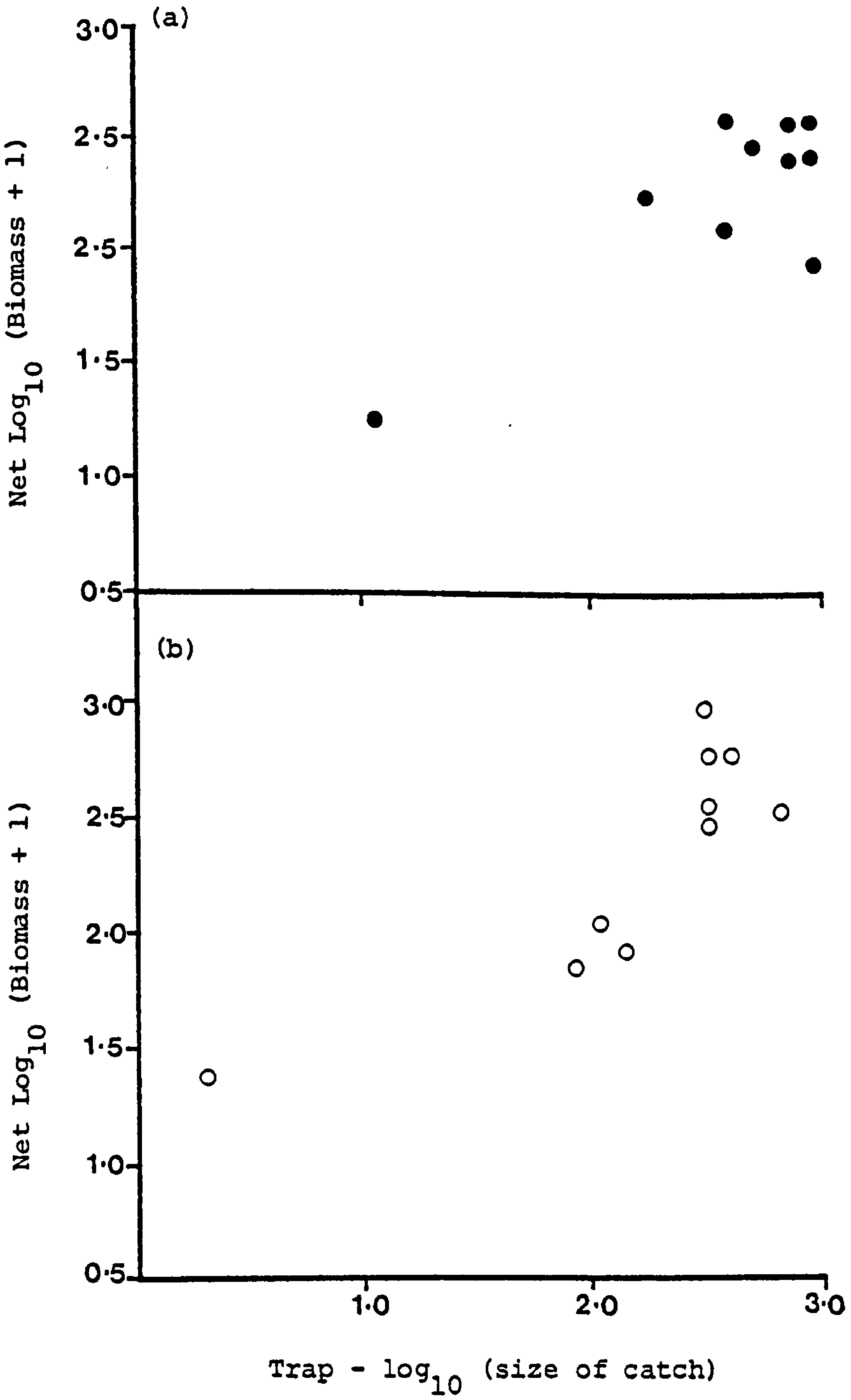
Figure 2.5

Comparison of net and suction trap catches -

(a) Numbers of items in the catches,

(b) Biomass of the catches.

One site, the catch of which was very variable, due to the irregular presence of livestock, is omitted from the comparison.


(a)
Net Log$_{10}$ (Biomass + 1)
3·0
2·5
2·5
1·5
1·0
0·5
(b)
Net Log$_{10}$ (Biomass + 1)
3·0
2·5
2·0
1·5
1·0
0·5
1·0
2·0
3·0
Trap - log$_{10}$ (size of catch)

So, although the net used over a full day and at more than one site correlates well with the suction trap catch, any individual sample may differ because of weather conditions, time of day or local concentrations of insects.

2.6 Insect Size

A formula relating dry weight to wing length for all insect taxa combined was obtained:

$$\text{Dry weight (mg)} = \frac{\text{wing length}^{2.68}\,\text{(mm)}}{66.07} \quad .$$

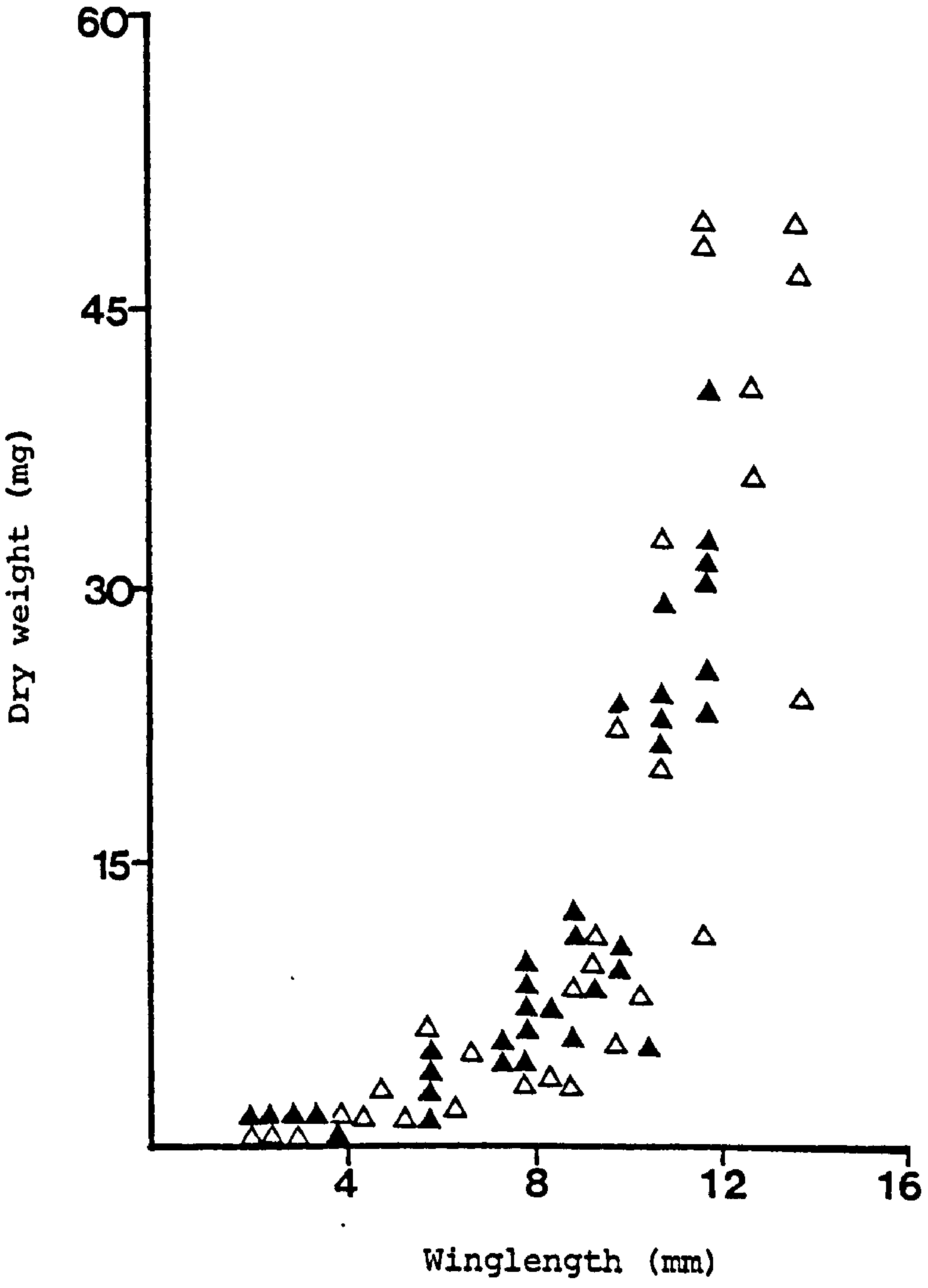
Formulae for individual taxa are given in Appendix 2A.

Logarithms of both dry weight and wing length were used since weight does not increase linearly with increasing wing length (Figure 2.6). The formulae were obtained from insects of all size classes but insects with similar wing lengths of more than 1 cm may vary in weight by 20 mg or more. Hence there could be some error for this size class. These very large items form about 4% by numbers of the Swallow's diet, less for the Sand Martin (this study) so the error is only slight.

A check was made by comparing direct weighings of food boluses of Swallows and Sand Martins with calculated weights, using these formulae, by a paired sample t-test. There was no significant difference between the means of the two sets of weights ($t = 0.25$ $p > 0.5$). However, 25% of the weights differed by 10 mg, the greatest difference being 23.8 mg (85 mg/61.2 mg).

Figure 2.6

The relationship between the dry weight of brachyceran (circles) and cyclorraphan (triangles) Diptera and the wing length of these insects.


60
45
30
15
Dry weight (mg)
4
8
12
16
Winglength (mm)

2.7 Insect Composition and Nutritional Value

The body composition of insects is shown in Table 2.2. Details of individual taxa are given in Appendix 2B.

Compared with other types of food (Table 2.3) insects are a good source of calcium, although shelled animals and Diplopoda are richer. Earthworms, too, may have a high calcium content in chalky areas (Bilby and Widdowson 1971). Reichle et al (1969) showed that the calcium content of some insects may also increase over the growing season. Insects, however, do not provide sufficient calcium at times of high calcium demand, such as during egg laying (see Discussion).

Insects are also a good source of protein including sulphur-containing amino-acids (SAA) which are essential for feather growth. Animal protein, in general, contains 0-6.3g SAA/100g protein whereas vegetable protein has 0-2.9g/100g (Tristram 1953).

The calorific value of insects compares very favourably with other forms of invertebrate and vertebrate prey types and is considerably better than many vegetable and cereal foods. Invertebrate foods are commonly taken when a diet high in calories and protein is required. Pintails, *Anas acuta*, for example, eat mainly plant food in autumn and winter but juvenile and laying birds take invertebrates (Krapu and Swanson 1977).

If only a few species of insect were taken, however, it is possible that they would not provide a balanced diet of, for instance, essential amino-acids (Greenstone 1979). It is thought that for this reason animals frequently take a mixed diet (Tinbergen 1960, Holling 1965, Barnett 1975). A deficiency is unlikely to occur in hirundines since they select items mainly by size rather than by

Table 2.2

The body composition of insects

The mean (± 1.s.d.) percentage composition of all taxa combined is given. Values for individual taxa are given in Appendix 2B.

Component	Percentage of dry weight	Percentage of total weight
Chitin	9.32 ± 4.18	2.52 ± 1.13
Calcium	0.34 ± 0.11	0.09 ± 0.03
Sulphur	0.77 ± 0.95	0.21 ± 0.26
SAA[1]	3.13	0.85
Nitrogen	10.29 ± 1.64	2.78 ± 0.44
Carbon[2]	46.21 ± 6.46	12.50 ± 1.75
Hydrogen[2]	7.67 ± 0.72	2.08 ± 0.19
Lipid	8.62 ± 4.97	2.33 ± 1.34
Ash	5.92 ± 1.15	1.60 ± 0.31
Water	-	72.94 ± 2.30

Calorific value (kcal/g dry weight) = 5.457 ± 0.218 (22.833 kJ)

Ash free calorific value (kcal/g ash free dry weight) = 5.80 (24.268kJ)

[1] SAA - sulphur-containing amino-acids (calculated - see Appendix 2B)

[2] Values for carbon and hydrogen were obtained during the analysis for nitrogen.

Table 2.3 Nutritional Value of Foodstuffs

Food	Calorific Value kcal/g dry wt	Protein g/g dry wt	Fat g/g dry wt	Calcium mg/g dry wt	Source
Oligochaetes	5.024	-	-	-	Griffiths 1977
Oligochaetes	-	0.68	0.06	5.5	McInroy 1971
Polychaetes	3.641	-	-	-	Griffiths 1977
Oyster	3.5	0.71	0.06	13.0	Long 1968
Snail (flesh)	4.33	0.77	0.07	-	Long 1968
Crayfish	4.11	0.83	0.03	4.40	Altman and Dittmer 1972
Diplopoda	-	-	-	327.3 (ash free)	Reichle et al 1969
Diplopoda	5.45 (ash free)	-	-	-	Cummins and Wuycheck 1967
Arachnida	5.82	-	-	-	Gibb 195~~7~~8
Insects	5.457	0.65	0.09	3.40	This study
Fish	4.928	-	-	-	Griffiths 1977
Salmon	5.96	0.62	0.37	2.17	Altman and Dittmer 1972
Amphibia	4.992	-	-	-	Griffiths 1977
Reptiles	4.826	-	-	-	Griffiths 1977
Birds	5.291	-	-	-	Griffiths 1977
Chicken	4.37	0.88	0.08	0.22	Altman and Dittmer 1972
Mus musculus	5.68	-	-	-	Golley 19~~59~~61
Rabbit	5.40	0.70	0.27	0.67	Altman and Dittmer 1972
Cereals	3.6 - 4.3	-	-	-	Petrucevicz and Macfadyen 1970
Sunflower seeds/					

Table 2.3 (continued)

Food	Calorific Value kcal/g dry wt	Protein g/g dry wt	Fat g/g dry wt	Calcium mg/g dry wt	Source
Sunflower seeds	6.46	-	-	-	Petrucevicz and Macfadyen 1970
Roots, legumes	3.4 - 3.8	-	-	-	Petrucevicz and Macfadyen 1970
Green plants	2.6 - 3.1	-	-	-	Petrucevicz and Macfadyen 1970
Fruit	3.3 - 3.8	-	-	-	Petrucevicz and Macfadyen 1970
Heather	1.3	0.07	-	0.48	Moss 1977
Cherries	2.54	0.03	trace	0.86	Long 1968

species (this study) so their diet seems to be both varied and nutritious.

2.8 Comparison of Boluses and Faecal Samples

The proportions of items in the boluses and in the faeces are shown in Figure 2.7. There is a good correlation for the Sand Martin ($r_s = 0.74$, $n = 8$, $p < 0.05$) but this is improved if the Ephemeroptera are excluded ($r_s = 0.89$, $n = 7$, $p < 0.01$) suggesting that insects with large fragile wings are under represented in faecal samples. For the Swallow the correlation is also good ($r_s = 0.78$, $n = 9$, $p < 0.05$) but this is improved if Psocoptera are omitted ($r_s = 0.83$, $n = 8$, $p < 0.05$). These items were found in only a third of the boluses from one sample period and probably represent a very local and transitory food source. Waugh (1978) also found a close correlation between the proportions of items in the faeces and boluses from Swallows and Sand Martins.

Boluses are obviously the best means of examining the nestling diet over short time periods since all the prey taken can be easily identified. Faecal analysis is a good substitute for adults or if collaring is not possible or desirable or a long sampling period is necessary. The possible under-representation of certain taxa, however, must be taken into account.

2.9.1 Body Composition and Growth of Nestlings

Swallow nestlings reached a peak weight of 22.8 ± 1.7g ($n = 19$) on the fourteenth day after the last youngster had hatched, and then declined until the nestlings fledged, Figure 2.8, (mean fledging day 21.1 ± 1.9, mean fledging weight 20.2 ± 1.9g, $n = 14$). The peak weight was 18.8% higher than the mean adult weight (19.2 ± 1.7g, $n = 51$). The magnitude of the weight recession was less than for

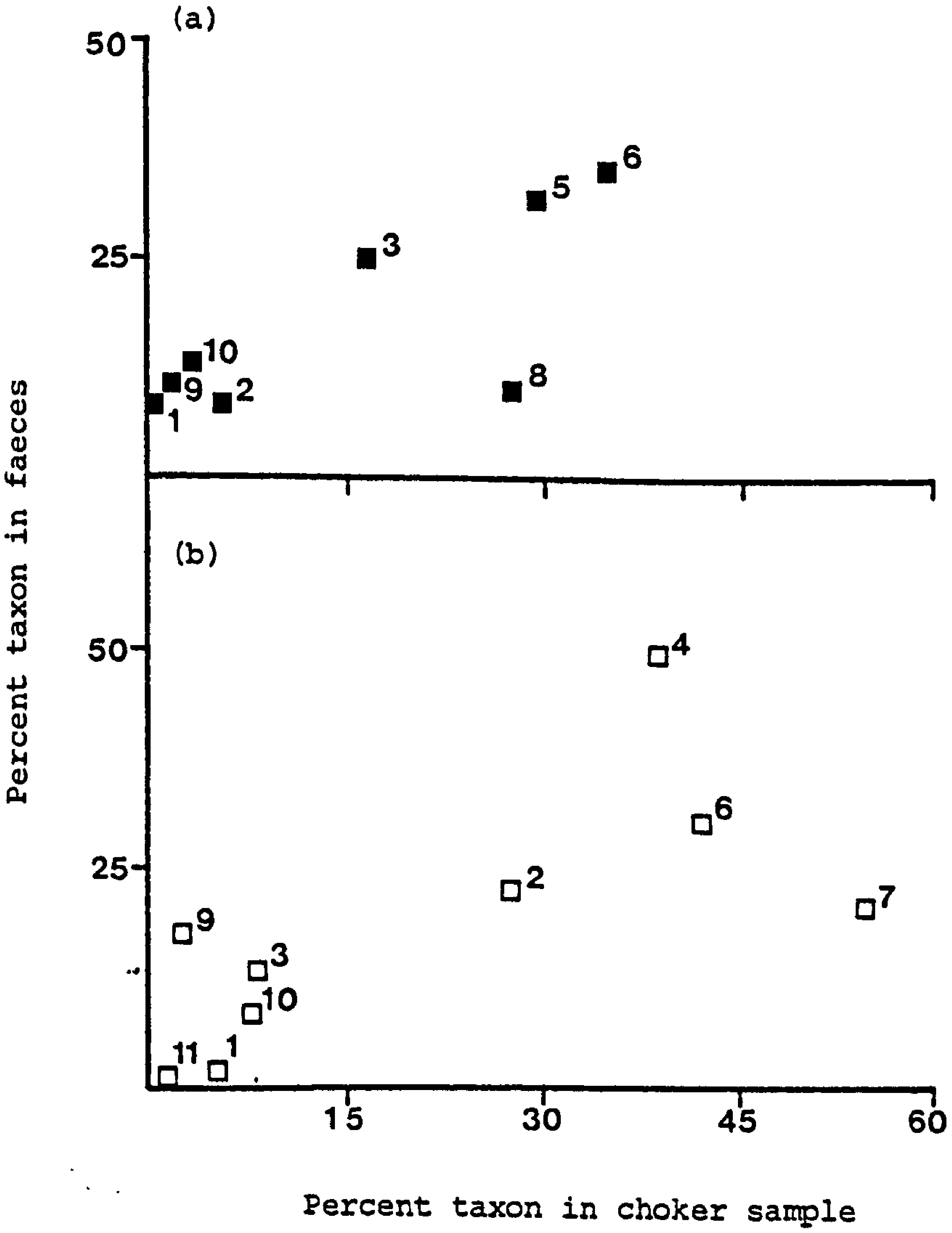
Figure 2.7

The relationship between the percentage of prey taxa in choker samples and the percentage of prey remains in faecal samples from (a) Sand Martin and (b) Swallow nestlings.

1. Nematocera,
2. Brachycera,
3. Acalypterae,
4. Calypterae,
5. Bibionidae,
6. Aphidoidea,
7. Psocoptera,
8. Ephemeroptera,
9. Hymenoptera,
10. Coleoptera,
11. Lepidoptera.

Spearman's rank correlation coefficient =

(a) 0.74, $p < 0.05$; (b) 0.78, $p < 0.05$.


(a)
50
25
■1
■9
■10
■2
■3
■8
■5
■6
(b)
50
25
□4
□6
□2
□7
□9
□3
□10
□11
□1
15
30
45
60
Percent taxon in faeces
Percent taxon in choker sample

most hirundines (Ricklefs 1968) but was greater than that of the American Barn Swallow (20.3%, Stoner 1935). In this sub-species adult and nestling weights were also lower. Weights would not be substantially altered by the presence of food in the gut which, in House Martins, averages under 2% of the live weight (Bryant and Gardiner 1979).

Sand Martin nestlings reached a peak weight of 16.9 ± 1.4g (n = 38) on the thirteenth day and declined to 13.2 ± 0.9g around the fledging day (22.5 ± 2.1, n = 49), giving a weight recession of 23.4%, Figure 2.9. The Bank Swallow shows a smaller weight recession (Petersen 1955).

Age-specific weights are influenced by a number of factors including time of year, brood size, food supply, weather conditions and hatching order (Bryant 1978a and b), consequently growth curves for different brood sizes would be affected by other factors. A multiple regression equation was therefore obtained for nestling weights of different age and brood sizes. After the 9th nestling day, nestlings in large broods were lighter than those in small broods (Appendix 3). In Sand Martins brood size explained 18% of the variance in nestling weight. In Swallows it was less important explaining only 7% of the variance, paralleling the Swallow's lesser needs, compared to the Martins, for fat stores and brood reduction as means of minimising the effects of an unpredictable food supply.

Wing length increased linearly from the seventh day onwards (Figures 2.8 and 2.9), and was used for aging some nestlings when hatching date was unknown.

Percentage water and water indices decreased during the nestling

Figure 2.8

Growth curve of the Swallow: weight (circles, mean ± 1 s.d.) and wing length (squares). Triangles = weights of fledglings.

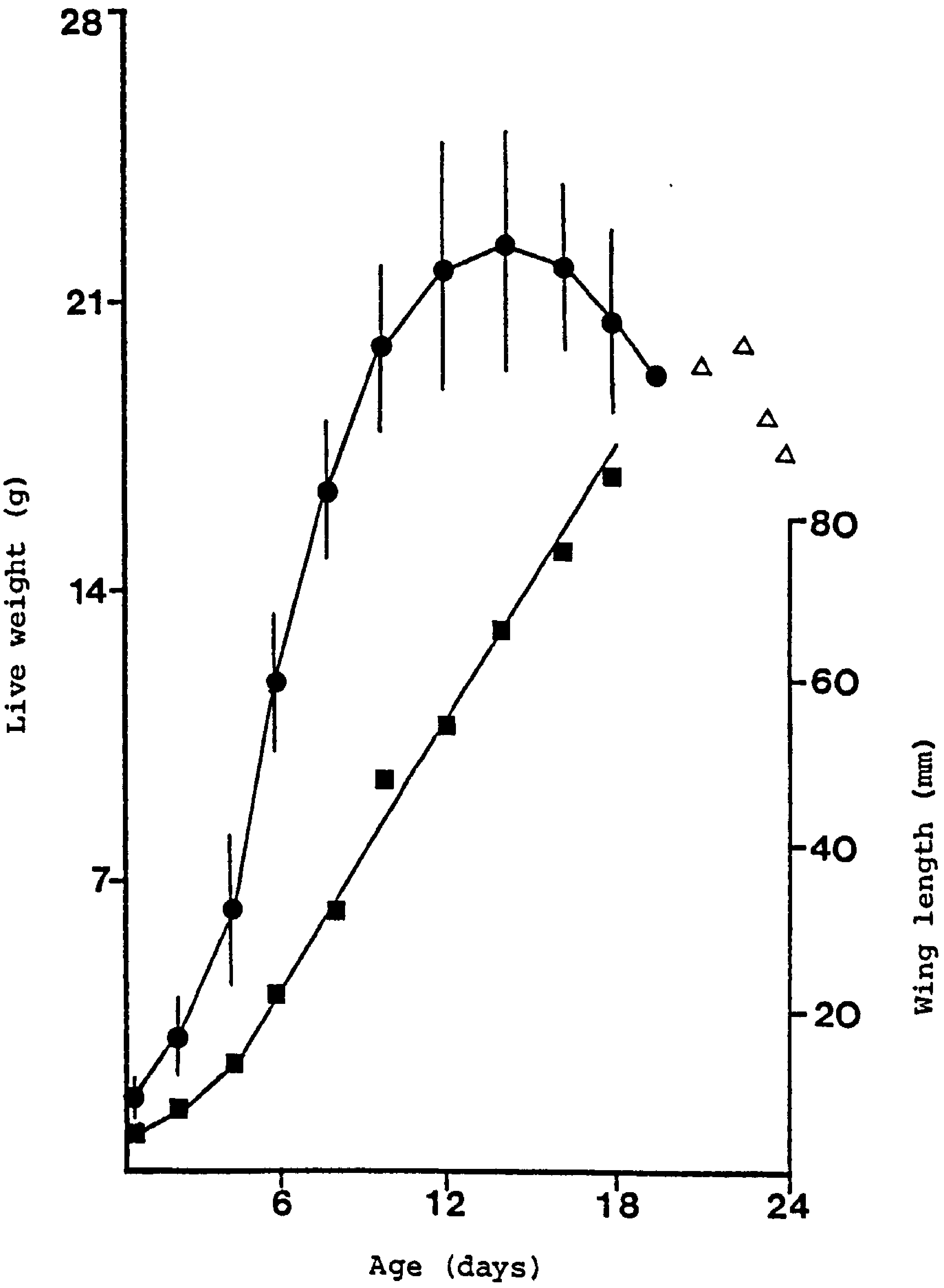
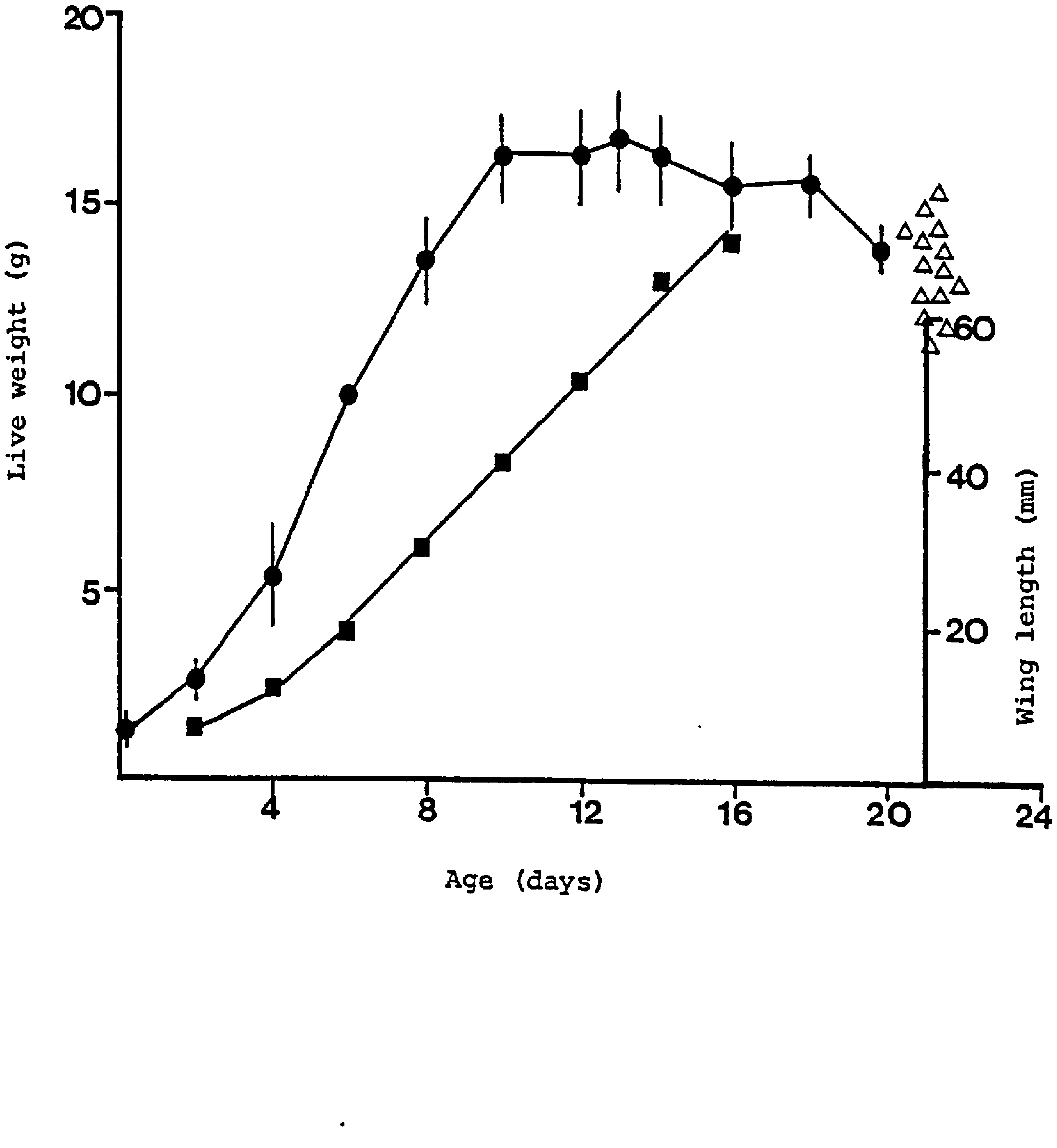

28
21
14
7
Live weight (g)
80
60
40
20
Wing length (mm)
6
12
18
24
Age (days)

Figure 2.9

Growth curves of the Sand Martin:
weight (circles, mean ± 1 s.d.) and wing length (squares).
Triangles = weights of fledglings.


20
15
10
5
Live weight (g)
60
40
20
Wing length (mm)
4
8
12
16
20
24
Age (days)

period (Figures 2.10 and 2.11). The weight recession in hirundines is due to a decrease in water content in maturing tissues (Ricklefs 1968). The lean component remained more constant after peak weight.

Lipid indices increased during nestling growth but were variable around and after peak weight was reached (Figures 2.10 and 2.11). Values for older Sand Martins (0.4 - 0.8) were higher than for older Swallow nestlings (0.3 - 0.6) but were less than for House Martins (0.5 - 0.9) and Swifts (over 1), (Turner and Bryant 1979).

The energy content of the nestling increased during growth due both to the decrease in water content and to the deposition of fat. The energy density of the Swallow was slightly lower than that of the Sand Martin since the fat store was lower (Figure 2.12).

Heavy nestlings had a high water content, dry weight and lipid weight compared to light nestlings; abundant food also resulted in high nestling weights (Table 2.4).

Assimilation values (the energetic requirements for growth and metabolism) for broods of 4 are shown in Figure 2.13. Assimilation increased up to a peak on the 8th to 10th day and then declined.

These assimilation figures can be taken as minimum values for two reasons: (1) the metabolic rates of Swallows and Sand Martins may be higher than those for House Martins since Swallows are in open nests, thereby exposed to lower ambient temperatures, and mature Sand Martin nestlings are active, often running along the burrow to meet their parents returning with food; (2) a disproportionately large amount of energy may need to be ingested in order to provide sufficient nutrients such as sulphur for feather formation.

Table 2.4

Correlations for Sand Martin nestling weights

Variable	Units	All ages	≥ peak weight
Sample size	-	21	13
Dry weight	g	0.87 ***	-
Lean dry weight	g	0.87 ***	-
Lipid weight	g	0.82 ***	-
Lipid index	-	0.79 ***	-
Water weight	g	0.95 ***	0.93 ***
Wing length	mm	0.58 **	-0.64 **
Age	days	0.63 **	-0.66 **
Food abundance	$\log_{10}$ (volume + 1)	0.42 *	-

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Only significant correlations are shown.

Table 2.5

A comparison of calculated assimilation (growth plus respiration) and daily energy budget (DEB) values for nestling Swallows and Sand Martins

Age (days)	Assimilation kcal dy^{-1}	DEB kcal dy^{-1}
12 (Brood of 5 Swallows)	47.41	63.34
12 (Brood of 5 Sand Martins)	34.62	52.14
16 (Brood of 5 Swallows)	26.51	63.34
16 (Brood of 5 Sand Martins)	28.05	52.14

Figure 2.10

Lipid index, percent water and water index in relation to age in nestling Swallows.

Circles = lipid index (lipid weight/lean dry weight of carcase)

Open squares = water content as a percentage of live weight

Closed squares = water index × 100 (water content/lean dry weight)

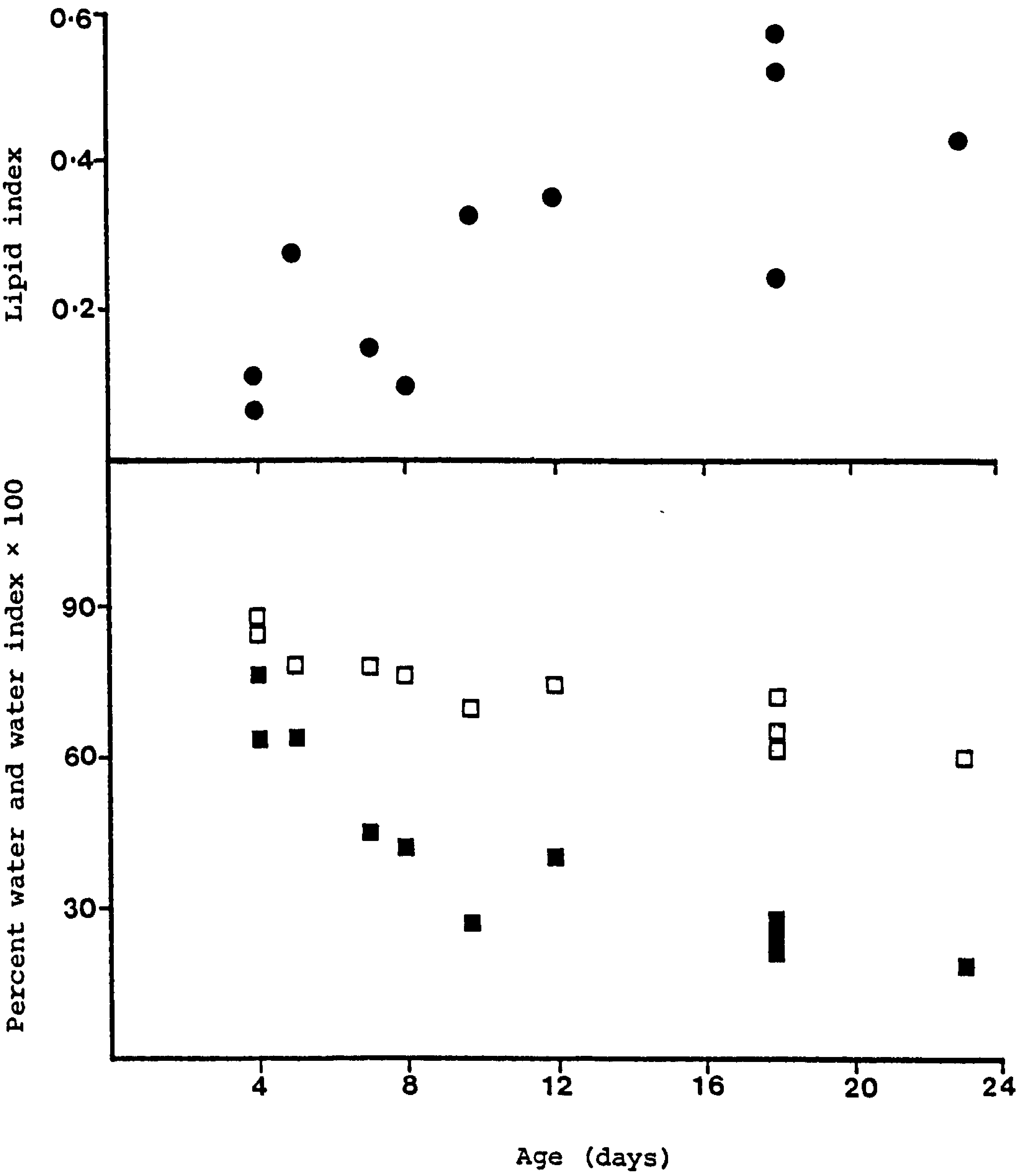

0·6
0·4
0·2
Lipid index
90
60
30
Percent water and water index × 100
4
8
12
16
20
24
Age (days)

Figure 2.11

Lipid index, percent water and water index in relation to age in nestling Sand Martins.

Circles = lipid index (lipid weight/lean dry weight of carcass)

Open squares = water content as a percentage of live weight

Closed squares = water index × 100 (water content/lean dry weight).

The data for lipid indices include figures from Bryant in Turner and Bryant (1979).

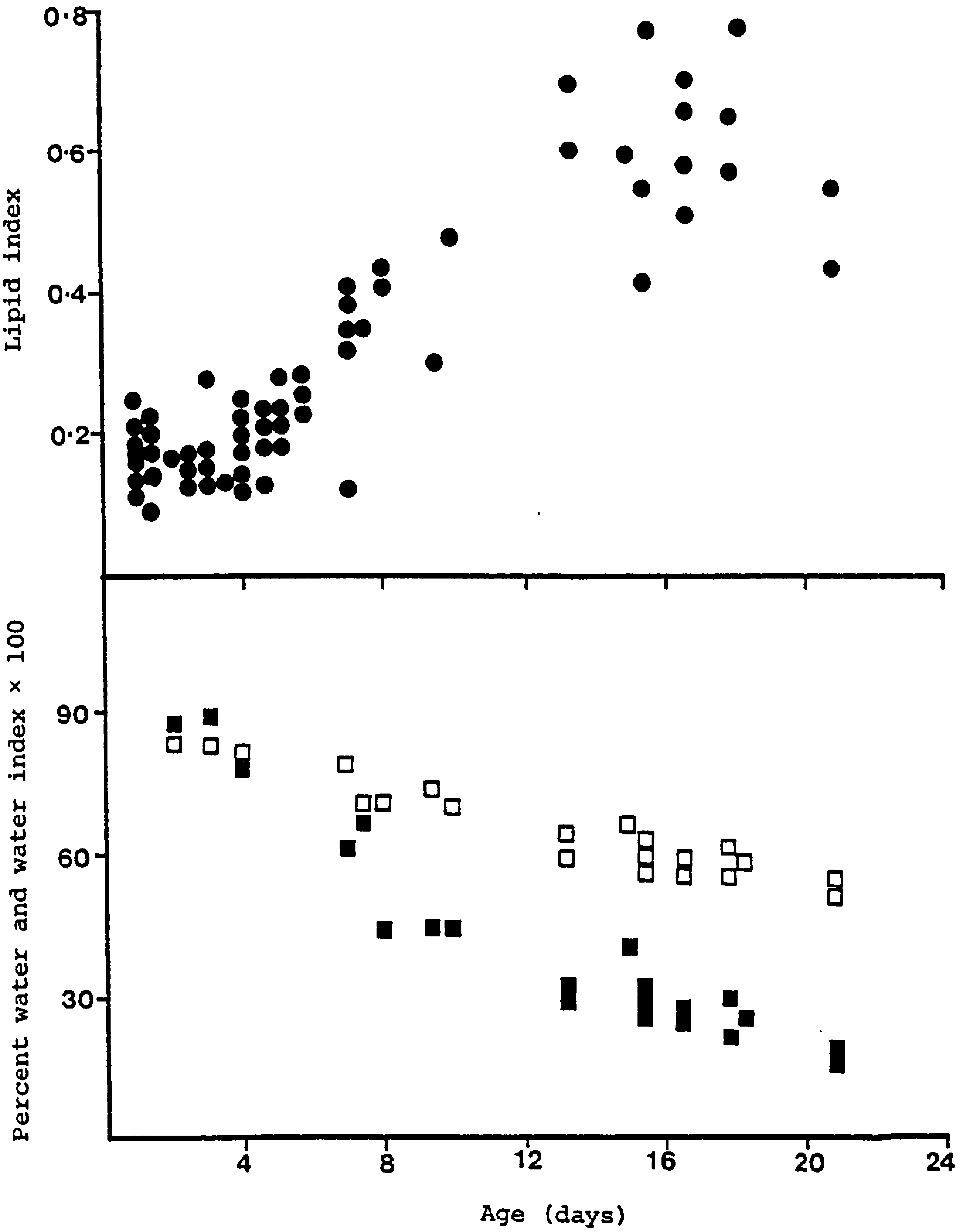
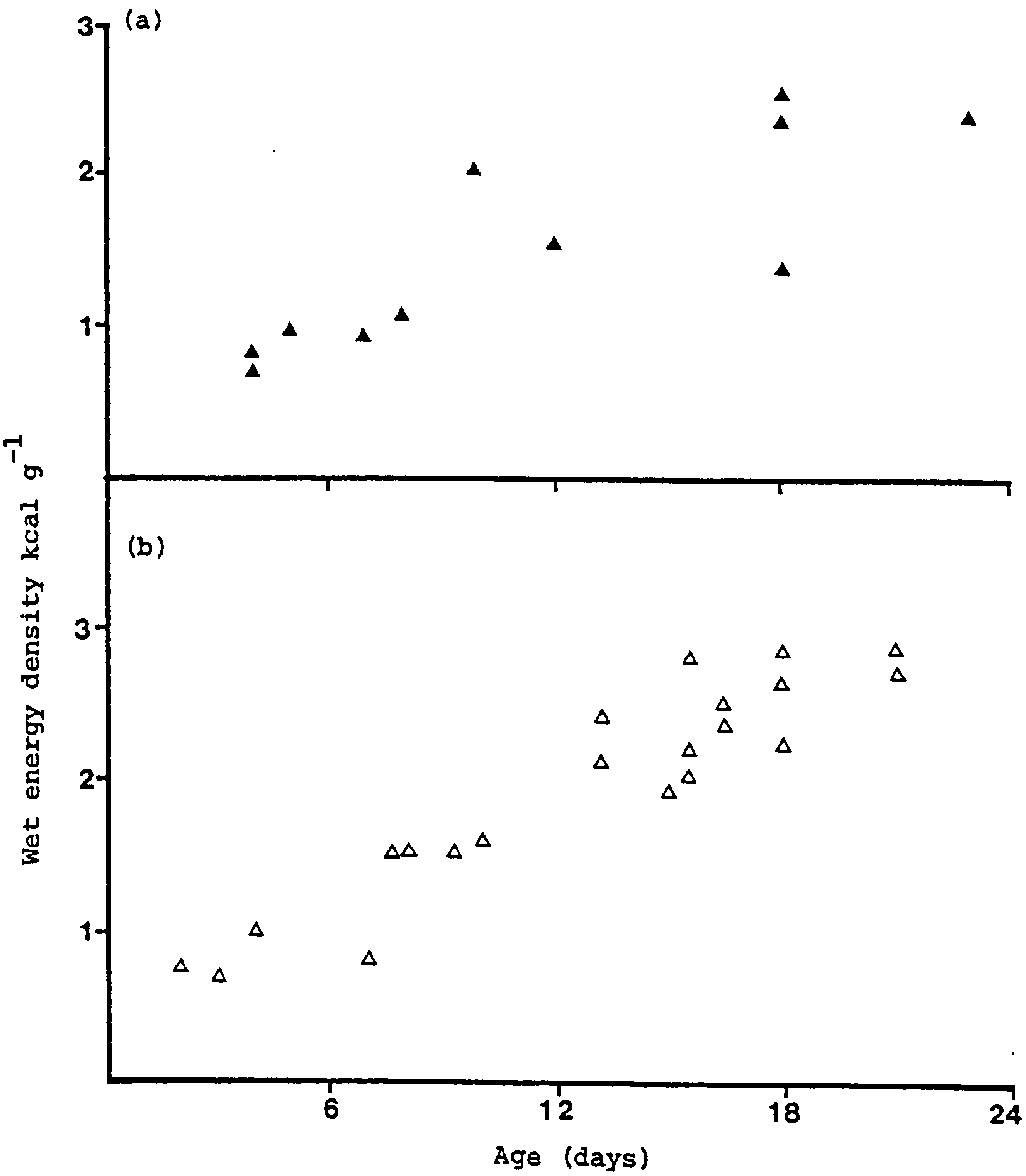

0·8
0·6
0·4
0·2
Lipid index
90
60
30
Percent water and water index × 100
4
8
12
16
20
24
Age (days)

Figure 2.12

Wet energy density in relation to age in nestling Swallows (a) and Sand Martins (b).


(a)
(b)
3
2
1
3
2
1
Wet energy density kcal g^{-1}
6
12
18
24
Age (days)

The daily energy budgets of nestling Swallows and Sand Martins, measured in the field, were higher than the calculated assimilation figures. The energy brought to the nest increased with age up to the peak weight and then remained more constant (Figures 2.13 and 2.14).

For Swallow and Sand Martin broods the daily energy budget (DEB) is given by the following equations (and see Figure 2.15):

$\leq$ 12 days old DEB (kcal dy^{-1}) = $1.88x^{0.76}$ ($n = 14$, $r = 0.94$, $p < 0.001$) . . 1

After 12 days DEB (kcal dy^{-1}) = $1.47x^{0.82}$ ($n = 12$, $r = 0.92$, $p < 0.001$) . . 2

Assimilation and DEB values are compared in Table 2.5 and Figure 2.13.

Comparable daily energy budgets have been obtained for other nestlings and for young precocial birds in experimental conditions (for example Penny and Baily 1970, Sugden and Harris 1972, Norton 1973, Westerterp 1973).

The energy demands of the nestlings plateau between the ages of about 9-16 days (Snapp 1973, Waugh 1978, this study, Figure 2.13). Bryant (1972) found that the feeding rate to House Martin broods was broadly constant 9-20 days after hatching.

2.9.2 Faecal Output

For the first few days after hatching, the parents ingested or carried away the faecal sacs of the nestlings. Sand Martin adults continued to carry faeces away for the majority of the nestling period but Swallow nestlings began to defaecate out of the nest after 5-6 days and all faeces were ejected in this way by the ninth day. The faecal output (dry weight) of a brood of four Swallows was found

Figure 2.13

Assimilation values (A) and Daily Energy Budgets (DEB) for (a) Swallow and (b) Sand Martin broods (of four nestlings) in relation to age. DEB has been calculated from equations 1 and 2 (see text). Values for assimilation have been calculated from daily growth increments (see text) and metabolic rates (calculated from equations given in Bryant and Gardiner 1979).

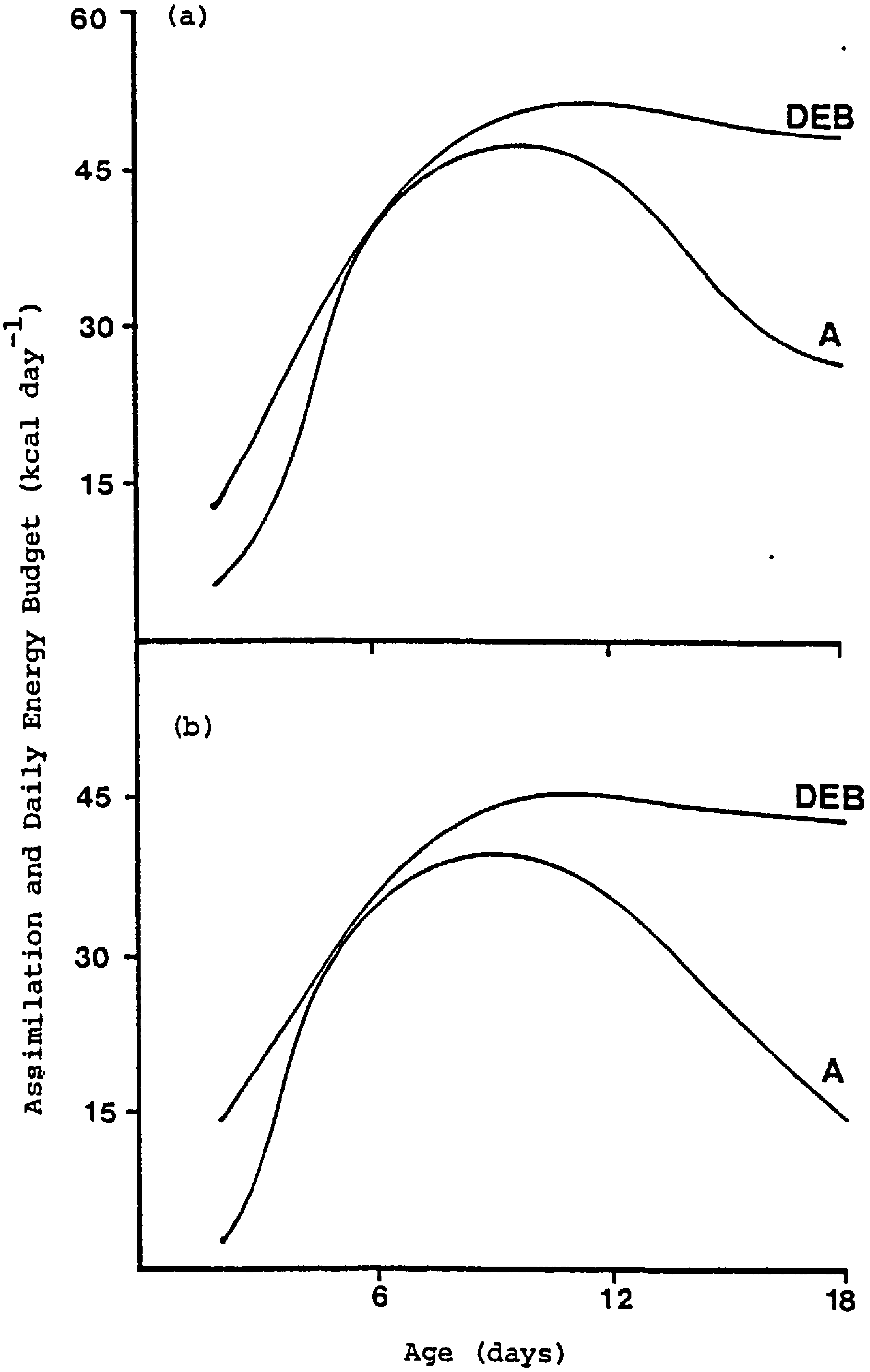

(a)
60
45
30
15
DEB
A
(b)
45
30
15
DEB
A
6
12
18
Assimilation and Daily Energy Budget (kcal day^{-1})
Age (days)

Figure 2.14

Assimilable energy (kcal day^{-1}) brought to broods of five Swallows (closed symbols) and Sand Martins (open symbols) in relation to age. Assimilation efficiency is 70%. The values are calculated from observed feeding rates to the brood and the mean size of the food bolus collected on that day.

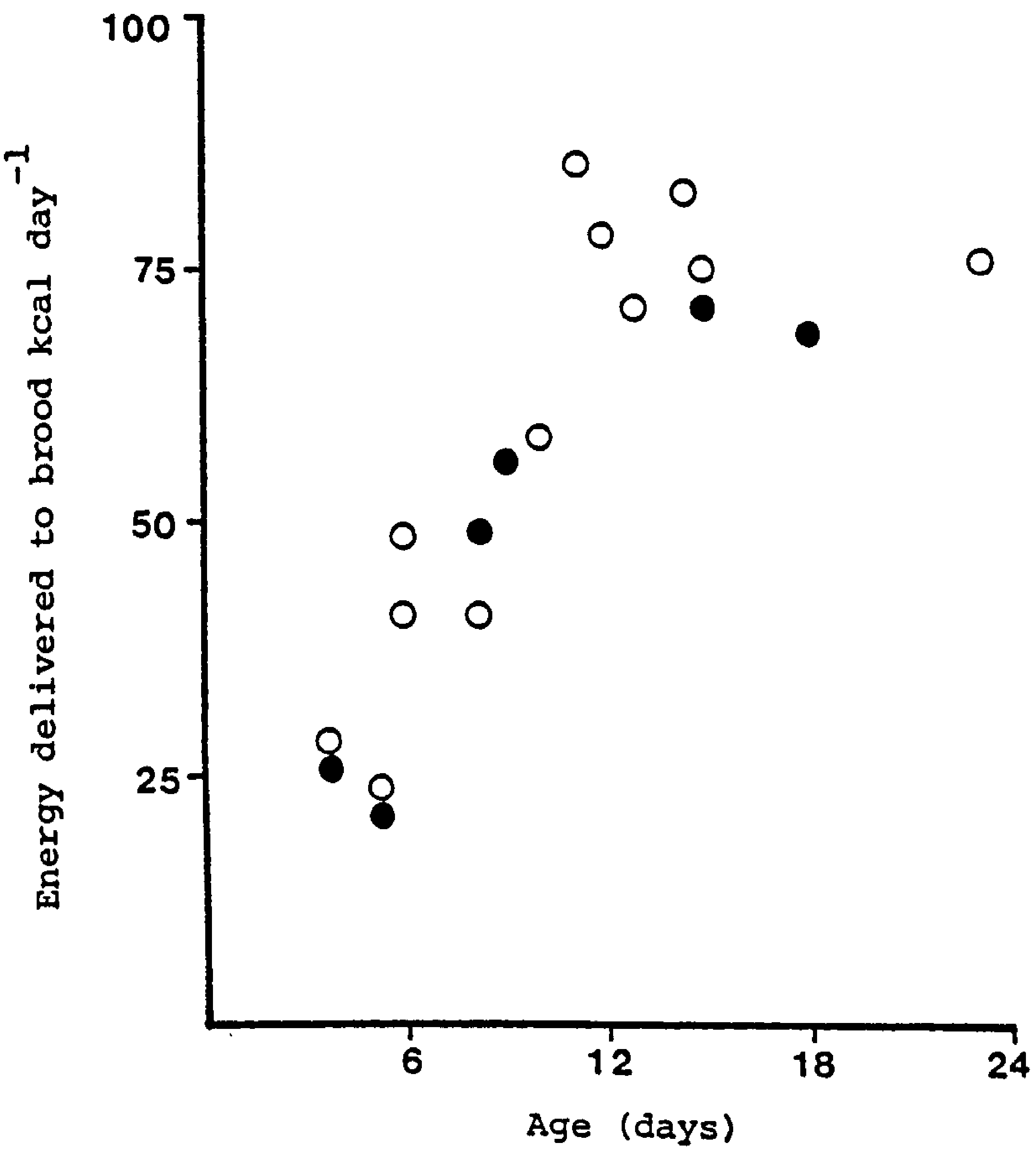
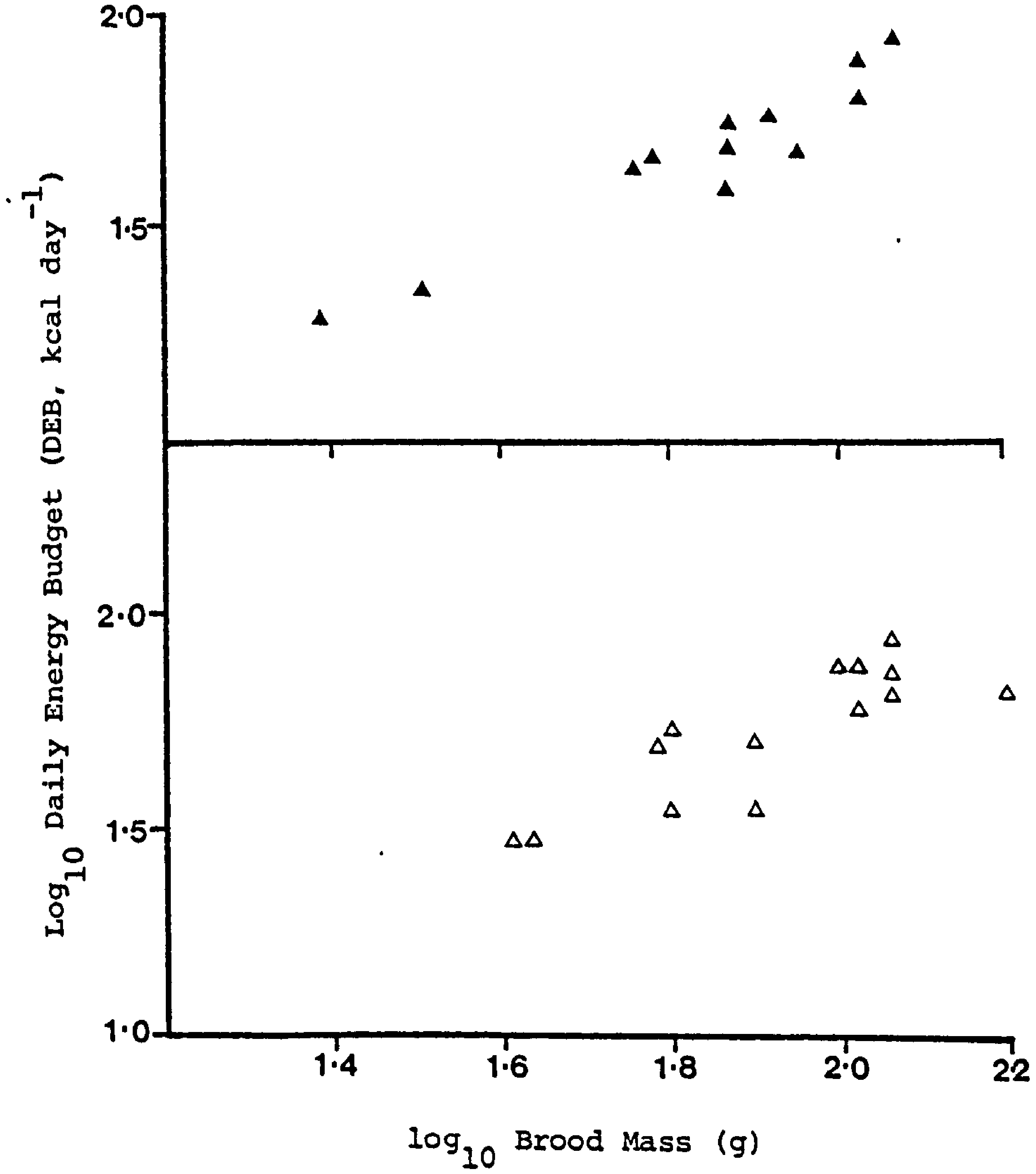

100
75
50
25
Energy delivered to brood kcal day^{-1}
6
12
18
24
Age (days)

Figure 2.15

Assimilable energy (DEB, kcal day^{-1}) brought to broods of Swallows and Sand Martins in relation to brood mass. Assimilation efficiency = 70%. Values calculated as for Figure 2.14.

Closed symbols = broods ≤ 12 days old,
DEB = 1.875 $Mass^{0.7646}$,
$r = 0.93$, $p < 0.001$.

Open symbols = broods > 12 days old,
DEB $\overset{=}{\cancel{8}}$ 1.472 $w^{0.8155}$, $r = 0.89$, $p < 0.001$.


2·0
1·5
2·0
1·5
1·0
1·4
1·6
1·8
2·0
2·2
Log$_{10}$ Daily Energy Budget (DEB, kcal day^{-1})
log$_{10}$ Brood Mass (g)

to be 4.83 ± 2.18g dy^{-1}, n = 22 nest days (nestlings aged 8-17 days). The mean dry weight of a faecal pellet was 0.125 ± 0.112g, n = 65.

The faecal output of a brood of four Sand Martins was estimated from the mean dry weight of a faecal pellet (taken from beneath the colony, 0.114 ± 0.049g n = 23) and the number of faeces which the parents carried away from the burrow (37.0 ± 12.0, n = 30 hours of observation). Hence the estimated faecal output would be 4.22g dy^{-1} for a brood of four.

Bryant and Gardiner (1979) found that House Martin nestlings in large broods received less food and had a lower faecal output than nestlings in small broods. Their relationship between faecal output and brood size was

Faecal output = $1.74x^{0.83}$g dy^{-1} where x = brood size.

The calorific value of Swallow and Sand Martin faeces was 3.22 ± 0.58 kcal g^{-1} dry weight (n = 3 nest days).

2.9.3 Assimilation Efficiency

The results of measurements of the assimilation efficiencies of nestling Swallows and Sand Martins are shown in Table 2.6.

Table 2.6 Assimilation efficiencies of nestling Swallows and Sand Martins, (calorific values)

Species	Age (days)	Percent. of Insects (net weight) in diet	Assimilation Efficiency as a percentage
Swallow	9-10	28	74.13
"	17-18	24	70.36
Sand Martin	12-13	28	77.16
"	17-18	36	69.87
			$\bar{x}$ 72.88

There was a tendency for the assimilation efficiency to decline with age and as more insects were incorporated into the diet. Westerterp (1973) and Myrcha, Pinowski and Tomek (1972) have also reported a decline in assimilation efficiency towards the end of the nestling period in Starlings, Sturnus vulgaris, and Sparrows, Passer spp., respectively. Bryant and Gardiner (1979) suggested that the relative decline in energy content and mass of the digestive organs in House Martins with age indicated a reduction in digestive capacity.

Other studies have given similar values for nestling assimilation efficiency: e.g. 75.3% for six passerines on insect/meat diets (Blem 1973), 70% for Redbacked Shrikes, Lanius collurio, (Diehl 1971) and House Martins (Guy, unpubl. data), and 64% for Starlings (Westerterp 1973). For the purpose of further analysis the assimilation efficiency is taken as the mean for this and the other studies referred to above (70%). This value is also used for the assimilation efficiency of the parents.

2.9.4 Nutritional Requirements for Nestling Growth and Egg Laying

As well as energy, the nestlings need protein and minerals for growth. Calcium for skeletal production and sulphur-containing amino-acids (SAA) for feather development are probably the two limiting requirements. Nutrients, especially calcium, are also necessary for egg production.

The calcium demand of nestlings has been examined for Blackbirds, Turdus merula, and Song Thrushes, T. philomelos by Bilby and Widdowson (1971). At hatching, nestling Thrushes and Blackbirds contain 793mg calcium per 100g lean dry weight (LDW) and at fledging 2265mg Ca/100g LDW. If calcium concentrations are similar in hirundines the Swallow at hatching contains 3mg calcium (0.4g LDW, see Appendix 3 for nestling and egg composition) and 115mg at fledging (5.069g LDW). The corresponding values for the Sand Martin are 1.85~~g~~mg (0.25g LDW) and 86.23mg (3.087g LDW). Most of the calcium is deposited from day 2 or 3, up to the time of fledging (a period of 19 days and 20 days for the Swallow and Sand Martin respectively). An indication that calcium is still being deposited beyond the peak weight is the increase in ash index of legs and wings for House Martins at this stage (Bryant and Gardiner 1979) and the continuing growth of the tarsus in the Sand Martin (Turner and Bryant 1979). To obtain the required amount of calcium the Swallow nestling must ingest 1.73g dry weight of insects per day and the Sand Martin 1.25g dry weight of insects per day. A linear deposition of calcium with age is assumed although the rate of deposition and thus the demand for calcium may increase during the most rapid growth phase.

The sulphur-containing amino-acids cystine and cysteine (SAA) are important constituents of feathers. Ward and Lundgren (1954) found a concentration of SAA of 6.8 to 8.2g per 100g total protein in feathers; a higher concentration than in animal protein (0 to 6.3g per 100g) or vegetable protein (0 to 2.9g per 100g) (Tristram 1953). Dolnik and Gavrilov (1979) found a total of 105mg SAA (7.5% of the plumage weight) in recently moulted Chaffinches, <u>Fringilla coelebs</u>. They showed that food consumption, protein catabolism and body temperature increased during molt indicating a requirement for protein and oxidation of other food components. The efficiency ratio of feather synthesis for the Chaffinch was only 5.5% of net productive energy compared to about 80% for the formation of eggs and somatic tissue. Nestlings, during feather growth, might also need to consume a high level of food in order to obtain sufficient SAA. Assuming a concentration of SAA of 7.5% of the plumage weight the Swallow contains 121mg SAA and the Sand Martin 80mg. A Swallow thus needs 5.03g dry weight of insects and a Sand Martin 3.32g of insects over about 9 to 11 days (day 7 to 18) for feather growth alone.

Nitrogen, as protein, is also necessary for growth. A Swallow gains 3.96g ash free lean dry weight (ALDW) from day 4 to peak weight and a Sand Martin 2.42g. If the ALDW is assumed to be mainly protein (although there is also some carbohydrate present) the Swallow needs to ingest 8.01g and the Sand Martin 4.89g dry weight of insects over this period of rapid growth. During periods of food shortage protein may have to be used for metabolism so extra would need to be ingested.

The parent also requires nitrogen for maintenance. The adult male chicken and the Tree Sparrow, _Passer montanus_, both need about 8% dietary protein (Martin 1968). An adult hirundine thus requires about 0.3g - 0.5g protein per day.

During egg laying the female Swallow requires 0.14g protein, 0.002g sulphur and 0.08g calcium for each egg. The female Sand Martin similarly requires 0.10g protein, 0.0015g sulphur and 0.06g calcium (Appendix 3).

CHAPTER 3

3. TIME AND ENERGY BUDGETS

3.1 Introduction

The Swallow and Sand Martin may live for seven or eight years (Stoner 1938, 1942, Beklovà 1976) but usually they live for much less. Uchida (1932), in a limited ringing study, retrapped few Swallows of three or more years of age. The mortality rate of first year Swallows is about 70% (von Vietinghoff-Riesch 1955, Beklovà 1976); the mortality rate of adult Swallows is lower (50-63% Lack 1949, von Vietinghoff-Riesch 1955, Beklovà 1976); in Sand Martins first year mortality is about 80% and adult mortality 58-65% (Harwood and Harrison 1977, Cowley 1979 and Mead 1979). Most mortality occurs outside the breeding season: in House Martins adult mortality at this time averages 57% whereas mortality during nesting is probably less than 5% (Bryant 1979). In other small passerines the annual adult mortality tends to be lower than in hirundines at 40-60% (Lack 1954). Because of the high mortality risk over the winter it is likely that a hirundine will attempt to rear as many nestlings as is possible each year without reducing its long term contribution to the gene pool. Double brooded female House Martins, however, have a greater mortality risk than single brooded females (Bryant 1979). Hence there must be a balance between yearly and life time reproductive effort (defined here as the parental expenditure of time and energy during breeding).

In order to maximise the contribution to the gene pool over its short life time the parent must optimise the allocation of time and energy for various activities during the breeding season. It must do this within the constraints imposed by the prevailing environmental conditions: for example, foraging time must be increased when food is scarce.

Optimal time and energy allocation also necessarily depends on the stage of the breeding cycle. During nestling rearing much of the daylight period can be spent foraging. Utter (1971) suggested that this period required the greatest expenditure of energy and foraging time. However, the critical stage for a parent could equally be earlier in the season; during incubation, for example, food may be scarce and available foraging time is necessarily restricted by nest attendance duties.

In this study 24 pairs of Swallows and 46 pairs of Sand Martins were time and energy budgeted so that critical periods for the birds in the breeding season could be assessed. In this section details of the time and energy budgets are given. As a necessary background to the time budget studies the breeding biology of Swallows and Sand Martins is briefly described and relevant information from the literature is detailed.

METHODS

3.2.1 Time Budgets

The present study was designed so that the effects of a wide variety of variables on the behaviour of the birds and the constraints imposed by these variables could be assessed.

These variables, listed in Appendix 4, include characters of the adult bird such as weight and wing disc loading, characters of the clutch or brood such as the number of nestlings and their age, characters of the feeding environment such as ambient temperature and available prey size, characters of feeding behaviour such as distance travelled to a patch of insects and miscellaneous variables such as time of day and day length.

Observations were made throughout the breeding season on birds which were colour marked with a waterproof dye. Observation periods usually lasted an hour. Several were made during each day but single observations were also taken where there was an opportunity to include a value for a variable which was rarely encountered (such as extremes of temperature). Note was taken of the time spent by each sex in each activity (perching, feeding, fighting, brooding etc.). Most variables could not be manipulated but brood size was altered to create unusually large or small broods in order to increase the influence of this variable. The number of variables which were used depended on the stage of the breeding cycle but 50-60 were normally used.

Stepdown multiple regression analysis was used to assess the effect of these variables on each behaviour in each stage of the breeding cycle. Despite its usefulness in unravelling a complex situation there are limitations to this approach. Inevitably many of the 'independent' variables are intercorrelated. The variables used in the multiple regression were those which both correlated well with the behaviour concerned and were biologically sound in that context. Also, some variables, both dependent and independent were not easy to measure accurately or were estimated subjectively (e.g. cloud cover). Time spent feeding, for instance, may include some perching time when the bird is not visible. Thirdly, the correlations between independent and dependent variables may not be perfectly linear. The data were transformed where necessary but a good fit was not always obtained. Fourthly, the method is based on correlations and does not prove cause and effect. Despite these drawbacks this approach remains a valuable technique for investigating the behaviour of free living birds.

Time budget studies alone can not, however, give a complete description of the effects of the environment and brood size on the adult bird without energetic and other costs and benefits of the activities being taken into account. These time budget studies were thus combined with measured and calculated energy expenditures and with measured rates of food collection for a more detailed analysis. Calculations of energy budgets are described in Appendix 5.

3.2.2 D_2O^{18} Measurements

The D_2O^{18} technique is a useful tool for measuring metabolic rates directly and is the only means of obtaining accurate data for small free-living animals. Validation studies comparing this technique with other methods of estimating CO_2 production have shown errors of 3% to 12.4% with a mean of 7.07% (Hails and Bryant 1979).

The technique was used on four Swallows and seven Sand Martins during the summer of 1978 by K. Westerterp and myself. Each run consisted of a bird or a pair of birds (all feeding nestlings) being caught and given an intraperitoneal injection of the stable isotopes. After an initial blood sample was taken the bird(s) was released and time budgeted until it was recaptured 24 to 48h later, when a final blood sample was taken for analysis of the isotopic concentration (by K.W.). Details of the technique are given in Hails (1977), Hails and Bryant (1979) and Bryant and Westerterp (in press).

3.2.3 Nest Temperature Measurements

The energy expenditure of a bird depends on ambient temperature especially when the bird is roosting or incubating, whereas heat produced during flight as well as the heat increment of feeding will contribute towards thermoregulation during the day. During incubation the heat required by the eggs also depends on the nest temperature.

Measurements were made of burrow temperatures and air temperatures around eggs and young nestlings in a Swallow's nest with a thermistor. The temperature within a dummy egg made of papier mâché and filled with glycerine, which was placed in a nest with a normal clutch, was also measured. The measurements were taken over periods of an hour.

3.2.4 Mate Removal Experiments

In order to assess the importance of the male's contribution to incubating, a series of experiments were made, each over a period of 9-12 hours. One partner of a pair of incubating Sand Martins was caught early in the day and retained while observations were made on the bird's partner. The captured bird was fed at intervals on minced beef to prevent a weight loss and was released at the end of the experiment. Similar observations were made on two pairs of Swallows.

3.2.5 Feeding Rates and Flight Costs

Observations were made, over periods of an hour, of the feeding rate to 33 Swallowbroods and 30 Sand Martin broods, by each sex. Both Swallows and Sand Martins fed nestlings in bouts interspersed with longer periods of self feeding. It is unlikely that the adults fed themselves at the same time as they were collecting food for the nestlings since they usually fed the nestlings very rapidly (Sections 3.7 and 4.4). The time interval between successive visits to the nest by each sex was measured. For each observation period, the highest 10% of these times, for each sex, were assumed to be bouts of self-feeding. This method would sometimes include times when the parent was collecting food for the nestlings and would sometimes exclude short self feeding times but a robust value is nevertheless obtained in the absence of knowledge of exactly when the adult is feeding itself. Inevitably a small part of the nominal self feeding time is taken up with collecting a bolus of food before the parent returns to the nest.

Measurements were made of flight costs during feeding. Hirundines employ two methods of flight: gliding and flapping. The proportion of gliding flight was measured by timing the birds' active and gliding flight simultaneously for 5-10 minutes after a time budget observation period. Note was also made of the site in which the birds fed and its distance from the nest site. Each individual was timed for 15-60 seconds. It was usually possible to observe colour-marked Swallows for which a time budget had just been obtained since they stayed close to the nest site. The flight behaviour of Sand Martins was noted on a flock basis, the colour-marked birds being watched if visible. The individuals in the main flock might include several stages of breeding. Hence the measurements are less precise than for the Swallow.

Throughout the text means are given ± 1 standard deviation. Energy values are given in calories (1 calorie = 4.184J).

RESULTS

3.3.1 Nest Site Selection and Nest Building - The Swallow

In their first breeding season Swallows return to their natal area, although not usually to the same site, whereas adults, especially the males, come back to the same barn and often to the same nest (Uchida 1932, Mason 1953).

There are usually only a few nests per farm (1-6 in this study, mean 4.1 ± 1.2, n = 23), but in the USA and continental Europe 25-30 pairs may not be uncommon (Bent 1942, von Vietinghoff-Riesch 1955, Lind 1964, Snapp 1973). Several nests may be located in the same barn but an area of a metre or so around the nest may be defended against intruders (pers. obs.).

The nest is built of mud and straw or grass, usually on beams or under the rafters in barns or occasionally under the eaves of buildings. The lining is of dry grass and feathers, often white (pers. obs.).

Nests may be reused for a second brood, and in subsequent years, although not necessarily by the same birds. Some nests may last 10-15 years (von Vietinghoff-Riesch 1955). The rim of the nest is strengthened with mud for each brood so old nests can become very large and robust.

Swallows arriving early in the spring usually laid in an old nest, late-comers tended to make a new nest. Hence, the mean date of laying for birds building a new nest in this study was the 4th June ± 3 days (n = 7) whereas the mean first laying date was 16th May. 71% of these late birds had only a single brood, suggesting that they were first year birds. Their nests tended to be shallow with thin walls and floor, less robust than older nests.

If a nest only needs to be repaired and a lining made, the work can be finished in a couple of days but a new nest may take a week to complete (pers. obs.). Bad weather or very dry weather delays the building further. von Vietinghoff-Riesch (1955) notes eight days as normal for nest building, 12-16 days in bad weather.

The following description of behaviour is supported by multiple regression analyses shown in Table 3.1.

Both sexes worked on the nest but the female tended to do a little more than the male (Purchon 1948, this study). Most of the work was done early on in the day leaving time for feeding in the afternoon, perhaps to build up fat for overnight maintenance.

In good conditions less time was needed for feeding and the male perched for longer and sang, usually just outside the barn where the nest was sited. The female then sometimes spent more time sitting on the nest but the time she spent perching did not itself depend on feeding conditions.

Both male and female guarded the nest site from intruders intent on trying to steal feathers and the male also guarded the female from other males. The number of chases and songs per bird per hour depended on the number of pairs per farm but also on the laying date of the pair.

On average a female spent 2.08 ± 2.17h a day on building and foraged for 8.48 ± 3.32h. The male worked for 1.56 ± 1.90h and foraged for 8.57 ± 3.39h. He sang outside the barn for 0.8 ± 0.75h but also spent some time gliding over the farm and singing.

The mean round trip time to collect mud and add it to the nest was 2.01 ± 0.45 min (n = 75 over 6h observation). The mud was usually taken from 10 to 30m away depending on availability. Most of the trip consisted of short flights with a few seconds on the ground. The birds may be at a high risk to predators at this stage, especially to cats which were common at the study site.

Wood (1937) calculated that a pair of Swallows took 1359 trips over six days to collect sufficient mud for a nest. von Vietinghoff-Riesch (1955) noted that a nest may be built from up to 1400 pieces of mud each with a wet weight of 0.48g although 750 pieces are adequate; some 16g of hay may also be used. Purchon (1948) estimated 1000 trips are necessary to build the nest. In Purchon's study the mean number of trips per hour was 26.5 early in the morning and 4.5 in the late afternoon. Herrick (in Bent 1942) found 22 times an hour as an average rate. In this study 8.5 times an hour was usual but during the most intense period of working the rate was 20-25 per hour.

3.3.2 Nest Site Selection and Nest Building - The Sand Martin

The first Sand Martins arrived at the colony about mid-April. More birds came in during May, the late comers being young, inexperienced birds (Mead and Harrison 1979). Adults tend to return to the same site while first years disperse from the natal colony (Mead & Harrison 1979).

A single bird sometimes started a burrow but it was only completed by a pair. The pair bond may have been weak at this stage and partners occasionally changed (in 3 out of 13 pairs caught during burrowing, although my disturbance may have affected this result). The favoured site for a burrow is near the top of a high vertical sand bank and at the top of the colony possibly to reduce the number of interactions with neighbours. Fine, homogenous and well-drained sand is preferred; tunelling will stop if stones are encountered (Stoner 1942, Spencer 1962). The tunnels were 60-100cm long and about 6cm in diameter with a nest chamber near, but not usually right at the back of the burrow (this study). The tunnel usually sloped upwards, perhaps to prevent flooding during periods of heavy rain.

A burrow took 5-10 days to complete (6.1 ± 1.6, n = 14) at a rate of 10-15 cm a day with both members of a pair excavating. Stoner (1942) gave a rate of 7.5 - 10cm a day and a final burrow length of 55 to 90cm. 1-3 days were spent making the nest, which was very shallow and constructed of grass, stems and feathers, usually white ones. Most of the nest material was collected by the female (pers. obs.). Stoner (1942) noted that feathers were not added to the nest until after the eggs were laid.

"Communal burrowing" has been noted (Hickling 1957) where several birds excavate a single burrow and many birds burrow simultaneously. I have never observed this and doubt that this occurs at all commonly. Lone birds will enter the burrow of a pair but they do not help to excavate it. Birds within a colony tend to go away to feed together and come back to the cliff face together; this may have led to the idea of "communal burrowing".

The following description of burrowing behaviour is supported by multiple regression analyses given in Table 3.1.

Burrowing activity was concentrated between the hours of about 0700 and 1600. Only an hour or so each day was taken up by digging, generally in short bursts of a few minutes, often interspersed with longer periods away from the burrow.

Heavy rain would interrupt burrowing but, in general, poor weather conditions did not affect the time spent burrowing except indirectly as the birds then had to spend more time feeding. Most of the day was spent feeding away from the burrows especially in poor weather when food was scarce.

Table 3.1 Multiple Regression Analyses of Nestbuilding/Burrowing Behaviour

		Dependent Variable (time spent in each activity)	Independent Variable	Standardised Partial Regression Coefficient	Cumulative $r^2 \times 100$	n
1.	Swallow	Building (B)[1]	Time (TM)[1]	- 0.52 **	26	25
	(male/female)		Available Prey Size (PSN)	0.46 **	47	
2.	Swallow	Feeding (F)	Distance to patch (D)	0.74 ***	40	29
	(female)		Food Abundance (Fn)	- 0.47 ***	68	
			Cloud cover (C)	- 0.41 ***	83	
3.	Swallow	Feeding (F)	Intensity of rain (R)	- 0.27 *	38	29
	(male)		Distance of patch (D)	0.56 ***	57	
			Cloud cover (C)	- 0.44 ***	70	
			Time (TM)	0.31 **	79	
4.	Swallow	Perching (P)	Wind strength (W)	0.48 ***	35	46
	(male)		Temperature (T°)	0.39 **	49	
5.	Swallow	Singing (SG)	Temperature (T°)	0.37 **	19	46
	(male)		Wind strength (W)	0.33 *	30	
6.	Swallow	Number of chases/h	Laying date (D. Med)	0.54 ***	32	36
	(male)		'colony' size (Col)	0.34 *	44	
7.	Swallow	Number of songs/h	'colony' size (Col)	0.42 *	25	36
	(male)					
8.	Sand Martin	Burrowing (B)	Time (TM)	- 0.43 **	19	44
	(male/female)					

9./

Table 3.1 (continued)

	Dependent Variable (time spent in each activity)	Independent Variable	Standardised Partial Regression Coefficient	Cumulative $r^2 \times 100$	n
9. Sand Martin (female)	Feeding (F)	Available Prey Size (PS3)	- 0.38 **	25	44
		Cloud cover (S)	- 0.34 *	35	44
10. Sand Martin (male)	Feeding (F)	Intensity of rain (R)	- 0.49 ***	28	44
		Food abundance (Fn)	- 0.41 ***	44	
11. Sand Martin (male)	Spare time (ST)	Temperature (T°C)	0.40 **	16	44
12. Sand Martin (male)	Fighting (FT)	Stage of burrowing (Stl)	- 0.38 *	14	44
13 Sand Martin (male/female)	Perching (P)	Food abundance (Fn)	0.59 ***	56	44
		Stage of burrowing (Stl)	0.29 *	62	

[1] Symbols in parentheses correspond to variables described in Appendix 4

* $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$

Burrowing was sometimes interrupted by chasing and fighting other birds in the colony which perched at the entrance of the tunnel. This happened most often during the early stages of burrowing when the owners of the burrow were most exposed to their neighbours.

The rest of the time was spent perching and gliding around the colony. This spare time and perching time was greatest in good feeding conditions and in the late stages of burrowing. It may be useful to watch for predators and possibly to look for an opportunity to steal nesting material or promiscuous matings and to guard the burrow and mate.

The majority of birds built their own burrows rather than reusing old ones. This may be due to the presence of parasites (_Ceratophyllus sp_. and Hippoboscid flies) in old nests. Burrows may also collapse or be destroyed between breeding seasons.

The female spent 1.40 ± 1.66h a day burrowing and 10.66 + 3.25h foraging. The male spent 1.32 ± 1.59h burrowing and 10.89 ± 2.92h feeding.

3.4.1 Egg Production and Laying - The Swallow

The eggs were laid at a rate of one a day although laying may be suspended for a day in bad weather conditions (pers. obs., Bryant 1975). The average weight of a Swallow egg was 1.97 ± 0.05g $(n = 6)$.

The following description of behaviour is based on multiple regression analyses presented in Table 3.2.

Both male and female spent more time feeding in the afternoon. Foraging time was also increased in bad feeding conditions (Figure 3.1). The female spent some time collecting calcareous particles to form the eggshells; she also completed the lining of the nest.

While perching and flying near the nest the male spent some time singing, especially at dawn and dusk. He also chased and fought with other males particularly in large 'colonies'. This chasing increased from the time of arrival of the birds, reaching a maximum when the female was ready to copulate (Figure 3.2). Copulation usually took place on a wire near the nest site. The male guarded the female, perching and feeding close to her. There was a decrease in chasing and singing after the eggs were laid until the first brood was ready to fledge and the parents prepared for another brood.

Early arrivals tended to spend more time fighting during egg laying than late comers, possibly as the female was ready to copulate just when late birds were arriving and pairing. Unpaired males were not observed in this study but they may occur in larger colonies. A few cases of polygamous Swallows have been recorded (Richardson 1956, Löhrl 1962).

The female usually spent 9.22 ± 2.48h feeding at this stage except in very bad weather when both sexes stayed away from the nest site. Her mate spent 8.99 ± 2.78h feeding, 0.73 ± 0.84h chasing and 1.04 ± 0.70h singing.

3.4.2 Egg Production and Laying - The Sand Martin

Once the burrow was complete the male spent a lot of time at the entrance calling and guarding the nest and female, or gliding near to the burrow. When the female was ready to copulate the male guarded her very closely, following her when she went out to feed or to collect nesting material. Beecher and Beecher (1979) suggest that this guarding is undertaken to prevent other males copulating with the female. They showed that males will chase the pair and that the paired male will himself chase other paired birds when his own female has laid her eggs and is no longer available to other males. However, the male could equally guard in order to prevent his mate deserting. There are always lone males in the colony looking for mates.

The female spent some time looking for calcareous particles for eggshell formation. Tooby (1947) noted pieces of mussel shell in a nest, just before egg laying had started, which the female may have collected for this purpose. The eggs were laid at the rate of one a day, although laying may be suspended as in other hirundines (Bryant 1975).

The following description is based on multiple regression analyses presented in Table 3.2.

The time spent feeding depended on the prevailing feeding conditions (Figure 3.1), especially the available prey size and the rainfall intensity, although in very heavy rain Sand Martins would stop feeding altogether. The female was probably the bird which decided when and for how long to feed since she would leave and re-enter the burrow before the male. The male's feeding behaviour correlated strongly with hers ($r = 0.74$, $n = 79$, $p < 0.01$).

The female spent 9.13 ± 3.64h a day feeding, the male 10.20 ± 2.82h feeding and 0.36 ± 0.69h chasing and fighting. As the female approached the time of egg laying the male spent less time guarding at the entrance to the burrow and instead stayed with the female at the back of the tunnel. Males at the periphery of a colony spent more time guarding and fighting than central, upper level birds perhaps because they tended to be later arriving and had more neighbours to interact with (r position $= 0.29$, $n = 79$, $p < 0.01$, see Appendix 4). The amount of chasing increased as the time of egg laying approached (Figure 3.2).

Figure 3.1

The percentage of each observation period (1 hour) spent feeding by (a) the Swallow and (b) the Sand Martin in relation to the abundance of food shown by the suction trap catch.

(a) $r = -0.32, p = 0.014$

(b) $r = -0.41, p < 0.001$

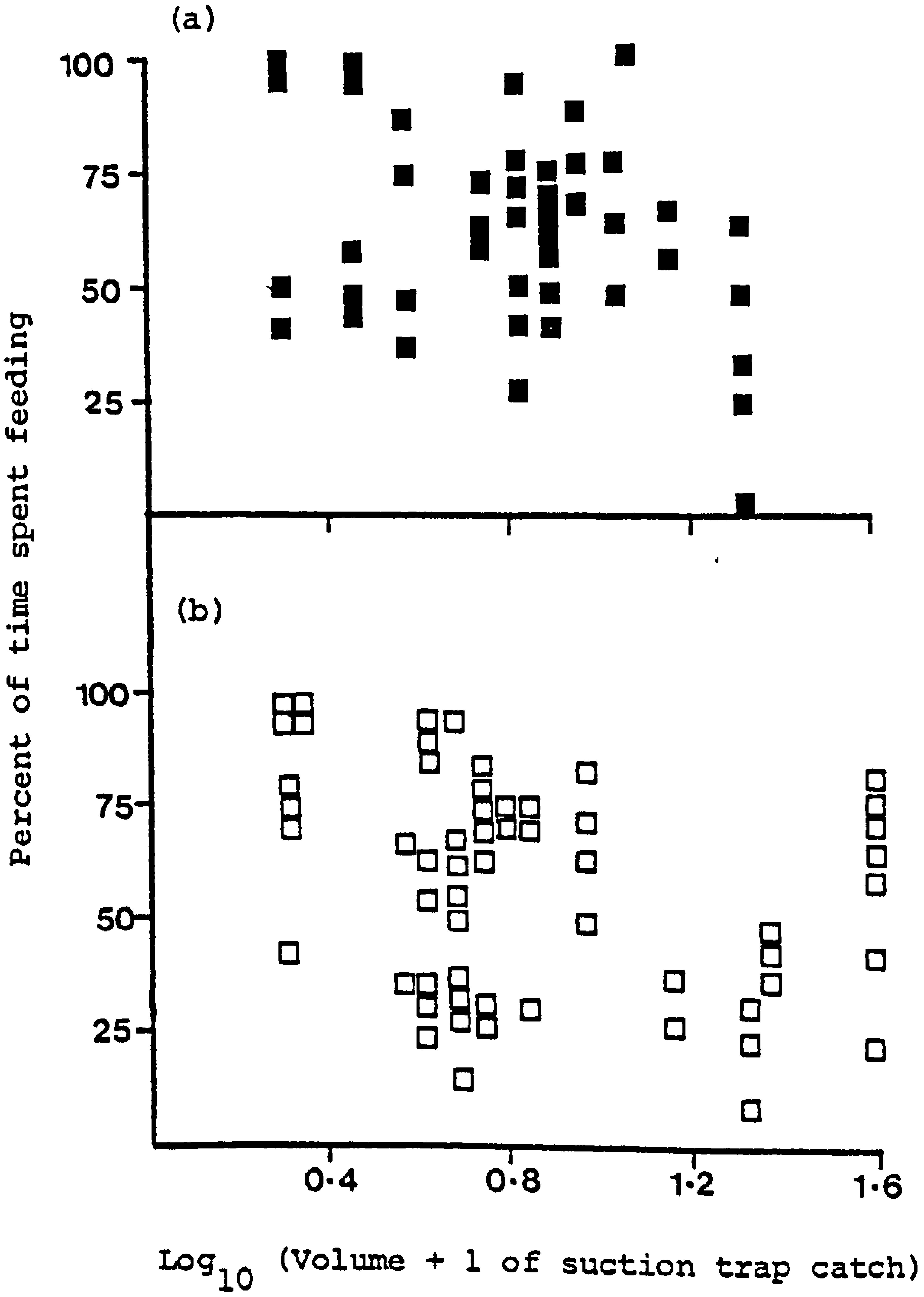

(a)
(b)
100
75
50
25
Percent of time spent feeding
0·4
0·8
1·2
1·6
Log$_{10}$ (Volume + 1 of suction trap catch)

Figure 3.2

The percentage of each observation period (1 hour) spend in agonistic behaviour by (a) the Swallow and (b) the Sand Martin in relation to the stage of the breeding season. Day 30 is the day on which incubation starts.

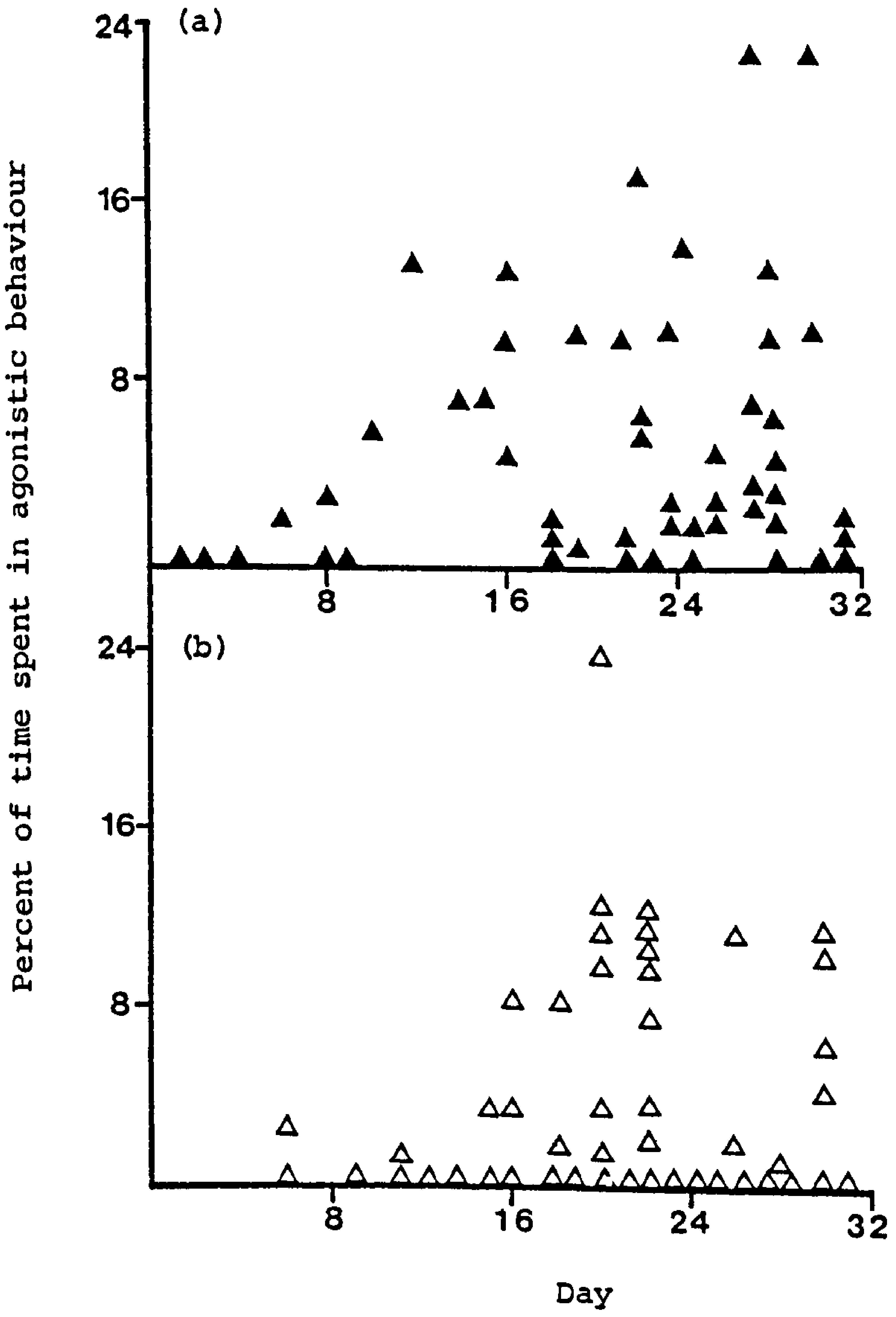

Percent of time spent in agonistic behaviour
(a)
24
16
8
8
16
24
32
(b)
24
16
8
8
16
24
32
Day

Table 3.2 Multiple Regression Analyses of Egglaying Behaviour

	Dependent Variable (time spent in each activity)	Independent Variable	Standardised Partial Regression Coefficient	Cumulative $r^2 \times 100$	n
1. Swallow (female)	Feeding (F)[1]	Available Prey Size (PSN)[1]	$- 0.51$ ***	18	35
		Time (TM)	0.46 **	38	
2. Swallow (male)	Feeding (F)	Time (TM)	0.37 **	17	47
		Intensity of rain (R)	$- 0.33$ *	28	
3. Swallow (female)	Spare time (ST)	Temperature (T°)	0.44 **	19	47
4. Swallow (male)	Spare time (ST)	Temperature (T°)	0.44 **	19	47
		'Colony' size (Col)	0.30 *	28	
5. Swallow (male)	Fighting (FT)	'Colony' size (Col)	0.40 **	12	47
		Laying date (DL)	$- 0.38$ **	26	
6. Swallow (male)	Singing (SG)	Time (TM±)	0.49 ***	24	47
7. Sand Martin (male/female)	Feeding (F)	Available Prey Size (PS1)	$- 0.44$ ***	33	62
		Intensity of Rain (R)	$- 0.30$ **	40	
		Laying Date (D Med)	$- 0.23$ *	45	
8. Sand Martin (male)	Guarding (G)	Time before Incubation (St2)	0.35 **	20	64

[1] Symbols in parentheses correspond to variables described in Appendix 4

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

3.4.3 The Timing of Laying

Of the three British hirundines the Sand Martin is the first to lay and the House Martin is the last. The Sand Martin starts to lay at the end of April in Southern Britain and in the first week of May in Northern Britain (Morgan 1979). Swallow clutches have also been recorded at the end of April and beginning of May (Adams 1957) but in two recent Scottish studies the earliest laying dates were in the second week of May (McGinn and Clark 1978, McGinn 1979). Laying is again earlier in Southern than in Northern Britain (Adams 1957). The earliest House Martins, in a study in Perthshire, Scotland, laid in the third week of May; the mean laying date for first clutches was 6th June (Bryant 1979). The mean laying date for House Martins in Southern Britain for first clutches was 29th May (Bryant 1975). Laying dates in the present study, for Swallows and Sand Martins, are in conformity with these results (Table 3.3), although here the sample sizes are small.

3.4.4 Clutch Sizes

The clutch size of both the Sand Martin and the Swallow varies from 3 to 6 eggs (Table 3.4). There is a decrease in clutch size in hirundines during the season partly due to a true decrease from first to second broods, and partly due to late arrivals, the younger birds, having smaller first clutches than the older, early birds (Bryant 1979).

Two broods were usual at the study sites; early birds could have had sufficient time for a third brood but I have no evidence of this for Sand Martins. Waugh (pers. comm.) noted one case of a third brood in Swallows in this study area. Petersen (1955) found no evidence of second broods of Sand Martins in his study area and

Table 3.3 Laying dates for Swallows and Sand Martins in this study

Year:	Range 1st brood	Median date	n	Range 2nd brood	Median date	n
Year: 1977						
Sand Martin	-	-		-	-	
Swallow	15th May - 4th June	25th May	9	12th - 19th July	16th July	7
Year: 1978						
Sand Martin	8th May - 7th June	19th May	13	13th June - 26th July	4th July	8
Swallow	16th May - 10th June	29th May	9	17th - 19th July	18th July	5
Year: 1979						
Sand Martin	3rd May - 8th June	19th May	13	15th June -	—	
Swallow	17th May - 6th June	3rd June	9	17th - 30th July	29th July	5

Table 3.4 Clutch Sizes of Swallows and Sand Martins

Swallows

Clutch Size	Source	Locality
4.4	Boyd 1935/36	U.K.
1st brood 4.5 2nd brood 4 3rd brood 3.5	Brinkmann 1938	Germany
1st brood 4.0 2nd brood 4.09	Buxton 1946	Bavaria
1st brood 4.25 2nd brood 3.34	Mason 1953	U.S.A.
June 4.34 September 3.0	Vietinghoff-Riesch 1955	Germany
5.02	Mizuta 1963	Japan
4.8	Snapp 1973	U.S.A.
May 5.06 August 4.08	McGinn and Clark 1978	Southern Scotland
4.67 - 3.75	McGinn 1979	Banffshire, Scotland
1st brood 4.70 ± 0.66 n=27 2nd brood 4.69 ± 0.55 n=23	This study	Central Scotland

Sand Martin

Clutch Size	Source	Locality
3 - 6	Cory 1909	Wisconsin, Illinois (USA)
3-7	Forbush 1929	New England (USA)
early 4 or 5, late 3 or 4	Stoner 1936	N.Y. State (USA)
5 (4-7)	Niethammer 1937	Germany
4-5	Witherby et al. 1940	U.K.
5 (4 - 6)	Lack 1947	Norway
Before June 15th 5.0, after 4.0	Petersen 1955	Wisconsin (USA)
4.8 (only one brood)	Svensson 1969	Lapland
5.0	Morgan 1979	Northern U.K.
4.64	Morgan 1979	Southern U.K.
1st brood 4.77 ± 1.12 n=20 2nd brood 4.63 ± 0.70 n=8	This study	Central Scotland

their occurrence undoubtedly varies according to local conditions. Early arrivals usually had two broods, late comers often had only one brood (e.g. all pairs of Swallows, in this study, laying before the median date of 27th May in 1977/78, had two broods, only 33% of pairs laying after that date, n = 18).

Of the double-brooded Swallows 78.3% had a second brood of the same size or larger (n = 23). So apart from the absence of clutches of six there was apparently little reduction in the clutch size of a particular individual in contrast to House Martins where only 0 - 30% have a second brood the same size as the first (D.M. Bryant pers. comm.). The sample size for Swallows is, however, too small for firm conclusions to be drawn.

3.5.1 Incubation

Incubation starts on the day of laying of the penultimate egg in Sand Martins (Asbirk 1976) and this is assumed to pertain to Swallows as well. Purchon (1948) observed intermittent incubation occurring in part-laid clutches of Swallows. Incubation periods are shown in Table 3.5.

3.5.2 Incubation of the Swallow

Only the female incubates although the male of the American race is said to do so. The male has been observed on the nest, apparently incubating by Smith (1933), Brewster (1937), Davis (1937), Wood (1937) and Herrick (in Bent 1942) all in the U.S.A., and by Moreau and Moreau (1939) and Berndt and Berndt (1942) in Europe. Wood (1937) found that after the third day of incubation the parents changed at intervals of 4-15 minutes and on the eleventh day at intervals of 6-36 minutes. Brewster (1938) also observed the birds changing over every 15 minutes. Smith (1933, 1937) and Moreau and Moreau (1939)

Table 3.5

Incubation periods of Swallows and Sand Martins

Swallow Incubation Period in days (last egg-last young hatched)	Study	Site
14 - 15	Brown 1924	U.K.
14 - 16	Smith 1933	U.S.A.
16	Wood 1937	U.S.A.
14 - 15	Allen and Nice 1952	U.S.A.
15 - 16	Kendeigh 1952	U.S.A.
15 - 25	Adams 1957	U.K.
16.3 ± 1.4 (n = 22)	This study (penultimate egg to last hatched)	Central Scotland

Sand Martin Incubation Period in days		
12 or 13	Evans (in Bergtold 1917)	U.S.A.
12 - 13	Burns 1921	U.S.A.
13 - 14	Baerg 1931	Arkansas U.S.A.
14 - 16	Stoner 1936	N.Y. State U.S.A.
12 - 16	Niethammer 1937	Germany
14 (12 - 16)	Witherby et al 1940	U.K.
15 (13 - 15)	Petersen 1955	Wisconsin U.S.A.
16.7	Svensson 1969	Lapland
12.6 ± 1.3 (10-14) n = 7	This study (penultimate egg to last hatched)	Central Scotland

state that there is not always an instantaneous changeover of the sexes. I have seen two males, on one occasion each, sitting on the eggs but for less than a minute each time with the female perching close by. Berndt (1942) and Kendeigh (1952) also saw the male briefly on the nest. Kendeigh (1952) recorded the heat applied to eggs by incubating Swallows and showed that males did not warm the eggs. The male's brood patch is feathered and not vascularised so he could not incubate as the female does. However, in bad weather a bird just covering the eggs to prevent them cooling too rapidly would allow the female more time to feed herself.

In this study the female warmed the eggs to a temperature of 35.7°C (Table 3.6). The egg temperature dropped by several degrees when the female was off the nest. The most frequent inattentive period was only 2-5 minutes (Figure 3.3). As energy is needed to reheat the eggs it is advantageous to the bird to keep the duration of inattentive periods to a minimum.

The following description of incubation behaviour is based on multiple regression analyses given in Table 3.8.

The female spent longer intervals on the nest when it was cold and at either end of the day (Figure 3.4, Table 3.7). The eggs require more heat as they approach hatching and so the inattentive period decreased with the stage of incubation.

During the egg laying period the female spent progressively more time on the nest, perhaps providing some warmth, especially at night. So the first laid eggs may start to develop before more constant incubation begins. The mean temperature of the air between the eggs in partly laid clutches was only 16.9 ± 1.5°C $(n = 10)$

Figure 3.3

Frequency of inattentive periods of incubating Swallows and the drop in egg temperature resulting from the inattentive period (squares). The inattentive periods are means of hourly intervals.

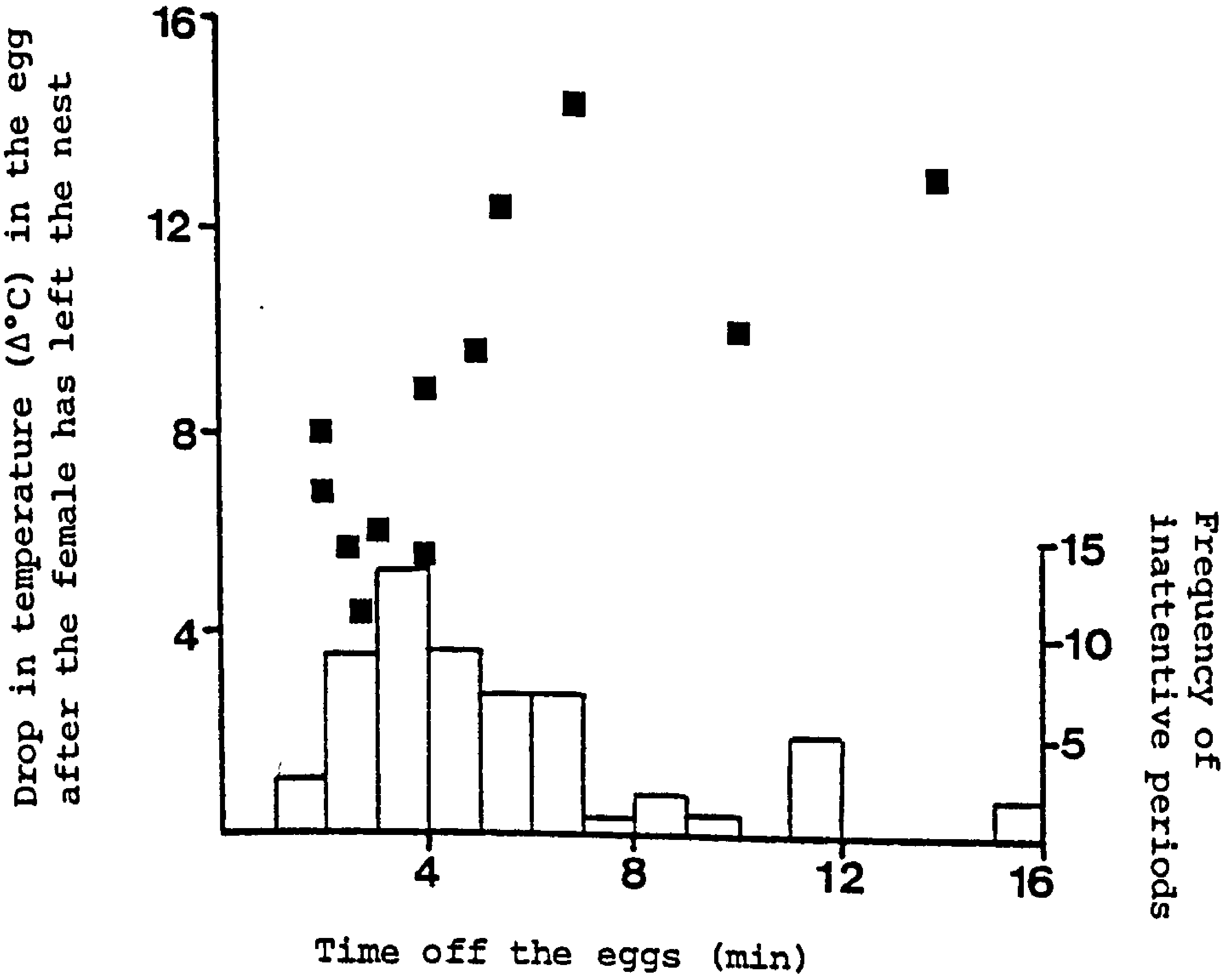

Drop in temperature (Δ°C) in the egg after the female has left the nest
16
12
8
4
Frequency of inattentive periods
15
10
5
4
8
12
16
Time off the eggs (min)

Figure 3.4

The diurnal variation in the duration of attentive periods of incubating Swallows at an ambient temperature of 20°C (shaded histogram) and 10°C (unshaded histogram). The duration of inattentive periods at 20°C and 10°C is indicated by the dashed lines A and B respectively. (The values are calculated from multiple regression equations)

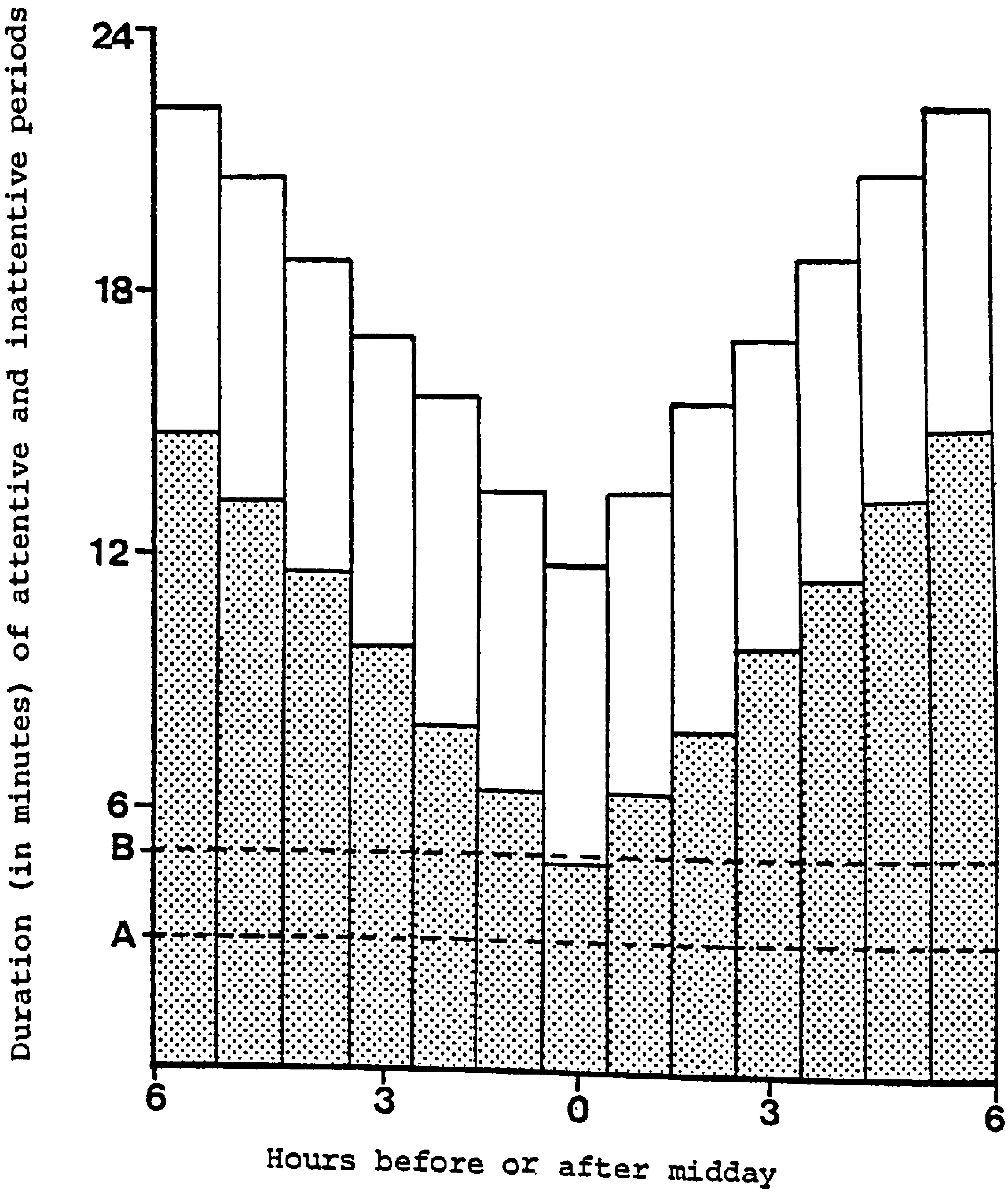

24
18
12
6
B
A
Duration (in minutes) of attentive and inattentive periods
6
3
0
3
6
Hours before or after midday

Table 3.6 Measurements of nest air and egg temperatures in Swallow clutches during the attentive (Tmax) and inattentive periods (T°C and Tmin) of incubation

Site	Cooling rate °C per °C-h	Mean maximum temperature Tmax	Mean temperature T°C	Mean minimum temperature Tmin	n
Air between eggs	2.93 ± 0.94	38.4 ± 0.4	32.2 ± 2.3	31.0 ± 1.7	25
Air above eggs	7.89 ± 1.95	41°	27.9 ± 2.2	26.5 ± 0.2	9
Inside egg	3.10 ± 1.48	35.7 ± 1.3	28.4 ± 3.4	25.5 ± 2.7	12

Table 3.7 Attentive Periods of the Incubating Swallow (in minutes, for all stages of incubation)

Ambient temperature, °C	n	Mean attentive period	Number day^{-1}	Mean Inattentive Period
9 - 12°	24	22.2 ± 15.3	28	7.6 ± 8.2
20 - 24°	10	10.0 ± 5.4	56	5.4 ± 4.3
		$t = 3.43$, $p < 0.01$		$t = 1.03$, n.s.

Table 3.8 Multiple Regression Analyses of Incubation in the Swallow

		Dependent Variable (time spent in each activity)	Independent Variable	Standardised Partial Regression Coefficient	Cumulative $r^2 \times 100$	n
1.	Female	Attentive Period (A)[1]	Time (TM±)[1]	0.33 **	14	65
			Temperature (T°C)	- 0.26 *	20	
2.	Female	Inattentive Period (IP)	Available Prey Size (PSN)	- 0.43 **	22	65
			Stage of Incubation (St3)	- 0.33 *	30	
			Clutch size (CS)	- 0.32 *	39	
3.	Female	Incubating (I)	Daylength (Ph)	0.46 **	21	65
4.	Female	Perching (P)	Temperature (TMx)	0.54 ***	30	65
			Time (TM)	0.31 *	39	
5.	Male	Feeding (F)	Temperature (T°)	- 0.41 **	26	44
			Rainfall (Rain)	0.31 *	34	
6.	Male	Spare time (ST)	1st or 2nd brood (1/2B)	- 0.34 *	14	44
			Time (TM)	0.31 *	24	

[1] Symbols in parentheses correspond to variables described in Appendix 4

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

whereas during incubation this value was more than 30°C (Table 3.6). Incubation rates (the percentage of time spent on the eggs by the bird) continued to be low during the first four or five days after the clutch was completed. The time spent incubating in the daylight period during the first five days (10.22 ± 2.40h, n = 22) was significantly lower than the time spent incubating after this period (12.21 ± 1.62h, n = 43, $t = 3.5$, $p < 0.001$). Incubation rates also increased in cold conditions ($r_{T°C} = 0.27$, $n = 65$, all stages, $p < 0.02$ and Figure 3.5).

The female spent most of the time off the nest feeding but when conditions were good, especially late in the day, she spent some time perching, usually close to the nest. The male Swallow spent some time perching near to the barn where the nest was sited or else gliding over the farmyard particularly during the incubation of the first clutch. At intervals he flew into the barn and often came out with the female. He either returned with her after she had fed or he went back to the perch, (out of 139 observations he stayed with the female 79 times, 57%). There was some chasing and fighting during this period but not as much as previously.

The male spent, on average, 9.12 ± 2.77h flying during the day, 0.61 ± 0.68h singing and 0.28 ± 0.41h in agonistic behaviour.

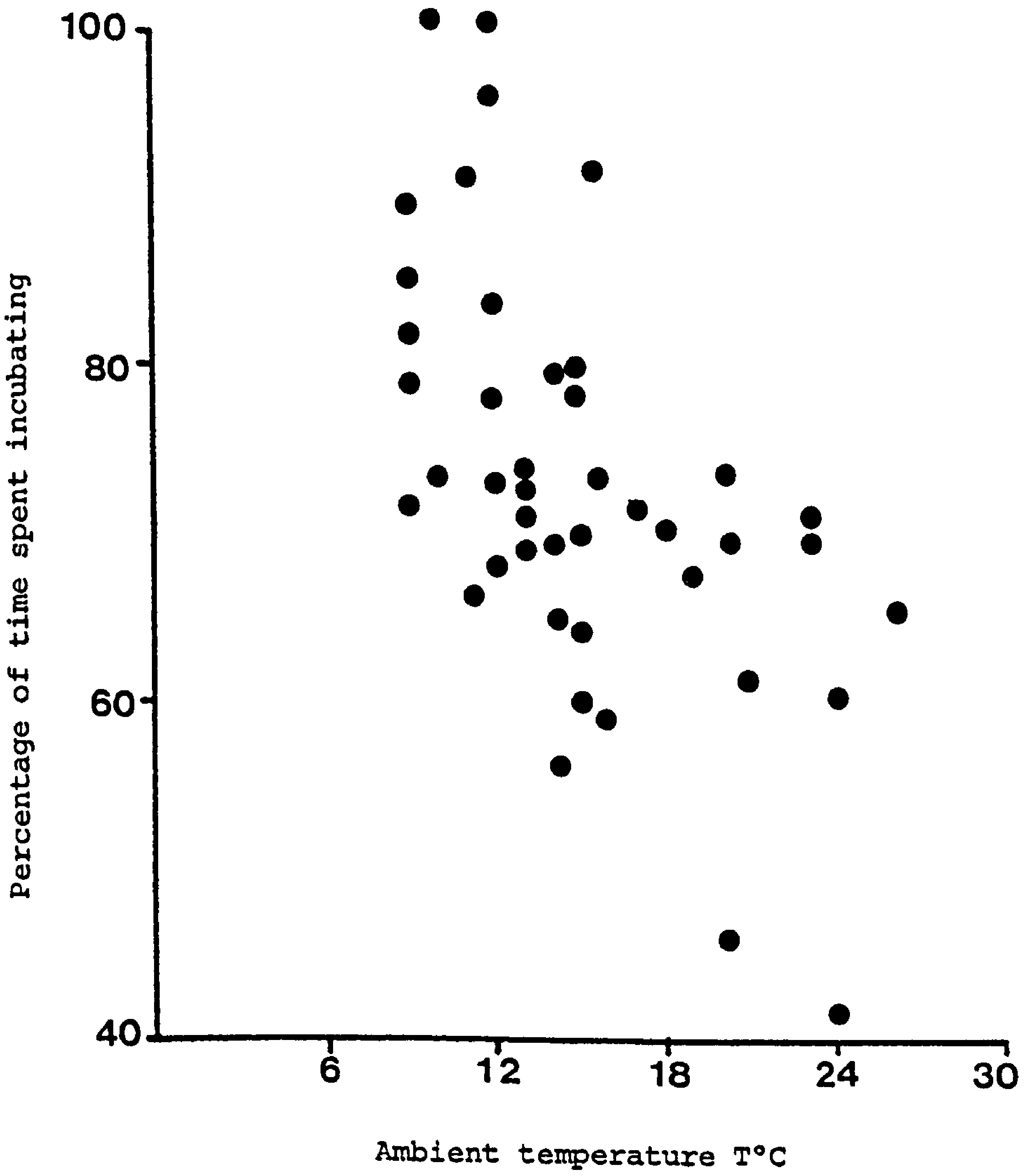
3.5.3 Incubation of the Sand Martin

Unlike the Swallow both the male and female Sand Martin incubate but while the female has a large, completely bare and well vascularised brood patch the male's brood patch is small and still partly feathered so it may be less effective for applying heat to the eggs. Petersen (1955) recorded the nest temperature when a male was on the eggs: the highest temperatures attained were 34.4° and 35.6°C during

Figure 3.5

The percentage of each hourly observation period spent incubating by the female Swallow in relation to the ambient temperature. Data points are shown for days 6 to 14 of incubation.

$r = 0.56, p < 0.001$


100
80
60
40
6
12
18
24
30
Percentage of time spent incubating
Ambient temperature T°C

incubation periods of 19, 17 and 18 minutes which suggests that the male is capable of incubation. In this study the incubation was shared unequally: 64% by the female and 34% by the male.

The birds were incubating in a fairly constant ambient temperature. The mean temperature of 31 nest chambers which contained nests with eggs or very young nestlings was 13.1 ± 0.6°C. The mean temperature of 18 chambers which contained one adult bird was 15.2 ± 0.9°C. The ambient temperatures outside the burrows ranged from 13° to 21°C. The metabolic heat produced by adults and by old nestlings can increase the burrow temperature. Stoner (1936) measured Bank Swallow burrow temperatures throughout the season:

Month	Mean Temperature °C	
	Occupied burrows	Unoccupied burrows
May	13.9	13.6
June	19.8	18.8
July	25.6	24.1

Soil temperatures and daily temperature variation decrease with depth so burrows are protected from extremes of temperature (White, Bartholomew and Kinney 1978).

The incubation rhythm of both sexes depended on maximum daily temperatures and rainfall intensity (Tables 3.9 and 3.10). The

Table 3.9

Attentive periods of incubating Sand Martins (in minutes, for all stages of incubation)

Maximum daily temperature	Attentive period of male	Attentive period of female	n
≤ 12°C	10.63 ± 5.80	23.00 ± 8.70	12
20 - 24°C	7.70 ± 3.00	13.79 ± 6.90	32
	$t = 1.67$, n.s.	$t = 3.30$, $p < 0.01$	

Table 3.10 Multiple Regression Analyses of Incubation in the Sand Martin

		Dependent Variable (time spent in each activity)	Independent Variable	Standardised Partial Regression Coefficient	Cumulative $r^2 \times 100$	n
1.	Male/female	Attentive Period (A)[1]	Temperature (TMx)[1]	- 0.37 ***	15	84
			Intensity of rain (R)	- 0.32 *	20	
2.	Male/female	Inattentive Period (IP)	Intensity of rain (R)	- 0.32 **	12	84
			Temperature (TMx)	- 0.30 **	20	
3.	Female	Incubating (I)	Incubation of ♂ (I)	- 0.68 ***	49	84
			Temperature (T°)	- 0.31 ***	59	
4.	Male	Incubating (I)	Incubation of ♀ (I)	- 0.69 ***	49	84
			Stage of Incubation (St3)	- 0.31 ***	58	

[1] Symbols in parentheses correspond to variables described in Appendix 4

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

percentage time spent incubating by the female was determined partly by the ambient temperature (Figure 3.6) but the male did not respond strongly to this. He incubated less as hatching time approached. Possibly the clutch needs more heat at this time and the female may be a more effective incubator. However, more of the variance in the data (49%) was explained by the behaviour of the mate than by weather conditions.

The incubating bird usually only left the nest when its partner entered the burrow so the eggs were rarely left unattended and then only in good conditions. Sometimes the male was away for a long time and the female then left to feed for a few minutes. On average the eggs were only left unattended for 0.36h a day. The egg temperature would thus be maintained at a high level and very little extra heat would be required to increase the temperature after an inattentive period by one bird.

Although the female incubated more in cold weather the male tended to increase his share of the incubation after a period of poor feeding conditions (Figure 3.7) perhaps allowing the female to replace body reserves by feeding for longer. On average, the male spent 6.82 ± 1.49h incubating during the day.

3.5.4 Mate Removal Experiments

Incubation rates of Sand Martins were measured on a per hour basis for six single males and six single females, ranging from Day 1 to Day 13 of incubation (Table 3.11). The median value for the males was 53.3% incubation (range 20.8 - 88.9) and for the females 70.8% (range 28.7 - 100.0). The difference between the incubation rates for males and for females is significant at the 5% level (Kolmogorov-Smirnov test).

Figure 3.6

The percentage of each hourly observation period spent incubating by female (closed circles) and male (open symbols) Sand Martins in relation to ambient temperature. The regression line for the female is shown.

Female : $r = -0.36$, $p < 0.001$

Percent incubation = 76.16 - 0.85T°C

Male : $r = 0.23$, $p < 0.02$

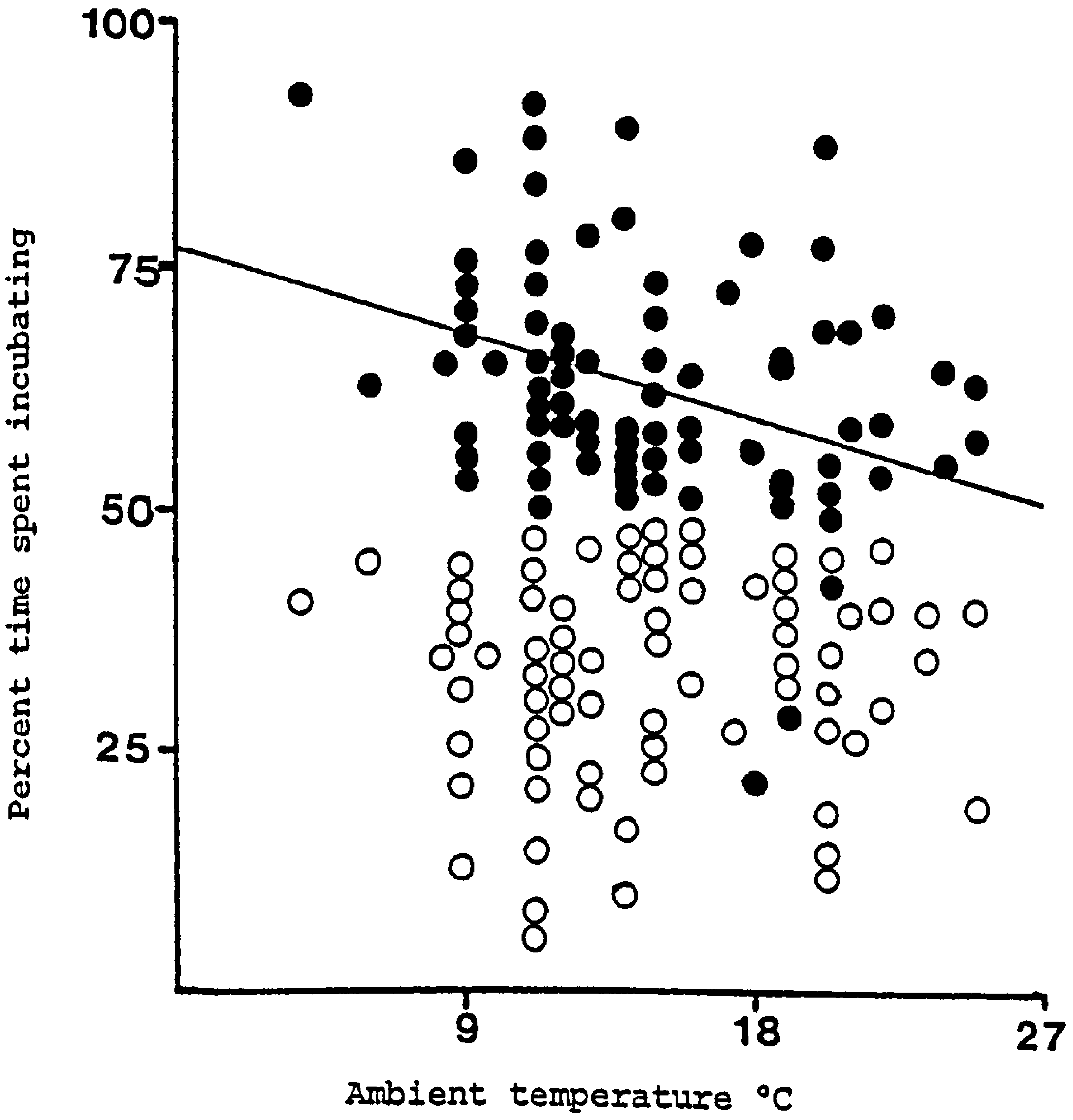
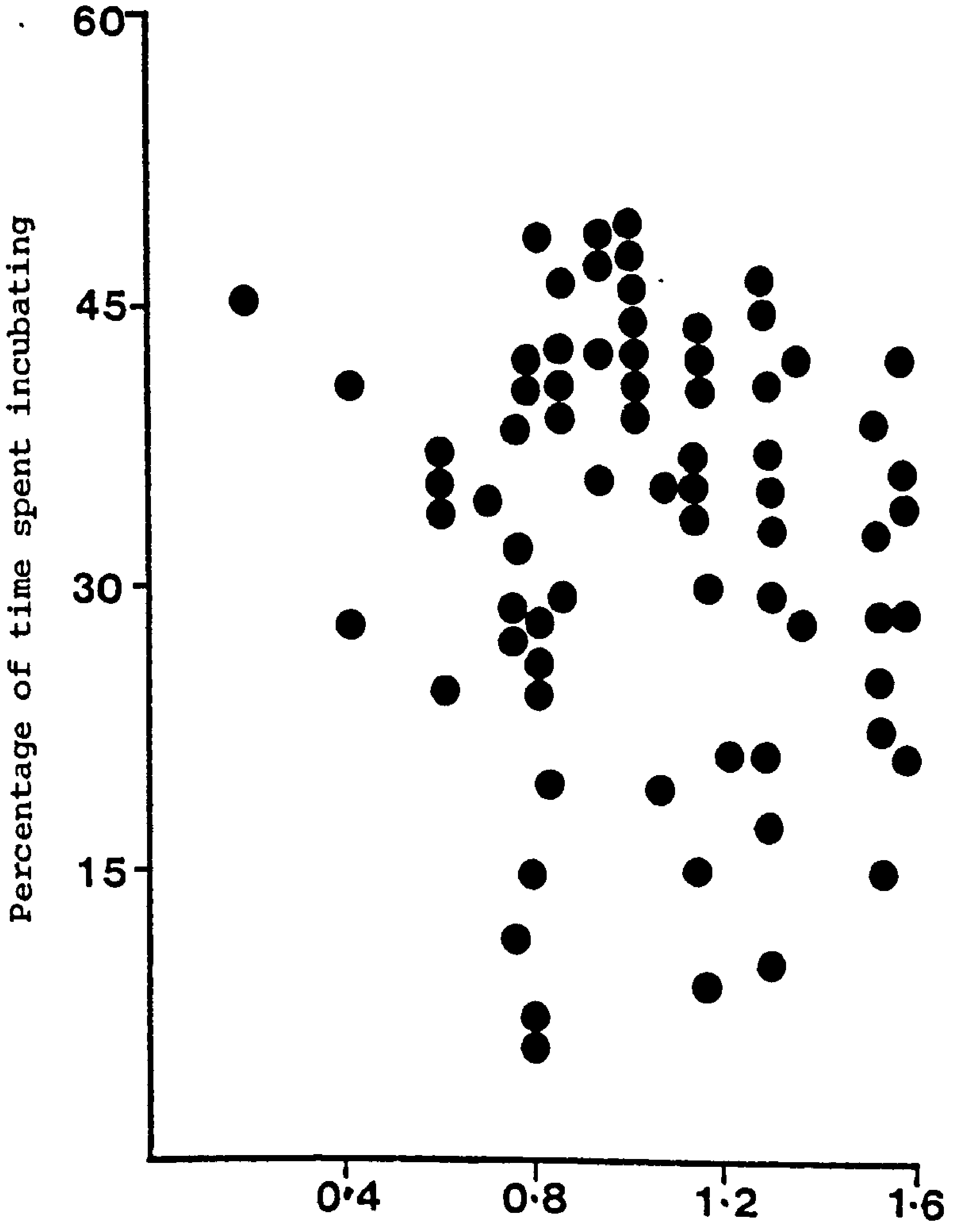

100
75
50
25
Percent time spent incubating
9
18
27
Ambient temperature °C

Figure 3.7

The percentage of each hourly observation period spent incubating by male Sand Martins in relation to the food abundance on the previous day.

$r = -0.25$, $p < 0.02$



log$_{10}$ (Volume + 1) of suction trap catch on day n - 1

Table 3.11

Incubation rates of Sand Martins incubating alone

Sex	Day of Incubation	Mean daily incubation rate (%)
M	1	56.02
M	7	35.24
M	7	72.39
M	6	81.37
M	12	60.62
M	13	52.69
F	1	47.68
F	7	72.39
F	7	64.42
F	9	75.58
F	10	73.90
F	13	91.38

The females (excepting the day 1 bird) were less variable than the males and consistently incubated at a high level throughout the day. The males began by staying on the nest for a long time but five out of the six males decreased their incubation rate by ≥ 20% by the end of the experiment whereas only one female did so.

Similar observations were made on two pairs of Swallows. The female of one pair was caught for a D_2O^{18} run (see Methods), retained for about 1½ hours and then released. She did not re-enter the room where the nest was located for a further three hours. During all this time the male flew into and out of the room occasionally but did not sit on the eggs. For part of the time, however, the female was perching close by on another building and her presence may have affected his behaviour.

Another incubating female was caught and retained for six hours. She was fed artificially and released at the end of the experiment. During this time the male frequently went to the nest and flew away again, at one time returning with another bird. For most of the time, however, he perched outside the barn.

The male Sand Martin is obviously able to contribute substantially to incubating the eggs but his role is secondary to that of the female. Two of the other nests in my study area were deserted by the female and in both cases the male deserted within a couple of days. I have no evidence of females incubating alone when the male has deserted but on one occasion a female House Martin at a colony at Muckhart, Perthshire, incubated a clutch when her partner had died, the eggs hatching successfully (D.M. Bryant, pers. comm.).

The male Swallow, on the other hand, is unable to incubate and apparently will not even cover the eggs when there is a risk of them becoming chilled.

3.6.1 Brooding - Introduction

The eggs may all hatch on one day or over two or three days, (Day 1 is the day on which all the nestlings have hatched). For the first few days after hatching the young altricial passerine is poikilothermic and needs to be brooded. The parent maintains the nestlings' temperature at a level similar to that of incubated eggs (Drent, in Farner 197~~2~~3). The body temperature increases and becomes more narrowly regulated as the nestling grows and becomes more homeothermic. Body temperatures of nestling Barn Swallows average 36.4°C, 39.8°C, 40.9°C and 42.2°C on the 1st, 5th, 10th and 17th day respectively (Stoner 1935).

Inattentive periods of brooding Swallows were generally short so the temperature in the nest fell very little (Table 3.12). The lowest temperature to which the nest air fell was 29°C after an absence of the female of seven minutes. The core temperature of the nestlings would probably remain more constant than their surface temperature. Kendeigh and Baldwin (1928) found that there was a drop of only 2.5 - 3°C in body temperature during the inattentive period of the female House Wren, Troglodytes aedon, at 10°C - 20°C just after hatching.

Table 3.12

Nest air temperatures of Swallow broods aged 1-4 days during the attentive period (T_{max}) and the inattentive period (T_{min})

Site	Cooling rate °C per °C-h	Mean maximum temperature, T_{max}	Mean minimum temperature, T_{min}	n
Air above nestlings	3.59 ± 2.08	28.8 ± 4.9	20.8 ± 1.7	8
Air between nestlings	0.90 ± 0.45	37.4 ± 2.0	30.2 ± 0.9	4

Marsh (1979) investigated the development of endothermy in the Bank Swallow. He concluded that the nestlings became homeothermic when they gained a weight of about 10g (6 days old) and that this was a result of the change in mass rather than an increase in insulation due to plumage development. Hence any delay in growth will delay the onset of homeothermy. The feather tips on the Sand Martin nestling do not sprout until the nestling is about eight days old and the bird is not well-feathered until 10-12 days. Sand Martins and Swallows of 1-6 days bear practically no down and are brooded for much of the time. However House Martins are covered with more down than the Sand Martin nestling, so they could be left alone on a bad weather day when the parents need to feed far from the nest (Bryant and Gardiner 1979).

3.6.2 Brooding in the Swallow (For nestlings aged 0-10 days)

The following description is based on multiple regression analyses given in Table 3.14.

The time spent brooding the nestlings was variable but the female was off the nest for only a few minutes at a time; the attentive periods decreased in duration as the brood mass increased. The male took no part in brooding.

The female usually just fed herself when she was away from the nest while the nestlings were very young, but the male would come in to feed them. The female increased her share of the feeding as the young grew.

The young were brooded at a decreasing rate until they were about six days old, but in bad weather the duration of brooding for any age was extended; nestlings up to about ten days were then also brooded (Figure 3.8). The female also covered the nest at night until 10-12 days after hatching.

Owen (1918) observed brooding by both male and female Swallows but Purchon (1948) only saw the female on the young. I saw the male occasionally stand over the nestlings but he never brooded them. The female left the nest for a minute or less when the male came in to feed the young. This was also noted by Purchon (1948) but this was in contrast to the behaviour noted by Owen (1918) and by Hosking and Newberry (1946) who found that the male passed food to the brooding female and she fed the nestlings.

Figure 3.8

The percentage of each hourly observation period that (a) Swallow and (b) Sand Martin nestlings are brooded during the day in relation to their age. Means ± 1 s.d. are shown. The number of periods over which the data were collected is indicated.

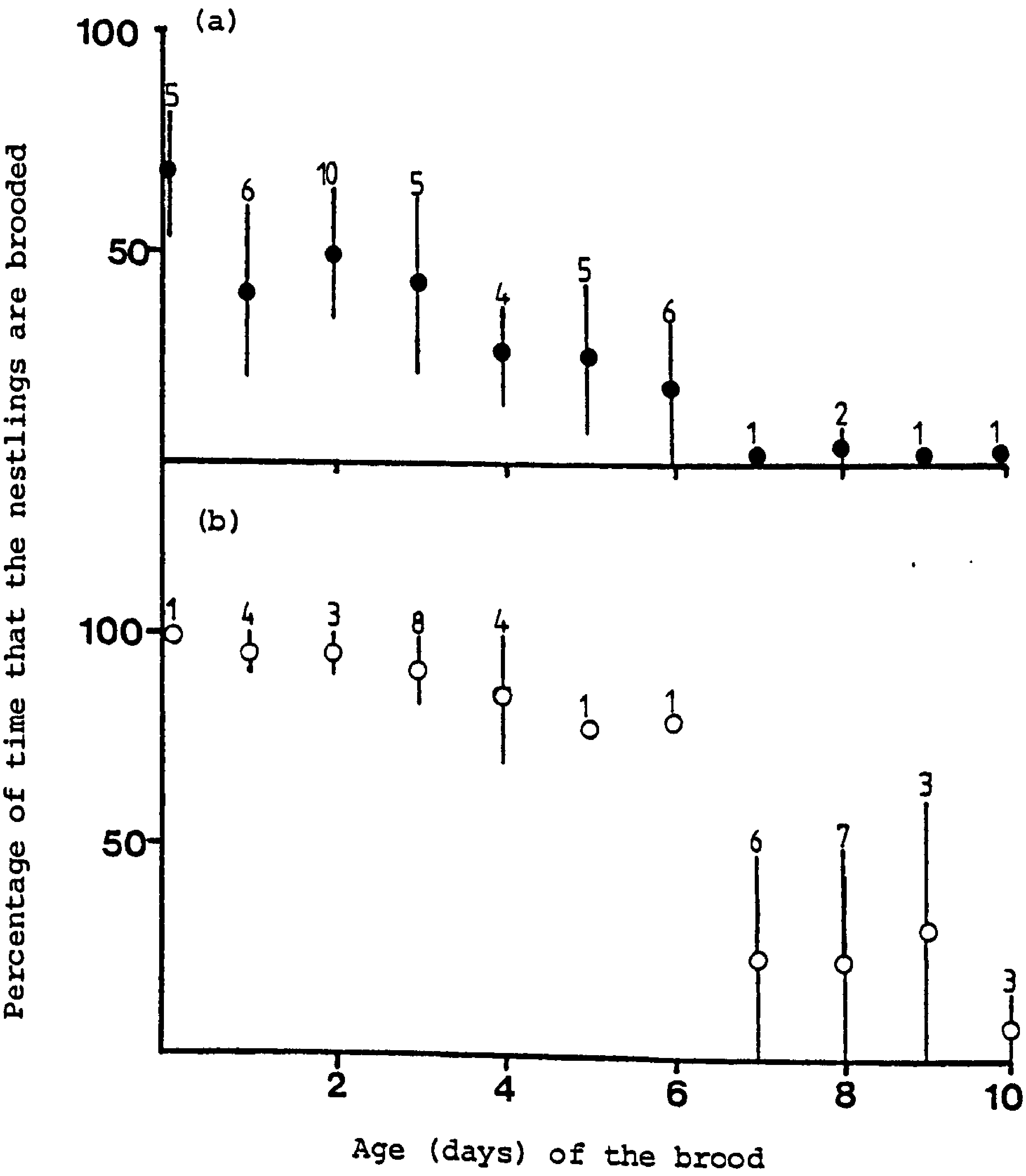

(a)
(b)
100
50
100
50
2
4
6
8
10
Percentage of time that the nestlings are brooded
Age (days) of the brood
5
6
10
5
4
5
6
1
2
1
1
1
4
3
8
4
1
1
6
7
3
3

Table 3.14 Multiple Regression Analyses of Brooding in the Swallow

		Dependent Variable (time spent in each activity)	Independent Variable	Standardised Partial Regression Coefficient	Cumulative $r^2 \times 100$	n
1.	Female	Attentive Period (A)[1]	Brood Mass (BM)[1]	- 0.56 ***	35	48
			Temperature (TMN)	- 0.23 *	40	
2.	Female	Inattentive Period (IP)	Intensity of rain (R)	- 0.45 ***	30	48
			Brood Mass (BM)	0.25 *	35	
3.	Female	Brooding (BR)	Brood Mass (BM)	- 0.70 ***	56	48
			Available Prey Size (PS3)	- 0.29	64	
4.	Female	Feeding Rate (FR)	Brood Mass (BM)	0.36 **	16	48
			Available Prey Size (PS3)	0.28 *	24	
5.	Male	Perching (P)	1st/2nd Brood (1/2B)	- 0.46 ***	23	48
			Brood Mass (BM)	- 0.35 **	40	
			Cloud cover (C)	0.32 **	49	
6.	Male	Feeding (F)	1st/2nd Brood (1/2B)	0.45 ***	23	48
			Cloud cover (C)	- 0.35 **	40	
			Brood Mass (BM)	0.33 **	50	
7.	Male	Feeding Rate (FR)	Time (TM)	0.58 ***	20	48
			Nestling Age (NA)	0.52 ***	45	

[1] Symbols in parentheses correspond to variables described in Appendix 4

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

The female increased her feeding time in response to an increase in brood mass (for second broods only) and available prey size since both led to a reduction in the brooding required. The male increased the time spent feeding the second brood relative to the first brood and unlike the female he responded to an increase in brood mass or age for both broods (Figure 3.9). The feeding rate increased with the age of the nestlings (Table 3.13). The male increased his feeding rate during the day.

The female spent an average of 8.4h brooding one day old nestlings and 3.1h brooding six day olds. The male spent 10.38h foraging on day 1 and 11.29h on day 6.

Table 3.13

Hourly Feeding Rates for Young Swallow Broods

Number	Age (days)	Feeding Rate h^{-1}	Study
3	3	24	Moreau and Moreau 1939
3	4	23	"
?	4	42	Williamson 1941
4	1	16	Purchon 1948
4	6	33	"
5	1	6.4 ± 1.9	This study
5	6	16.8 ± 2.9	"

3.6.3 Brooding in the Sand Martin (for nestlings aged 0-10 days)

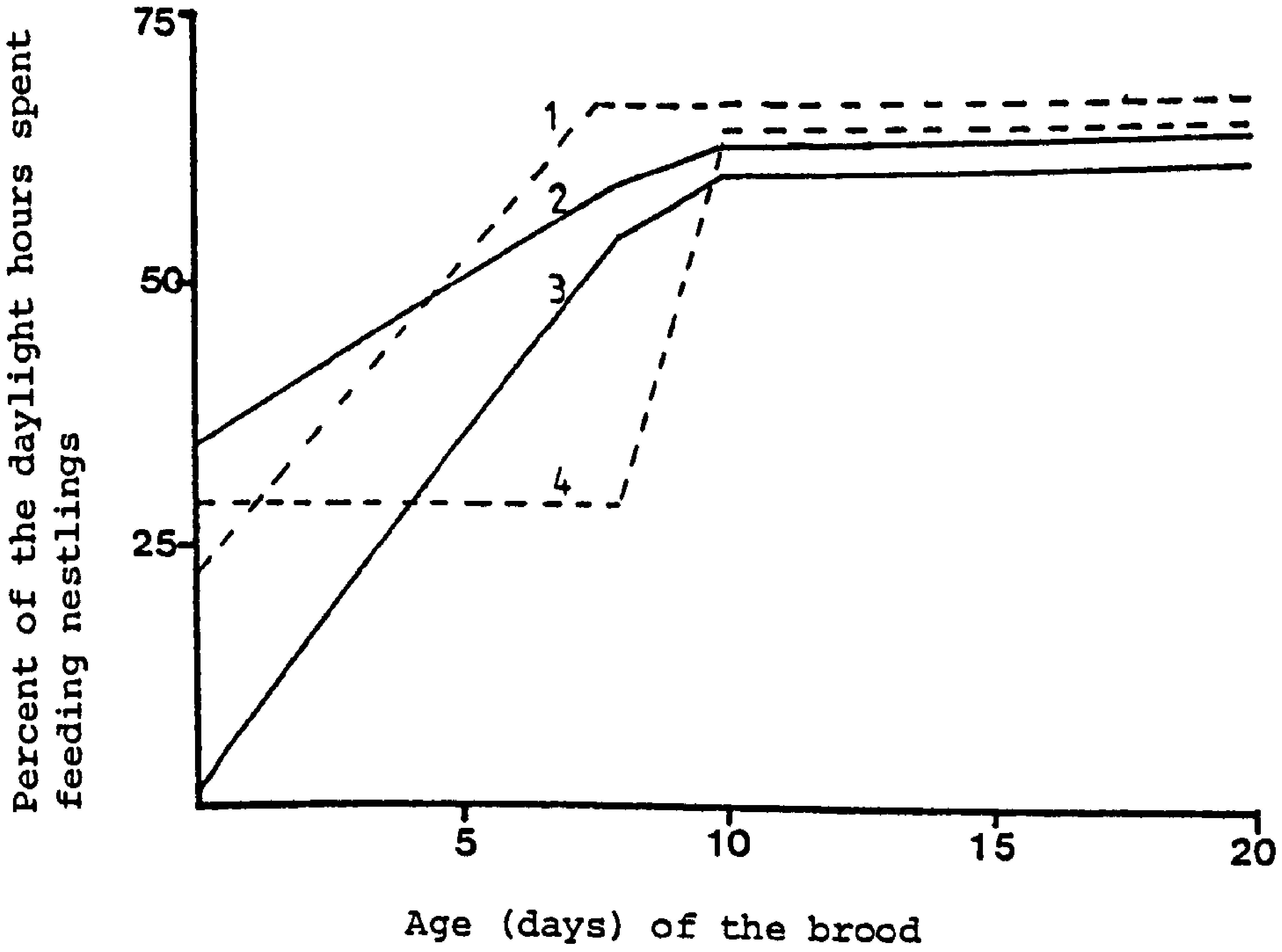
This description is based on multiple regression analyses presented in Table 3.16.

Both male and female Sand Martins brooded the young until they were about six days old (Figure 3.8). Each parent stayed on the nest for spells of about ten minutes, longer in bad weather.

Figure 3.9

The percentage of each hourly observation period invested in feeding nestlings during the day by male and female Swallows in relation to the age of the brood.

1. Female - Second broods
2. Male - Second broods
3. Male - First broods
4. Female - First broods


Percent of the daylight hours spent feeding nestlings
75
50
25
5
10
15
20
Age (days) of the brood
1
2
3
4

The mean time spent away also depended on the ambient temperature and the brood mass. The male spent less time brooding than the female (male 5.17 ± 2.72h, female 7.96 ± 4.07h, $n = 45$, $t = 3.82$, $p < 0.001$), particularly as the nestlings grew older. He tended to brood less on bad days presumably because the female has a more vascularised, hence more effective, brood patch so she did most of the work when brooding was most necessary.

Both sexes spent more time feeding second broods than first broods (Figure 3.10), but the male tended to increase his feeding time more than the female. Feeding rates increased as the nestlings grew but were affected by weather conditions (Table 3.15).

Table 3.15

Hourly Feeding Rates for Young Sand Martin Broods

Age (days)	Feeding Rates h^{-1}	Study	
3	24	Beyer 1938	
2-4	14.1	Stoner 1941	
1	6	Asbirk 1976	
>1	9	"	good conditions
	4.2	"	poor conditions
1-3	6.5 ± 3.7	This study	
4-8	12.6 ± 6.0	This study	

Asbirk (1976) observed that for the first 4-5 days the bolus was divided between two, rarely three, nestlings. His feeding rate measurements did not correlate with age or number of nestlings, however.

Figure 3.10

The percentage of each hourly observation period invested in feeding nestlings during the day by male and female Sand Martins in relation to the age of the brood.

1. Female - Second broods
2. Male - Second broods
3. Female - First broods
4. Male - First broods

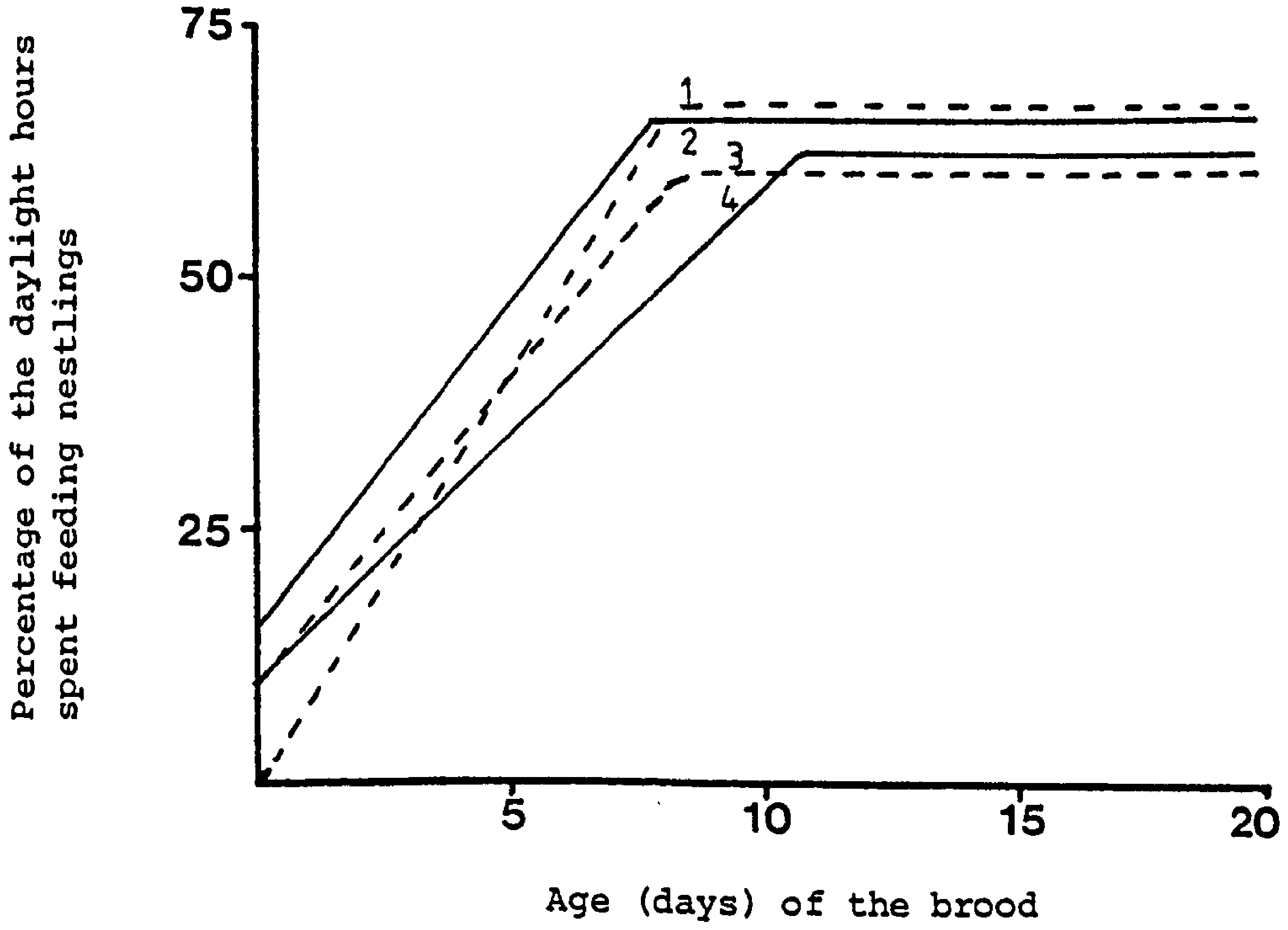

Percentage of the daylight hours spent feeding nestlings
75
50
25
5
10
15
20
Age (days) of the brood
1
2
3
4

Table 3.16 Multiple Regression Analyses of Brooding in the Sand Martin

		Dependent Variable (time spent in each activity)	Independent Variable	Standardised Partial Regression Coefficient	Cumulative $r^2 \times 100$	n
1.	Female	Attentive Period (A)[1]	Temperature (T°)[1]	- 0.35 *	20	45
			Intensity of rain (R)	- 0.33 *	30	
2.	Female	Inattentive Period (IP)	Brooding by ♂ (A)	0.50 ***	26	45
			Brood Mass (BM)	0.36 **	39	
3.	Female	Brooding (BR)	Brood Mass (BM)	- 0.56 **	45	45
			Available Prey Size (PS2)	- 0.34 **	54	
4.	Female	Feeding Rate (FR)	Brood Mass (BM)	0.54 ***	34	45
			Temperature (T°)	0.37 **	49	
5.	Male	Attentive Period (A)	Brooding by ♀ (A)	0.36 **	26	45
			Brood Mass (BM)	- 0.44 **	43	
			Intensity of rain (R)	- 0.38 **	56	
6.	Male	Inattentive Period (IP)	Temperature (T°)	- 0.55 ***	31	45
7.	Male	Brooding (BR)	Nestling Age (NA)	- 0.64 ***	45	45
			Food Abundance (Fn)	0.32 **	55	
8.	Male	Feeding Rate (FR)	Brood Mass (BM)	0.49 ***	23	45
			Temperature (T°)	0.37 **	37	

[1] Symbols in parentheses correspond to variables described in Appendix 4

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

3.7.1 Nestling Rearing - The Swallow (for nestlings aged 7 days to fledging)

The daily variation in feeding rates is shown in Figure 3.11. For first broods the feeding rate peaked at 1000-1400h but feeding occurred from about 0600 to 2000 depending on the demands of the brood and the available daylight hours. For second broods the feeding rate was higher, especially in the afternoon and evening; the peak rate was maintained for longer.

The feeding rate increased with increasing brood weight and the number of nestlings per brood:

Daily feeding rate = $13.50x^{0.76}$, $r = 0.78$, $n = 57$, $p < 0.001$,
x = brood weight (g)

Daily feeding rate = $135.13x^{0.74}$, $r = 0.78$, $n = 57$, $p < 0.001$,
x = number in brood

This increase in feeding rate does not increase linearly with brood weight hence each nestling in large broods received fewer feeding visits than a nestling in a small brood (Table 3.17).

Table 3.17

Daily Feeding Rates for Swallow Broods (≥ 10 days old)

Brood Size	Daily Feeding Rate	Nest days	Number of nests	Feeds/ nestling
1	179 ± 39	3	2	179
2	126 ± 56	4	2	63*
3	336 ± 90	5	2	112
4	390 ± 108	20	14	98
5	403 ± 117	19	9	81
6	588	1	1	98
**7	591 ± 84	5	3	84

* mainly bad weather ** artificially enlarged

Figure 3.11

Diurnal variation in feeding rates for broods of (a) Swallows and (b) Sand Martins.

Squares = female feeding rate,

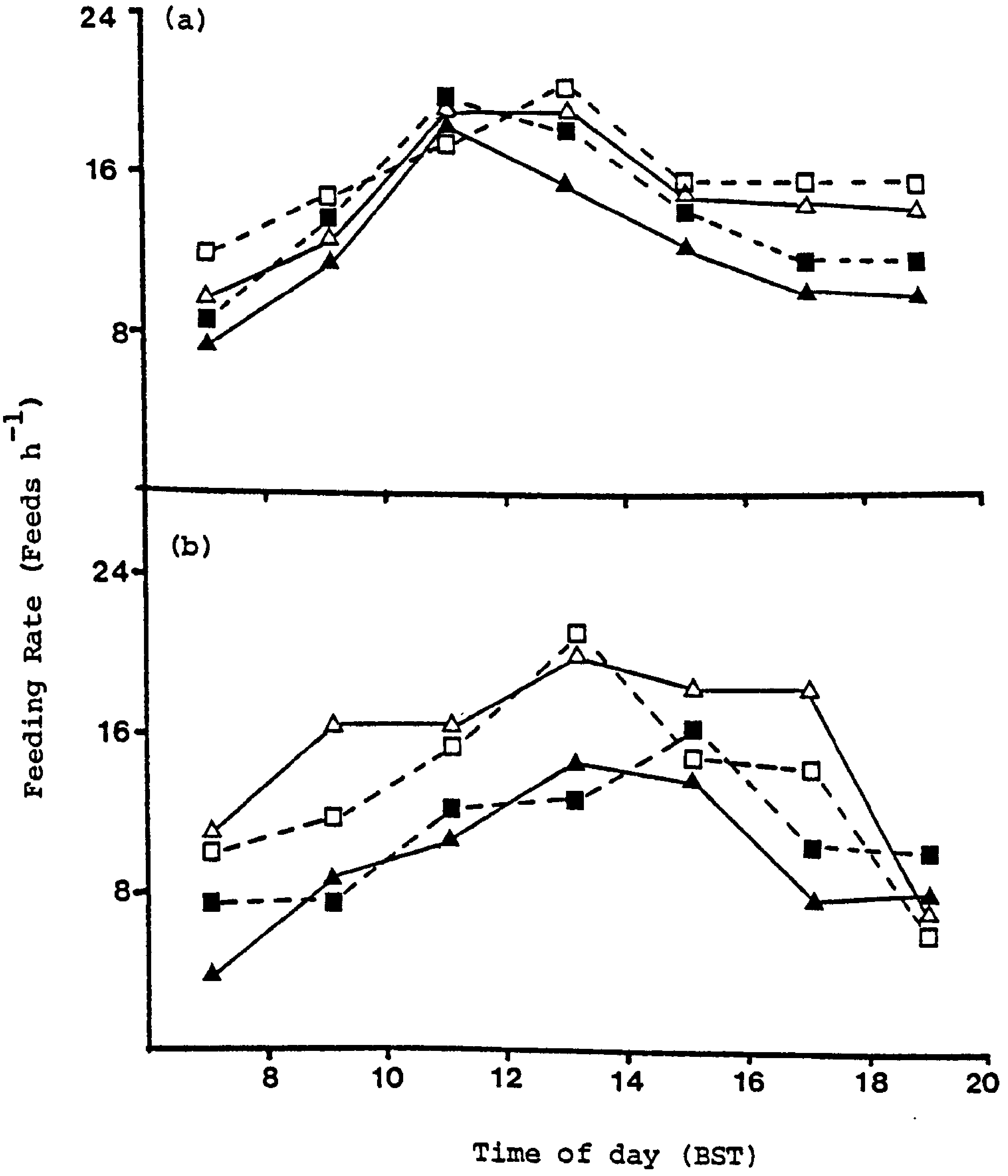
triangles = male feeding rate,

closed symbols = 1st broods,

open symbols = 2nd broods.

The data are for broods of 4 and 5 nestlings combined.

n = 27 nest days at 16 nests for the Sand Martin and 39 nest days at 13 nests for the Swallow.


(a)
(b)
24
16
8
24
16
8
8
10
12
14
16
18
20
Feeding Rate (Feeds h^{-1})
Time of day (BST)

This is equivalent to less food received since food bolus size is the same for all brood sizes (Waugh 1978, this study). Bryant and Gardiner (1979) found that, in House Martin nestlings, feeding frequency per unit of assimilate was lower in large broods and suggested that bolus size may be larger for the biggest broods but not sufficiently so to compensate for their greater demands.

The male made slightly fewer visits to the nest per hour than the female (Figure 3.12). Both sexes increased their feeding rates for second broods at this ~~stage~~ age (the male by 24%, $t = 2.55$, $p < 0.02$, the female by 20%, $t = 2.41$, $p < 0.05$). There was no significant difference between the feeding rates of the male and female to large or to small broods but the male fed the nestlings less than did the female in bad weather ($t = 2.64$, $p < 0.02$).

It is uncertain whether the artificial broods of seven could have been fledged successfully. Feeding rates may level out or drop for such large broods over a period of several days. The adults may also lose condition. Snapp (1973) noted a drop in individual nestling weight in artificial broods of seven and eight.

In poor weather conditions the female spent less time feeding herself (5.07 ± 1.97h, $n = 27$) than the nestlings (8.19 ± 1.67h, $n = 27$, $t = 6.28$, $p < 0.001$) whereas the male fed himself as much as he fed the brood (6.40 ± 2.80h self feeding, $n = 27$, 6.31 ± 2.84h nestling feeding, $n = 27$, $t = 0.12$, n.s.). In good feeding conditions more time was devoted to the nestlings than to self maintenance by the female (9.25 ± 1.25h and 3.13 ± 1.17h for a brood of five and self maintenance respectively $n = 50$, $t = 25.3$, $p < 0.001$) and by the male (8.74 ± 1.27h and 3.30 ± 1.9h respectively, $n = 50$, $t = 22.1$, $p < 0.001$), Figure 3.13.

Figure 3.12

Feeding rates for (a) Swallow and (b) Sand Martin broods of different sizes. The broods of 7 were artificially enlarged.

Open columns = female feeding rates,

shaded columns = male feeding rates,

B = feeding rates during bad weather.

The means ± 1 s.d. are shown.

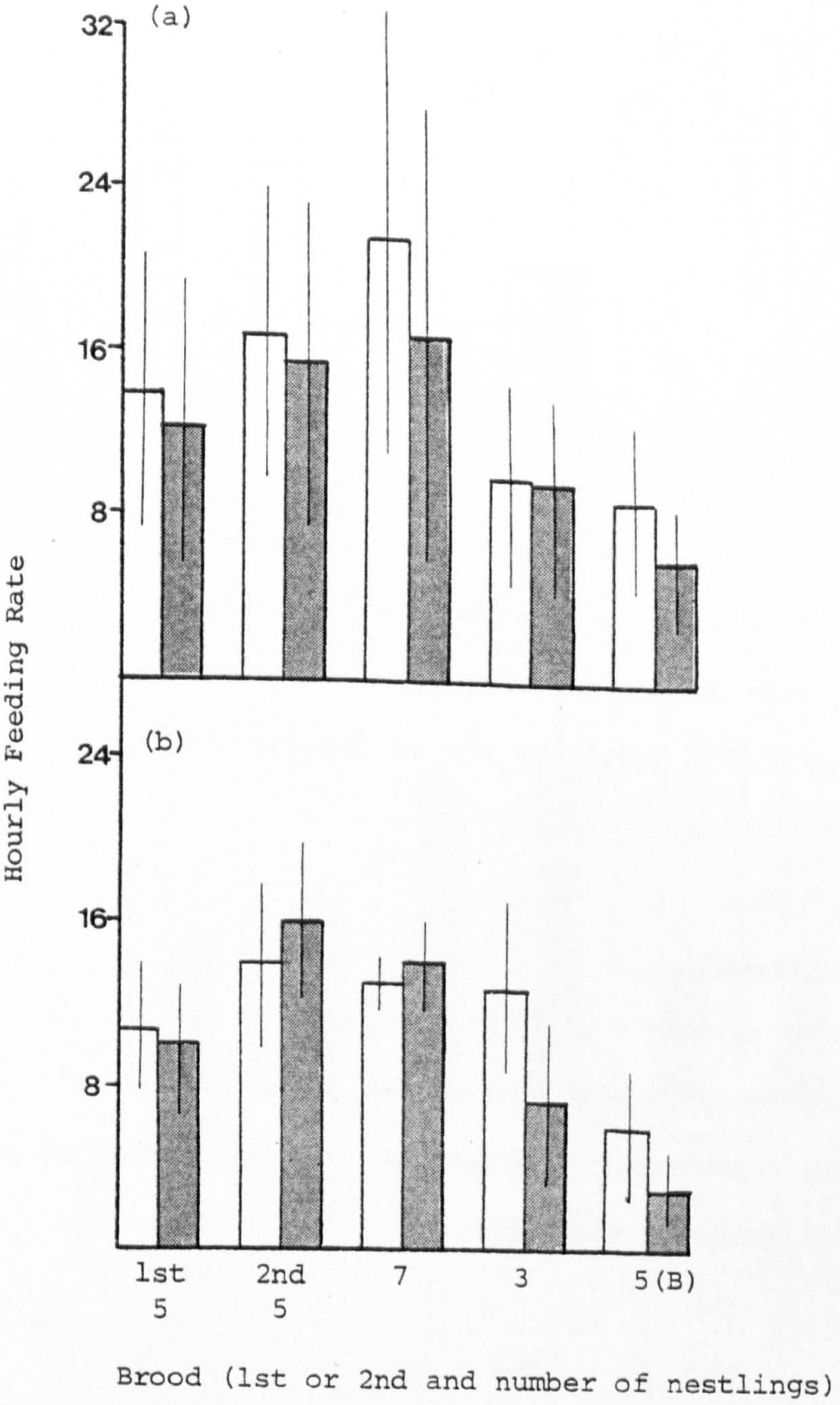

(a)
32
24
16
8
Hourly Feeding Rate
(b)
24
16
8
1st
5
2nd
5
7
3
5(B)
Brood (1st or 2nd and number of nestlings)

Figure 3.13

The time invested by (a) Swallows and (b) Sand Martins in feeding a brood of 5 nestlings in good weather and bad weather, in feeding an enlarged brood of 7 nestlings and in feeding themselves in similar conditions.

M = male

F = female

open columns = nestling feeding

shaded columns = self feeding time

The number of hourly periods over which data were collected is indicated.

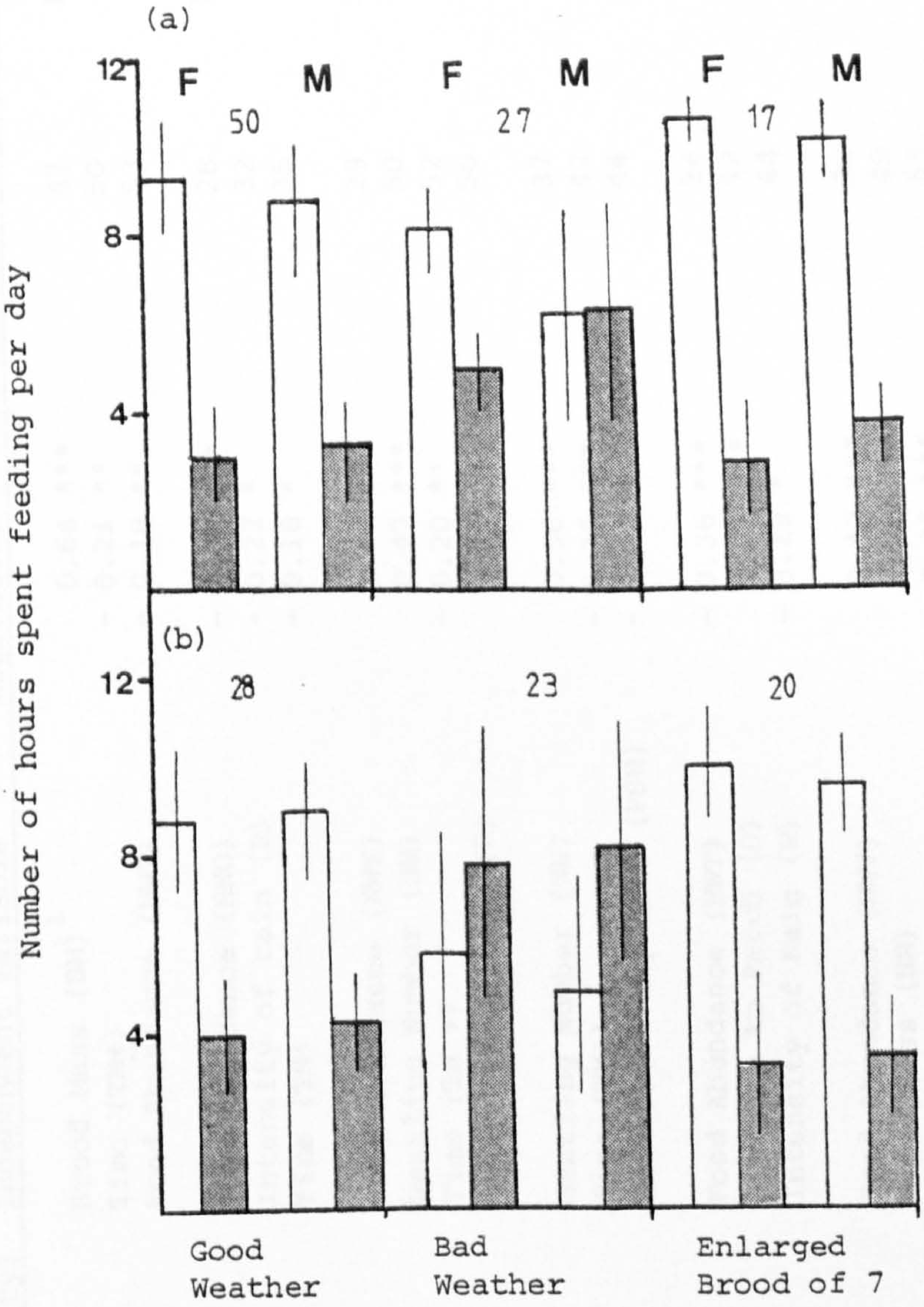

(a)
12
8
4
F
50
M
F
27
M
F
17
M
(b)
12
8
4
28
23
20
Number of hours spent feeding per day
Good Weather
Bad Weather
Enlarged Brood of 7

Table 3.18 Multiple Regression Analyses of Swallow Behaviour During the Nestling Rearing Stage

	Dependent Variable (time spent in each activity)	Independent Variable	Standardised Partial Regression Coefficient	Cumulative $r^2 \times 100$	n
1. Female	Feeding (F)[1]	Brood Mass (BM)[1]	0.64 ***	47	131
		Time (TM±)	- 0.21 **	50	
		Food Abundance (NWT)	- 0.18 **	53	
2. Female	Self-feeding (SF)	Food Abundance (NNO)	- 0.43 ***	28	131
		Intensity of rain (R)	- 0.22 *	32	
		Time (TM)	- 0.18 *	35	
3. Female	Feeding Rate (FR)	Food Abundance (NWT)	0.41 ***	29	131
		Nestling Number (NN)	0.47 ***	50	
		Time (TM ±)	- 0.20 **	52	
		Intensity of rain (R)	0.24 **	56	
4. Male	Feeding (F)	Nestling Number (NN)	0.56 ***	37	131
		Time (TM±)	- 0.25 ***	42	
		Available Prey Size (PSN)	- 0.15 *	44	
5. Male	Self-feeding (SF)	Food Abundance (NWT)	- 0.36 ***	34	118
		Distance to Patch (D)	0.27 ***	42	
		Intensity of Rain (R)	- 0.19 *	44	
6. Male	Feeding Rate (FR)	Food Abundance (NWT)	0.42 ***	32	131
		Brood Mass (BM)	0.40 ***	49	
		Time (TM±)	- 0.25 ***	53	
		Intensity of Rain (R)	0.22 *	56	

[1] Symbols in parentheses correspond to variables described in Appendix 4

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Table 3.18 shows the multiple regression analyses of Swallow behaviour during the nestling rearing stage. The total percentage of time spent feeding decreased near dawn and dusk and when prey was abundant. Feeding time was increased for large brood sizes. The female fed herself most early in the day. The male fed himself most when he had to travel a long way to a foraging site.

3.7.2 Nestling Rearing - The Sand Martin (for nestlings aged 7 to fledging)

The daily variation in feeding rates is shown in Figure 3.11. For first broods the peak feeding rate occurred at 1000-1600 hours but the nestlings were fed from about 0600 to 200h depending on the demands of the brood and the available daylight hours. The parents fed at a higher rate most of the day for second broods. The female's rate dropped off more markedly in the afternoon than the male's.

The feeding rate increased with increasing brood weight and the number of nestlings per brood:

Daily feeding rate = $7.53x^{0.82}$, $r = 0.71$, $n = 44$, $p < 0.001$,
x = brood weight (g)

Daily feeding rate = $63.09x^{0.90}$, $r = 0.70$, $n = 44$, $p < 0.001$,
x = number per brood

Nestlings in large broods thus received fewer visits each than those in small broods, (Table 3.19).

Table 3.19

Daily Feeding Rates to Sand Martin Broods ($\geq$ 10 days old)

Brood Size	Daily Feeding Rate	Nest days	Number of nests	Feeds/ nestling
2	134 ± 49	5	4	67
3	183 ± 23	6	5	61
4	251 ± 66	18	10	63
5	282 ± 101	9	6	56
6	335 ± 39	3	2	56
*7	316 ± 27	3	3	45

* artificially enlarged

Sex differences in feeding rates are shown in Figure 3.12. The male increased his feeding rate for second broods by 63% ($t = 6.75$, $p < 0.001$) and the female by 25% ($t = 3.50$, $p < 0.001$). The male, however, fed small broods at a lower rate than did the female ($t = 4.84$, $p < 0.001$) and he also fed nestlings at a lower rate in bad weather ($t = 3.44$, $p < 0.01$).

During peak periods the parents tended to feed as much as they could. Non-peak feeding rates were altered to meet the demands of different brood sizes. Similarly, House Martins stop feeding early in the afternoon when they have small broods (D.M. Bryant pers. comm.).

In poor weather conditions both male and female, unlike the Swallow, spent more time feeding themselves than the nestlings (5.32 ± 2.52h nestling feeding and 8.39 ± 3.16h self feeding by the male, $n = 23$, $t = 3.64$, $p < 0.001$, 5.78 ± 3.04h nestling feeding and 7.78 ± 3.14h self feeding by the female, $n = 23$, $t = 2.18$, $p < 0.05$). In good feeding conditions more time was devoted to the nestlings than to self maintenance by the female (8.88 ± 1.36h and 4.09 ± 1.29h for a brood of five and self maintenance respectively, $n = 28$, $t = 13.5$, $p < 0.001$) and by the male (8.96 ± 1.39h and 4.38 ± 1.4h respectively, $n = 28$, $t = 20.3$, $p < 0.001$), Figure 3.13.

When the nestlings were young the parents had to go to the back of the burrow to feed them; they also had to stay to remove faecal sacs which were then dropped outside the burrow. When the nestlings were 10-12 days old they began to run forward to meet the parent. After about 15 days they would stay at the entrance so the parent did not need to enter the burrow although it sometimes perched at the entrance. One or both parents stayed in the burrow overnight until the nestlings were about 15 days old.

Table 3.20 Multiple Regression Analyses of Sand Martin Behaviour During the Nestling Rearing Stage

	Dependent Variable (time spent in each activity)	Independent Variable	Standardised Partial Regression Coefficient	Cumulative $r^2 \times 100$	n
1. Female	Feeding (F)^1	Time (TM)^1	0.22 *	7	100
		Nestling Number (NN)	0.20 *	11	
2. Female	Self-feeding (SF)	Intensity of Rain (R)	- 0.49 ***	24	100
3. Female	Feeding Rate (FR)	Intensity of Rain (R)	0.37 ***	26	100
		Available Prey Size (PS3)	0.33 ***	42	
		Temperature (T°)	0.23 **	46	
4. Male	Feeding (F)	Time (TM)	0.40 ***	14	100
		Available Prey Size (PS3)	- 0.36 ***	29	
		Rainfall (Rain)	0.22 **	34	
5. Male	Self-feeding (SF)	Intensity of Rain (R)	- 0.48 ***	29	100
		Temperature (T°)	- 0.19 *	32	
6. Male	Feeding Rate (FR)	Temperature (T°)	0.42 ***	26	100
		Intensity of Rain (R)	0.29 **	33	

[1] Symbols in parentheses correspond to variables described in Appendix 4

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Table 3.20 shows the multiple regression analyses of Sand Martin behaviour at this stage. The total percentage of time spent feeding increased during the day and in bad weather. The feeding rates of both male and female were strongly influenced by the weather.

3.8 A Comparison of Swallow and Sand Martin Time Budgets

The seasonal time budgets of Swallows and Sand Martins are shown in Figure 3.14.

During nestbuilding and burrowing the activity of both species depended on the time of day (Figure 3.15a); work was done mainly in the early morning. The Swallow's building activity was also affected by the prey size available, reflecting its greater dependence on large prey items (see Sections 4.3 and 4.11). Both birds fed for longer when it was wet but whereas an increase in rainfall intensity from drizzle to heavy rain increased the feeding time of the Martin by 26% it only increased that of the Swallow by 15%.

During egg laying both species responded to the available prey sizes and to rainfall. Swallows also fed more late in the day. In Martins but not in Swallows early arrivals had less guarding and fighting to do than latecomers.

The female Swallow, during incubation, was more constrained by the weather and food supply than the Sand Martin. Also, the duration of attentive and inattentive periods depended on the stage of incubation in the Swallow but not in the Martin. These differences are probably.due to the female Swallow incubating alone whereas both male and female Martins incubated.

Ambient temperature, rather than brood size was important in determining the length of the attentive period of the female Sand

Figure 3.14

Seasonal time budgets of Swallows and Sand Martins.

Open columns = male Sand Martin

Light stippling = female Sand Martin

Grey columns = male Swallow

Dark stippling = female Swallow

N = Nest building stage

E = Egg laying stage

I = Incubation stage

B = Brooding stage

NR = Nestling rearing stage.

Percentages are percentages of 24 hours. Perching time does not include incubating or brooding.

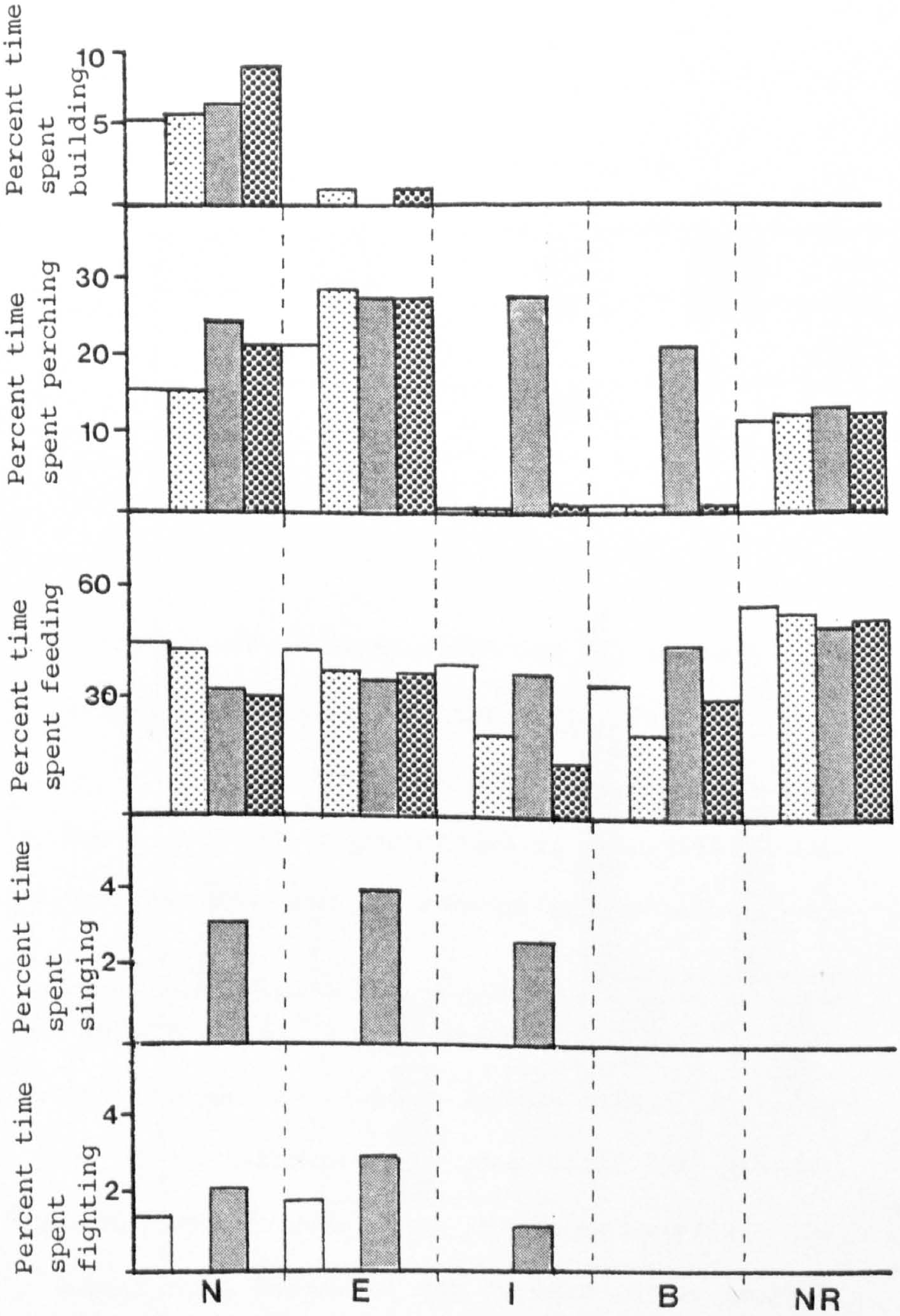

Percent time spent building
10
5
Percent time spent perching
30
20
10
Percent time spent feeding
60
30
Percent time spent singing
4
2
Percent time spent fighting
4
2
N
E
I
B
NR

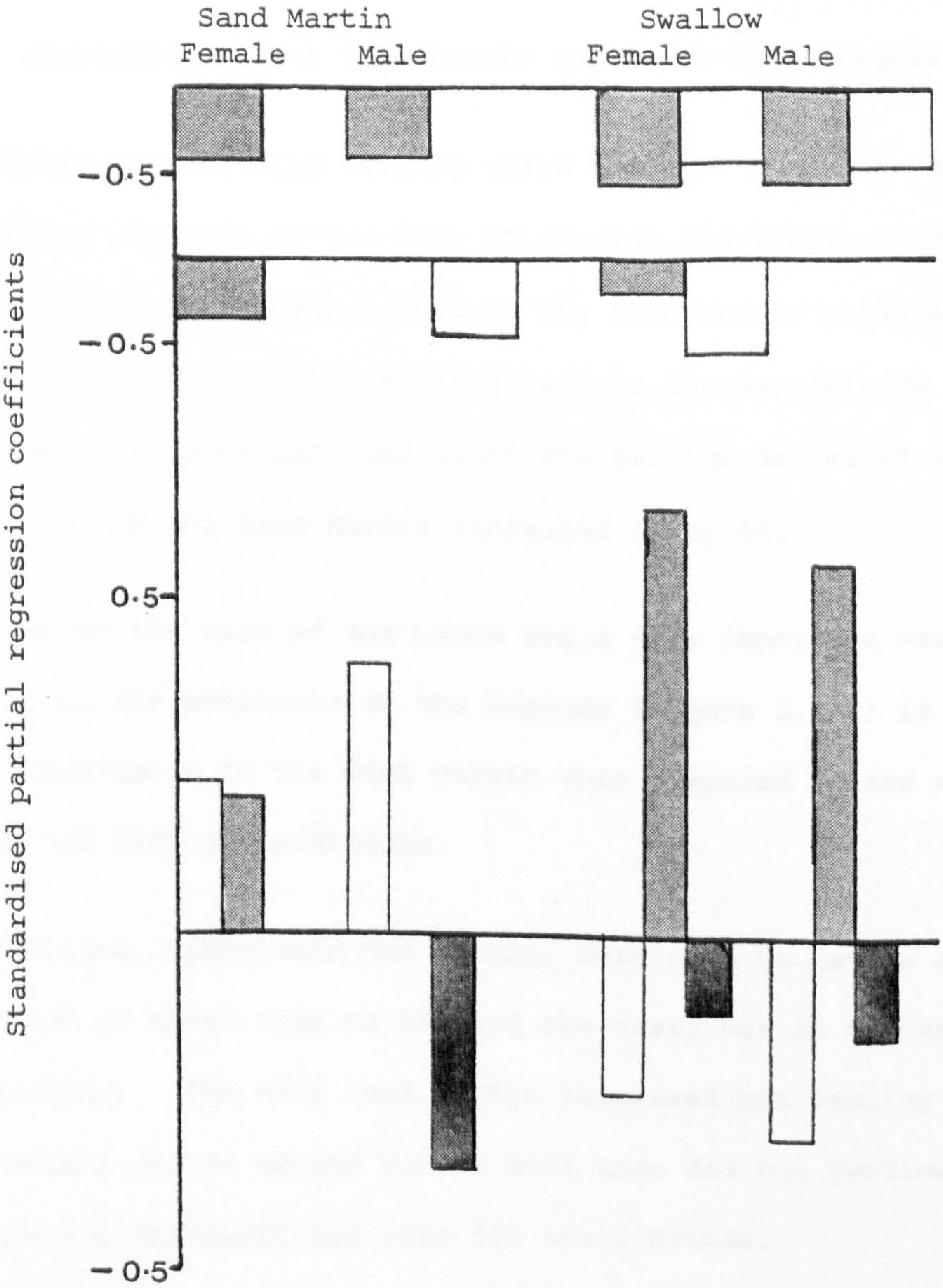
Figure 3.15

Species and sex differences in the partial regression coefficients of time budget parameters in relation to environmental and other factors.

(a) Differences in dependence of the time spent building on the time of day (shaded columns) and the available prey size (unshaded).

(b) Differences in dependence of the length of the attentive period during brooding on ambient temperature (shaded) and brood mass $^{0.67}$ (unshaded).

(c) Differences in the dependence of the time spent feeding on the time of day (unshaded), the number of nestlings in the brood (light shading) and food abundance (dark shading) during the nestling rearing stage (time of day for the Swallow is the time before or after midday).


Sand Martin
Swallow
Female
Male
Female
Male
Standardised partial regression coefficients
-0.5
-0.5
0.5
-0.5

Martin when brooding, but not of the male since the female probably has the more effective brood patch. The female Swallow, brooding alone, responded to both temperature and brood mass (Figure 3.15b).

During the nestling rearing stage the time spent feeding by both species was affected by the time of day but the Swallow reduced its feeding time in the evening whereas the Sand Martin still spen~~d~~t a substantial amount of time feeding late in the day (Figure 3.15c); for example, between 1600 and 1800h the Swallow decreased its feeding time by 8% and the Sand Martin increased it by 6%.

Whereas the size of the brood was a very important variable in determining the behaviour of the Swallow (Figure 3.15c) it was of little importance to the Sand Martin when compared to the effects of weather and feeding conditions.

Swallows, especially the female, were able to devote a greater proportion of their time to feeding the nestlings in bad weather than Sand Martins. The male Sand Martin increased his feeding rate for large broods and to second broods more than did the Swallow but he also greatly decreased his rate for small broods.

Over the whole season, the Sand Martin, being a less efficient feeder (see Section 4.12) tended to spend more time feeding than the Swallow and less time perching (Figure 3.14).

3.9 D_2O^{18} Measurements

These must be considered as preliminary results due to the small sample analysed to date.

Swallows

The measured daily energy expenditures and flight costs of the four Swallows are given in Table 3.21.

Table 3.21

Daily energy expenditure and flight costs of Swallows measured by the D_2O^{18} technique

Sex	Daily Energy Expenditure (DEE) kcal dy^{-1}	kcal $g^{-1}h^{-1}$	Flight costs kcal $g^{-1}h^{-1}$
Female	20.10	0.0439	0.0724
Female	27.77	0.0547	0.0964
Male	26.59	0.0547	0.0960
Male	19.22	0.0445	0.0744

The Swallows' flight costs were calculated as follows:

E_{PR} = Perching costs ($BMR_{15°C}$ × 1.5 × time spent perching)

+ Roosting costs ($BMR_{15°C}$ × time spent roosting)

Flight costs = (DEE (kcal $g^{-1}h^{-1}$) - E_{PR})/time spent flying

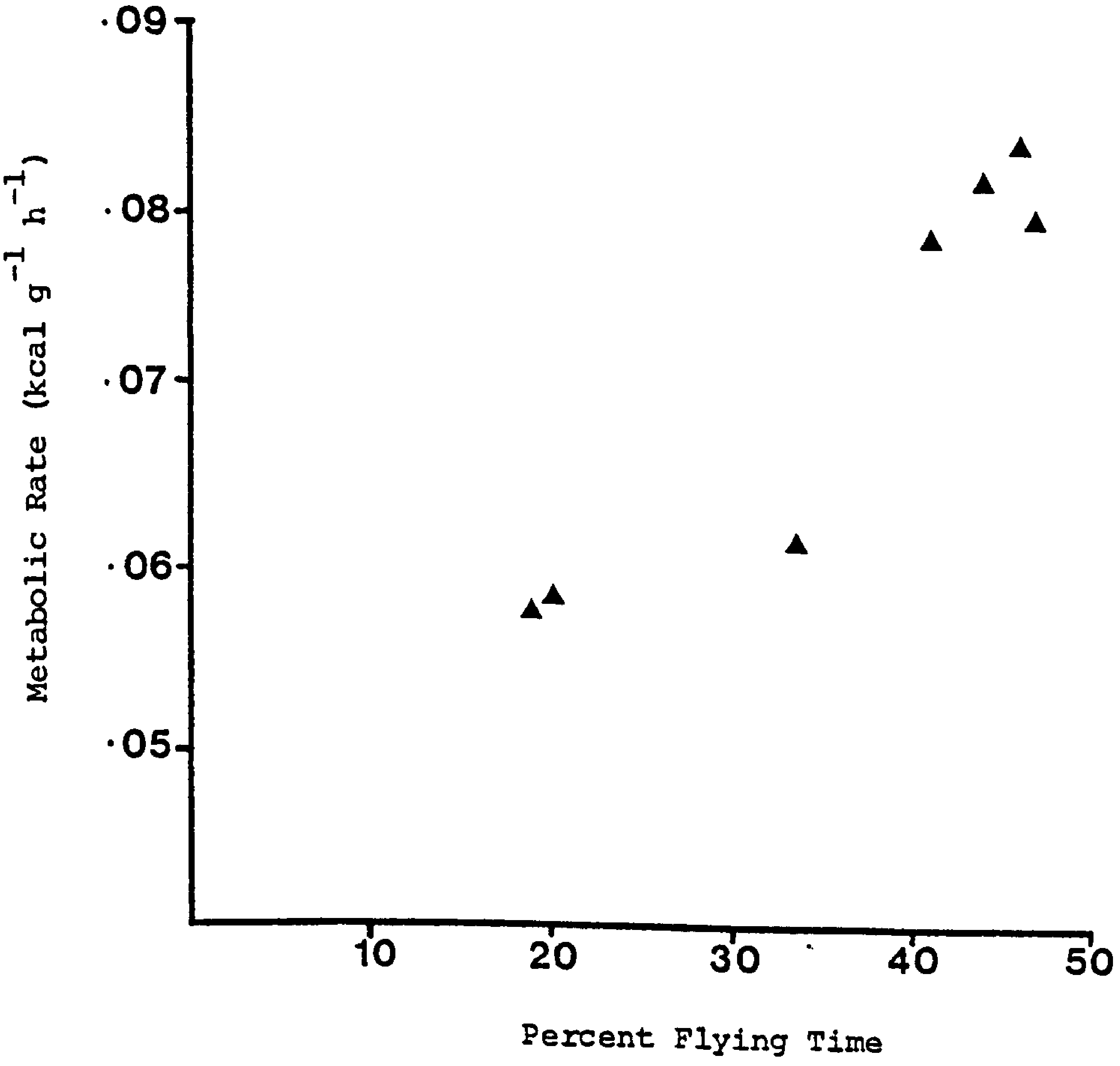
(see Appendix 5 for the calculation of BMR).

All the Swallows were feeding second broods of five nestlings and the average time spent in flapping flight was 93% of total flying time. For calculation of energy budgets the average of the flight costs for Swallows given in Table 3.22 were used since the sample size obtained in the present study was too small to yield a significant correlation with time budget data.

Hails (1977), also using the D_2O^{18} technique, obtained daily energy expenditures of 0.0262 kcal g^{-1} h^{-1}, 0.0394 kcal $g^{-1}h^{-1}$ and 0.0669 kcal $g^{-1}h^{-1}$ for Swallows rearing broods of four, three and five nestlings respectively.

Figure 3.16

The metabolic rate (kcal g^{-1} h^{-1}) of Sand Martins derived from the D_2O^{18} technique in relation to the percentage of the day (24h) spent flying.


·09
·08
·07
·06
·05
Metabolic Rate (kcal g^{-1} h^{-1})
10
20
30
40
50
Percent Flying Time

Sand Martins

The daily energy expenditure of seven Sand Martins ranged from 18-25.5 kcal dy^{-1}. The regression of metabolic rate on flying time is $y = 0.00089x + 0.0398$, $r = 0.95$, $n = 7$, $p < 0.001$, where $y = \text{kcal } g^{-1}h^{-1}$ and $x = \%$ flying time (Figure 3.16). The Sand Martins were feeding late first broods or second broods and the average time spent in flapping flight was 88% of total flying time.

3.10.1 Flight Costs

For many birds energy expenditure in flight is some twelve times the level of BMR (Raveling and Lefebvre 1967). Hirundines and Swifts, however, have a lower flight metabolism than any other bird of similar size. There is a reduction of 72.6% from the "expected" value (based on data for other species of similar weight) for House Martins, 62.4% for Swallows and 49% for Purple Martins, *Progne subis*, 2.9-5.7 × BMR (Hails 1979). In this study the flight cost for Swallows was 5.7 × BMR, and the flight cost for Sand Martins was 7.9 × BMR. Flight costs for hirundines are shown in Table 3.2.2.

Hirundines have relatively long wings for their size with a low wing loading (weight supported by unit area of wing). Relatively little power is thus required to support their weight while in flight compared to other birds of similar size. The hirundine is also streamlined, with a short neck and so drag is reduced. Their high aspect ratio ($\text{wingspan}^2/\text{area}$) lowers the drag induced by the wings when flapping. Both the low wing loading and high aspect ratio favour gliding flight which also contributes to the low overall flight costs (Hails 1979).

Table 3.2.2[1] Estimates of flight costs for Hirundines

Species	Flight Cost kcal $g^{-1}h^{-1}$	Study	Method Used
Progne subis	0.066	Utter and Lefebvre 1973	D_2O^{18} technique
Delichon urbica	0.045	Lyuleeva 1970	Weight loss during homing
Delichon urbica	0.034-0.050	Keskpaik 1968	i. Weight loss during flight, ii. Heat loss estimates iii. Extrapolation from O_2 consumption after flight iv. Theoretical model
Delichon urbica	0.040-0.057	Hails 1979	D_2O^{18} technique
Hirundo rustica	0.068	Lyuleeva 1970	Weight loss during homing
Hirundo rustica	0.059	Hails 1979	D_2O^{18} technique
Hirundo rustica	0.0848	This study	D_2O^{18} technique
Riparia riparia	0.1288	This study	D_2O^{18} technique

[1] Adapted from Hails (1979)

3.10.2 Seasonal Changes in Flight Costs

Hirundines employ two methods of flight: gliding and flapping. The former is energetically inexpensive and the latter is expensive. Heart beat rates of gliding gulls, for instance, are more similar to those of resting gulls than to those of flapping individuals (Kanwisher, Williams, Teal and Lawson 1978).

The percentage of flapping flight used increased during the season (Figure 3.17, Table 3.23). This may have been partly due to birds having more 'spare time' early on hence gliding more and partly due to a true increase with changing environmental conditions. The inexpensive method of gliding would have been, in theory, more suitable when feeding conditions were poor (Norberg 1977, Krebs in Krebs and Davies 1978).

Table 3.23

Seasonal changes in the proportion of gliding flight used by Swallows and Sand Martins

Stage	Swallow	Number of Observations	Sand Martin	Number of Observations
Pre-breeding	0.39 ± 0.10	6	0.32 ± 0.14	6
Nest building	0.22 ± 0.08	23	0.32 ± 0.14	13
Egg laying	0.21 ± 0.08	23	0.20 ± 0.11	13
Incubation	0.22 ± 0.21	32	0.21 ± 0.11	22
1st brood	0.20 ± 0.20	71	0.14 ± 0.10	60
2nd brood	0.07 ± 0.05	61	0.09 ± 0.08	35

Insufficient data were available to separate egg laying and incubation into first and second broods.

On arrival in Spring the hirundines stayed around lochs and reservoirs in the study area, presumably to feed up after their migration before moving to their nest sites in the locality. They then became more constrained in where they could feed since they had to return to the nest site after feeding. The cost of travelling to and from the foraging area would increase the energy expended in feeding. The constraint was greatest when there were eggs or young in the nest to which the parents had to return after only a few minutes to incubate, brood or feed nestlings. The distance travelled to a patch decreased during the season (Figure 3.17, Table 3.24).

The Swallow always fed fairly close to the nest site. The range of distances travelled contracted considerably during second brood feeding. The Sand Martin travelled up to a kilometre away early in the season but when the nestlings were being fed the distances travelled were comparable to the Swallow's. The seasonal decrease in distance was thus more marked in the Martin. The House Martin will feed even further away (1½-2km) than the Sand Martin and it shows a more noticeable contraction in distance, especially during incubation (D.M. Bryant, pers. comm.).

Table 3.24

Seasonal changes in nest site - feeding site distances (m) for Swallows and Sand Martins

Stage	Swallow	Number of Observations	Sand Martin	Number of Observations
Pre-breeding	-	-	-	-
Nest building	295.2 ± 153.5	21	600 ± 224.5	25
Egg laying	312.8 ± 182.4	39	439.2 ± 233.4	60
Incubation	269.0 ± 133.6	42	388.5 ± 235.0	26
1st brood	188.3 ± 146.8	78	216.0 ± 185.3	59
2nd brood	138.1 ± 40.9	56	143.6 ± 56.2	34

Figure 3.17

Seasonal changes in the proportion of gliding flight used (a) and the distance travelled from the nest site to the feeding site (b) by the Swallow (closed symbols) and the Sand Martin (open symbols).

PB = Prebreeding stage

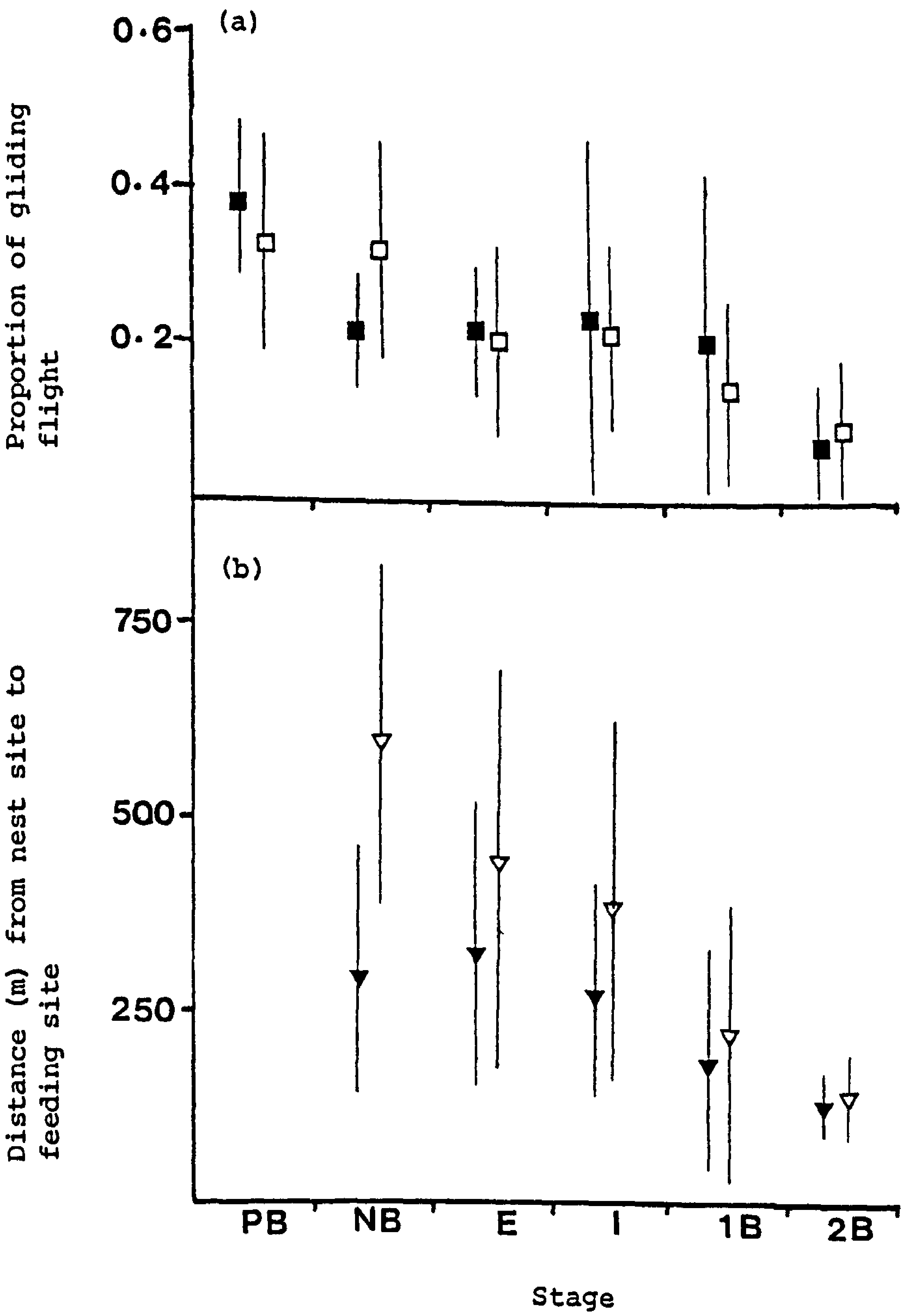
NB = Nest building

E = Egg laying

I = Incubation

1B = 1st brood period

2B = 2nd brood period


(a)
0·6
0·4
0·2
Proportion of gliding flight
(b)
750
500
250
Distance (m) from nest site to feeding site
PB
NB
E
I
1B
2B
Stage

3.10.3 Effects of Size on Flight Costs

Bryant and Westerterp (1979) showed that the average daily metabolic rate (ADMR) of House Martins is negatively correlated with weight. House Martins are heaviest early in the season at the time of low-cost pre-nestling stage activities (Bryant 1975b). Swallows and Sand Martins also showed a seasonal decrease in weight, Table 3.25 (although my data are limited).

Table 3.25

Seasonal changes in weight (g) of Swallows and Sand Martins

	Pre-breeders	Incubators	Nestling rearers
Swallow	-	21.9 ± 2.6 n = 6	18.8 ± 1.2 n = 45
Sand Martin	14.5 ± 0.9 n = 36	13.4 ± 0.6 n = 34	12.6 ± 0.8 n = 52

Besides the seasonal decrease in weight there is also a difference in size between individuals. Size has been measured mainly in terms of weight and wing length; Bryant and Westerterp (in press) have used keel length, although the bird has to be measured on several occasions to obtain an accurate result.

Both weight and wing length affect the wing loading which thus varies between individuals and within individuals during the year. A low wing loading improves the gliding performance and so reduces energy costs. Hence a long wing is advantageous. Wing length may sometimes grow for a year or more after fledging (Bryant 1979, Table 3.26).

Most of the birds in Table 3.26 were first caught as adults hence their ages were designated as 1(+) on first capture.

Table 3.26 Growth of wing length in adult Sand Martins

Bird: ring number/sex	Age (yrs)	Wing length (mm)	Age (yrs)	Wing length (mm)	Increase yr^{-1}
JX67121/F	1(+)	101	4(+)	108	2.3
KJ78319/F	1(+)	103	3(+)	108	2.5
JR99285/F	1(+)	100	4(+)	104	1.3
JV63050/M	1(+)	109	4(+)	113	1.3
JR76959/F	1(+)	105	4(+)	109	1.3
KJ78318/F	1(+)	109	3(+)	112	1.5
KR70138/F	1(+)	103	2(+)	106	3.0
KV58532/F	1(+)	110	2(+)	110	0
A107355/M		104	1	104	0
A107396/F		105	1	108	3.0
A107360/F	1(+)	106	2(+)	106	0

$\bar{x} = 1.47 \pm 1.09$ mm yr^{-1}

3.11 The Energy Budget

The calculated daily energy budgets (DEB) for average birds at different stages of the breeding cycle are presented in Table 3.27 and Figure 3.18. A comparison is also made with the measured energy budget of the House Martin. Despite its smaller size the Sand Martin shows higher values than the Swallow and House Martin because of its high flight costs. All three hirundines have DEBs of 2.6 to 4.8 times the basal metabolic rate (BMR, see Appendix 5) with the highest values during the nestling rearing stage. Burrowing may also be energetically expensive for the Sand Martin; building a nest, however, is not very energy demanding for Swallows especially since old nests are frequently reused.

The percentage of the day spent flying is least for the Swallow which is the most efficient feeder (see Section 4.12). Flying time is very much reduced for incubating females hence their DEBs are low.

Energy expenditure is also reduced when feeding conditions are poor because the bird employs a higher proportion of low-cost gliding flight. During the nestling rearing stage energy expenditure is also decreased in bad weather by the parent spending less time feeding the nestlings and hence spending less time on travelling between nest site and food source (see Section 3.7).

Figure 3.18

The daily energy budgets of (a) the Swallow and (b) the Sand Martin at different stages of the breeding season.

N = nest building/burrowing

E = egg laying

I = incubation

BR = brooding

NR = nestling rearing. (A in good weather, B in bad weather)

Solid line = female's daily energy budget

dashed line = male's daily energy budget

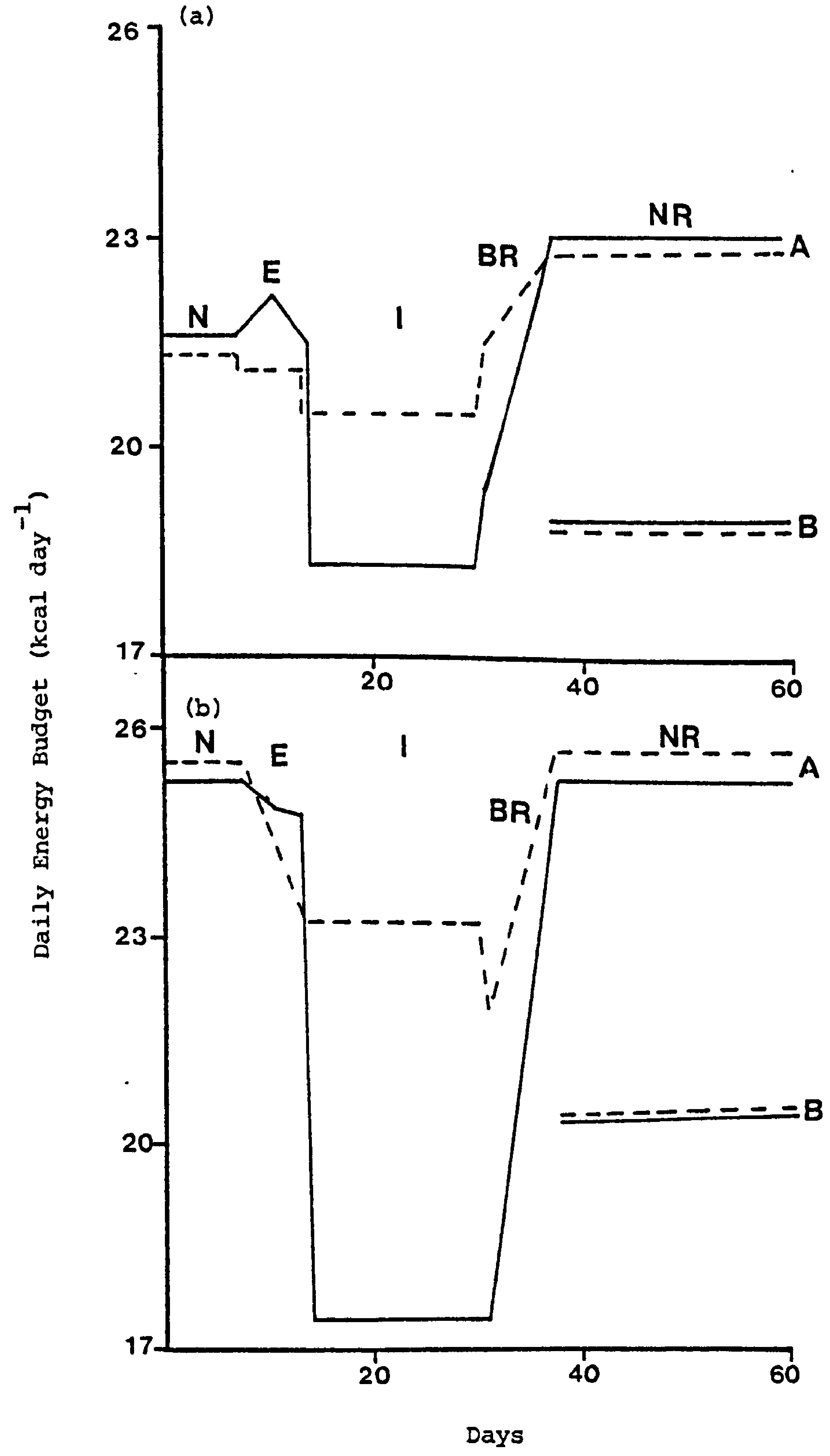

(a)
26
23
20
17
N
E
I
BR
NR
A
B
20
40
60
(b)
26
23
20
17
N
E
I
BR
NR
A
B
20
40
60
Daily Energy Budget (kcal day^{-1})
Days

Table 3.27 <u>Daily energy budgets (DEB) of hirundines during the breeding season</u>

The values for Swallows and Sand Martins are calculated (see Appendix 5); the values for House Martins are from Bryant and Westerterp (in press). The DEB is also given as a multiple of the basal metabolic rate (BMR); values are also given for the percentage of the day (24h) spent in flight and the percentage of flapping flight used.

<table>
<tr><th rowspan="2">Stage</th><th rowspan="2"></th><th colspan="2">Swallow</th><th colspan="2">Sand Martin</th><th colspan="2">House Martin</th></tr>
<tr><th>Female</th><th>Male</th><th>Female</th><th>Male</th><th>Female</th><th>Male</th></tr>
<tr><td>Nest building</td><td>DEB</td><td>21.59</td><td>21.33</td><td>25.24</td><td>25.51</td><td></td><td></td></tr>
<tr><td></td><td>×BMR</td><td>3.19</td><td>3.16</td><td>4.68</td><td>4.73</td><td></td><td></td></tr>
<tr><td></td><td>% Flight</td><td>35.33</td><td>25.71</td><td>44.42</td><td>45.38</td><td></td><td></td></tr>
<tr><td></td><td>% Flapping</td><td>78</td><td>78</td><td>68</td><td>68</td><td></td><td></td></tr>
<tr><td>Non breeding</td><td>DEB</td><td>20.04</td><td>19.21</td><td>24.73</td><td>25.02</td><td colspan="2">-</td></tr>
<tr><td></td><td>×BMR</td><td>2.96</td><td>2.84</td><td>4.58</td><td>4.63</td><td colspan="2">2.66</td></tr>
<tr><td></td><td>% Flight</td><td>35.33</td><td>35.71</td><td>44.42</td><td>45.38</td><td colspan="2">47.1</td></tr>
<tr><td></td><td>% Flapping</td><td>78</td><td>78</td><td>68</td><td>68</td><td colspan="2">33.2</td></tr>
<tr><td>Egg laying</td><td>DEB</td><td>22.10</td><td>21.03</td><td>24.80</td><td>24.29</td><td colspan="2">-</td></tr>
<tr><td></td><td>×BMR</td><td>3.27</td><td>3.11</td><td>4.59</td><td>4.50</td><td>2.70</td><td>-</td></tr>
<tr><td></td><td>% Flight</td><td>38.42</td><td>37.46</td><td>38.04</td><td>42.50</td><td colspan="2">39.6</td></tr>
<tr><td></td><td>% Flapping</td><td>79</td><td>79</td><td>80</td><td>80</td><td colspan="2">20.0</td></tr>
<tr><td>Incubation</td><td>DEB</td><td>18.33</td><td>20.49</td><td>17.46</td><td>23.34</td><td colspan="2">18.32</td></tr>
<tr><td></td><td>×BMR</td><td>2.71</td><td>3.03</td><td>3.23</td><td>4.32</td><td>2.72</td><td>2.93</td></tr>
<tr><td></td><td>% Flight</td><td>15.79</td><td>38.00</td><td>20.96</td><td>38.50</td><td colspan="2">26.4</td></tr>
<tr><td></td><td>% Flapping</td><td>78</td><td>78</td><td>79</td><td>79</td><td colspan="2">45.8</td></tr>
</table>

Brooding/

Table 3.27 (continued)

Stage		Swallow		Sand Martin		House Martin	
		Female	Male	Female	Male	Female	Male
Brooding Day 1	DEB	19.41	21.46	17.44	21.86		
	×BMR	2.87	3.17	3.23	4.05		
	% Flight	31.88	43.25	21.67	34.38		
	% Flapping	78	78	79	79		
Nestling Rearing	DEB	22.96	22.71	25.29	25.70		-
	×BMR	3.40	3.36	4.69	4.76		22.58
	% Flight	51.58	50.17	54.04	55.58		52.7
	% Flapping	87.5	87.5	88.5	88.5		37.7
Nestling Rearing (Bad Weather)	DEB	18.99	18.77	20.41	20.52		
	×BMR	2.81	2.78	3.78	3.80		
	% Flight	55.25	52.96	56.50	57.13		
	% Flapping	62	62	68	68		

CHAPTER 4

4. FORAGING ECOLOGY

4.1 Introduction

Foraging involves two main types of decisions: (a) when to forage and (b) how to forage. The parent bird must decide when to allocate time and energy to feeding; in this it is constrained in two ways. Firstly, during the breeding season, eggs and nestlings require a considerable amount of time to be spent on incubation and brooding as well as on collecting food. The age, number and collective brood weight of the nestlings inevitably affects parental time budgets. The decrease in clutch size during the season (Petersen 1955, Kuzniak 1967, Bryant 1975, this study) will also have an effect. Secondly, changes in feeding conditions are expected to result in changes in the bird's allocation of time.

The second type of decision, how to forage, on the other hand, is influenced primarily by the prevailing environmental conditions rather than by constraints imposed by other necessary activities. If demands on their feeding time are low, however, the parents may change their behaviour while foraging (see Section 5.4.2). Natural selection should favour those individuals which maximise their contribution to the gene pool but foraging models generally consider the short term goal of maximising the net rate of energy intake (Emlen 1966, MacArthur and Pianka 1966, Schoener 1971, Charnov 1973, Pulliam 1974). In order to maximise its net energy intake rate the bird must make inter-related decisions on where to feed, how to search for prey and what sort of prey to select. The resulting foraging strategy must also be flexible since variable environmental conditions will change such factors as patch location and the availability of different prey types.

In this section the questions of where Swallows and Sand Martins feed, what method of flight is used and what sort of prey are selected, are examined in relation to characteristics of the environment.

METHODS

4.2 Feeding Behaviour and Diet

Several measures of feeding behaviour were made: (a) the quantity and quality of food delivered to the nestlings, (b) the duration and distance of the foraging trips and (c) the height and speed of flying including the relative use of gliding flight. Data were obtained from twelve Swallow nests and fifteen Sand Martin nests.

The food was sampled by using collars on the nestlings (as described in Section 2 - Methods). The adult birds were observed through binoculars on their foraging trips while the nestlings were collared (usually a period of 1½ to 2 hours). The distances to specific points around the nest sites were measured so that an approximate distance per foraging trip could be estimated by noting to which points the birds fed closest. The available prey was monitored with the suction trap (for the Sand Martin) and the butterfly net (for the Swallow). The net allowed sampling to be made of the specific patches where the Swallows were feeding. A suction trap was impractical for such temporary recording of prey and also would have given an unmanageably large sample. Sticky traps were tried but were strongly biased towards wind drifted insects.

The feeding rate and thus bolus collection times were observed for an hour before boluses were collected from a brood. The lowest 90% of collection times were taken to calculate the mean for the observation period (see Section 3 - Methods). Nestlings of age

8-17 days were used in this study since energy demands do not vary much at this stage (Figures 2.13 and 2.14) and the birds are of a suitable size and age to allow easy handling.

It is not usually possible to observe capture of individual items by hirundines, although occasionally the birds can be seen taking a large item or insects which are visible against the sky in suitable light. Hence, an estimate of pursuit time was obtained in this study by timing the interval between obvious swerves or alterations in the flight path of the parent bird. It is assumed that insects are not taken while the bird is flying straight. The direction of turning after prey capture was also noted.

The speed of the birds while foraging was estimated by timing them over known distances with a stopwatch. Any times less then ten seconds were discarded as likely to be inaccurate. A subjective measurement was also made. The birds did not often go straight between objects of a known distance apart whereas an estimate of speed was required for each observation period. The flight speed was thus classed as fast, medium or slow for each pursuit time and the percentage gliding flight measured (Section 3 - Methods). A mean value was obtained for each period where precise measurements were not available. Fast, medium and slow speeds for the Swallow were taken to be 13.9, 10.4 and 6.9 m/s respectively and, for the Sand Martin, 11.7, 8.2 and 4.7 m/s (Appendix 5), inevitably these results are subjective but they did allow a comparison of speeds under different conditions to be made.

Although the diet and feeding behaviour of both Swallows and Sand Martins were examined in this study, the foraging strategy of the former was studied in greater detail for two reasons. The prey available to Swallows was monitored more easily and more accurately than that available to Sand Martins and individually marked Swallows were more easily observed when feeding.

Statistics are expressed as mean ± 1 s.d. Energy values are expressed in kilocalories (1 kcal = 4.184 kJ).

RESULTS

4.3.1 Characteristics of the Diet - Bolus Size and Composition

There was considerable variation in the size and composition of the food boluses delivered to the nestlings, much of which is due to differences in environmental conditions. The results of multiple regression analyses of bolus size and composition are shown in Table 4.3.

There was a reduction on bolus dry weight during the season (12% for the Sand Martin, 22% for the Swallow). The mean bolus weight for first brood Sand Martins was 64.37 ± 28.42 mg, n = 150, and for second broods 56.63 ± 23.47 mg, n = 122, t = 2.46, $p < 0.01$. The mean bolus weight for first brood Swallows was 82.80 ± 35.86 mg, n = 186, and for second broods 64.56 ± 27.93 mg, n = 246, t = 5.74, $p < 0.001$.

Sand Martins collected their largest boluses during periods when feeding conditions were poor and especially if they had to travel a long way to a patch of insects (Table 4.1, Figure 4.1). Bolus size also increased during the day. The largest Swallow boluses, however, were collected in good weather (Table 4.1). There was no positive correlation between bolus size and the distance travelled to the foraging patch (Figure 4.2). Bolus size increased around the middle of the day, when feeding conditions were at their best.

Figure 4.1

The mean dry weight of food boluses delivered to Sand Martin broods in relation to the distance travelled to the feeding site by the parent. Each data point represents the mean of boluses collected over a 2 hour period.

$r = 0.52, p < 0.001$

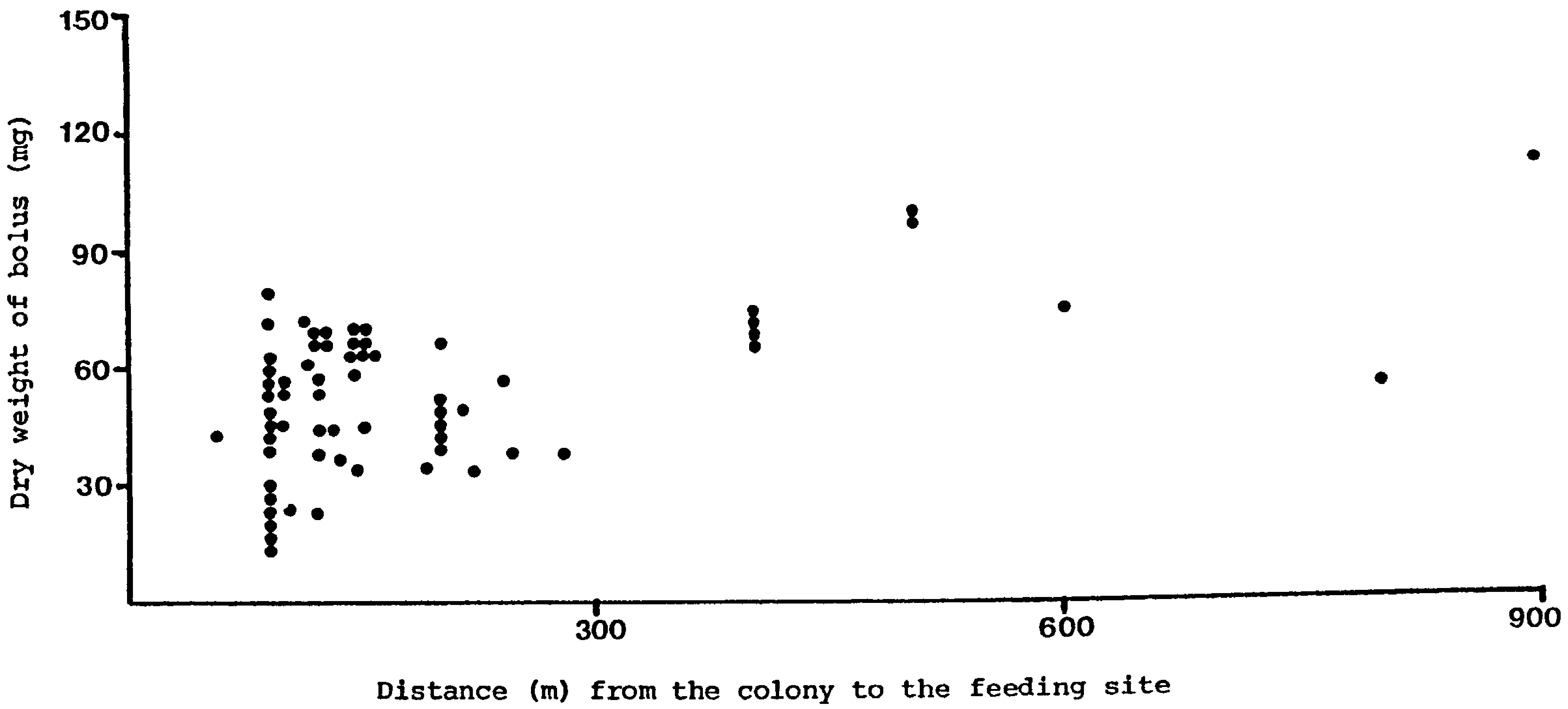

Dry weight of bolus (mg)
150
120
90
60
30
300
600
900
Distance (m) from the colony to the feeding site

Figure 4.2

The mean dry weight of boluses delivered to Swallow broods in relation to the distance travelled by the parent to the feeding site. The data points are means for boluses collected over 2 hour periods. The correlation is not significant.

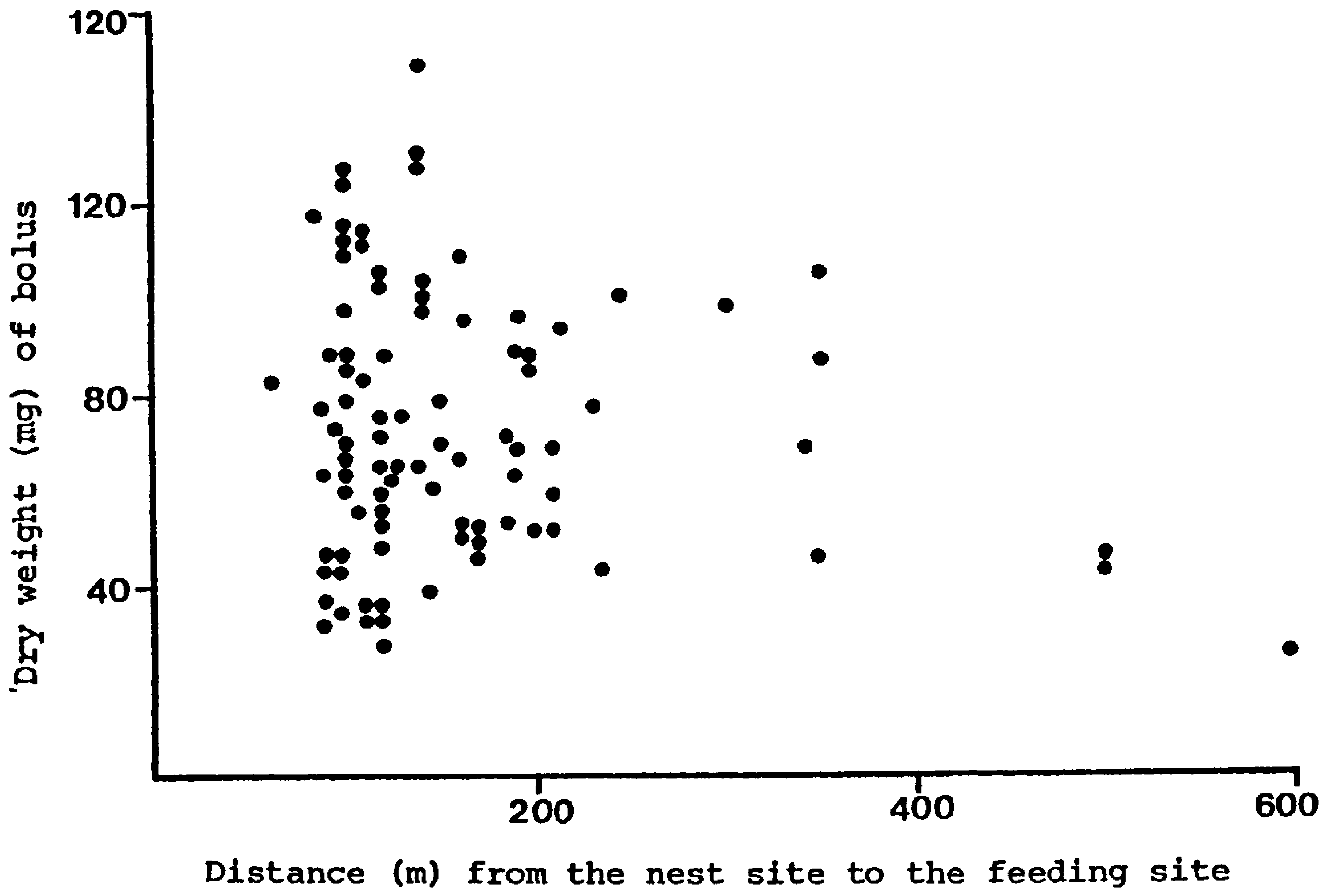

120
120
80
40
'Dry weight (mg) of bolus
200
400
600
Distance (m) from the nest site to the feeding site

Table 4.1

Bolus sizes (mg dry weight) of Swallows (a) and Sand Martins (b) taken in good and bad conditions; n = the number of observation periods

(a) Weather	Sand Martin	Bolus Size	t	p
Maximum daily temperature: ≥ 20°C	41.8 ± 11.7	n = 17	4.45	<0.001
Maximum daily temperature: ≤ 16°C	74.3 ± 21.3	n = 10		

(b) Weather	Swallow	Bolus Size	t	p
Rainfall: 0mm per day	75.0 ± 28.6	n = 55	5.52	<0.001
Rainfall: ≥ 75mm per day	47.4 ± 11.9	n = 14		

The number of prey items in a bolus varied greatly from one to well over a hundred (mean number = 59.7 ± 40.6 in the Sand Martin bolus, n = 67 observation periods, mean number = 18.1 ± 14.1 in the Swallow bolus, n = 92 observation periods). More items per bolus were taken when feeding conditions were poor.

The Sand Martin took, on average, 13.3 ± 5.5 different insect taxa (n = 67) and the Swallow 9.3 ± 4.8 (n = 92). The Sand Martin increased the variety of prey taxa taken in good feeding conditions, especially late in the season. The Swallow, on the other hand, was more selective of taxa in good conditions: the preferred items were large insect types of which Brachycera, Calypterates and Syrphidae are the most common. Sand Martins took smaller prey represented by a wider variety of taxa.

Both the Swallow and the Sand Martin increased the range of prey weights taken in good weather. The inclusion in the bolus of either very large items or a mixture of small and large items contributed towards a large size range.

4.3.2 Characteristics of the Bolus - Prey Size Taken

The mean prey size (mg dry weight) taken by the Swallow was 6.01 ± 5.64 mg, n = 4960 and the mean prey size taken by the Sand Martin was 1.26 ± 1.28 mg, n = 8080. Small items are here defined as those less than 0.32 mg for the Sand Martin and 1.5 mg for the Swallow (both 25% of their mean prey size). There was a decrease in prey size taken during the season by the Sand Martin (1.53 ± 1.58 mg for the first broods, n = 4516 and 0.90 ± 0.48 mg for the second broods, n = 3564, t = 25.4, $p < 0,001$), but there was an increase in prey size for the Swallow (4.89 ± 3.20 mg for first broods, n = 2129 and 6.58 ± 6.91 mg for second broods, n = 2831, t = 11.5, $p < 0.001$). Waugh (1978), however, noted a seasonal decrease in prey size taken for both species; hence, there may be some variation between years.

In good feeding conditions the mean prey size taken was large (Table 4.2) but large and small items were sometimes taken on the

Table 4.2

Prey size taken (mg dry weight) by Swallows (a) and Sand Martins (b) in good and bad conditions; n = the number of observation periods

(a) Weather/Food Supply	Swallow Prey Size		t	p
Dry conditions	6.41 ± 5.46	n = 85	3.00	<0.01
Heavy rain	3.14 ± 3.17	n = 12		
Large items abundant[1]	7.08 ± 6.65	n = 20	3.35	<0.01
Large items scarce[2]	3.09 ± 1.97	n = 36		

(b) Weather	Sand Martin Prey Size		t	p
Dry conditions	1.58 ± 1.44	n = 49	4.78	<0.001
Heavy rain	0.57 ± 0.19	n = 16		

[1] $\log_{10}$ (Number of large items in the net) (FLIN - see Appendix 4) ≥ 0.8

[2] FLIN ≤ 0.3

Table 4.3 Multiple Regression Analyses of Food Bolus Composition

		Dependent Variable	Independent Variable	Standard Partial Regression Coefficient	Cumulative $r^2 \times 100$	n
1.	SWALLOW	Bolus Size (BS)[1]	Time (TM ±)[1]	- 0.25 **	11	92
			Rainfall (Rain)	- 0.31 ***	20	
			Percent, Gliding (GF)	- 0.41 ***	27	
			Photoperiod (Ph)	0.39 ***	40	
2.	SAND MARTIN	Bolus Size (BS)	Temperature (TMX)	- 0.39 ***	32	67
			Time (TM ±)	0.31 ***	40	
			Travel Time to Patch (TP)	0.36 **	49	
3.	SWALLOW	No. of Items (NBS)	Rainfall (Rain)	0.38 ***	19	92
			Food Abundance (NNO)	- 0.33 ***	29	
4.	SAND MARTIN	No. of Items (NBS)	Prey Size Taken (PLI)	- 0.48 ***	35	67
			Intensity of Rain (R)	- 0.40 ***	50	
5.	SWALLOW	No. of Taxa (TX)	Cloud Cover (C)	- 0.29 **	15	92
			Distance to patch (D)	0.26 **	20	
6.	SAND MARTIN	No. of Taxa (TX)	Temperature (TMX)	0.39 ***	24	67
			Day (DY)	0.28 *	31	
7.	SWALLOW	Size Range (SRB)	Temperature (TMX)	0.29 **	11	92
			Photoperiod (Ph)	- 0.19 *	15	
8.	SAND MARTIN	Size Range (SRB)	Intensity of Rain (R)	0.45 ***	20	67

[1] Symbols in parentheses correspond to variables described in Appendix 4.

* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$

same foraging trip. The largest prey were taken at medium to high temperatures (Figure 4.3). Swallows took large prey when these were available but for Sand Martins there was a negative correlation between prey size taken (PST) and prey size available (PSA2), ($PST = 0.89 - 0.87 \log_{10} PSA$, $n = 73$ observation periods, $r = 0.2$, $p < 0.05$, PSA2 excludes chironomids and culicids from the calculation of prey size), indicating a preference for small, swarming items rather than large, more mobile prey (Figure 4.4).

4.4 Food Bolus Collection Times

The following description is based on multiple regression analyses shown in Table 4.6. Collection times (equivalent to foraging trips) for the Sand Martin were most variable late in the season and for Swallows in the middle of the season (Figure 4.5).

Short collection times for both species were strongly associated with good feeding conditions when the parent could forage close to the nest (Table 4.4). Low food availability, for instance, could triple the collection times of Swallows. Heavy rain increased the collection time and, if persistent, prevented Sand Martins from feeding at all. Swallows only desisted from feeding in the very worst of rain with associated low temperatures.

4.5 Feeding Station and Mode of Flight

Waugh (1978) found the mean foraging height of Swallows to be 7.4 ± 15.7m, of Sand Martins 15 ± 15m and of House Martins 21.5 ± 33.2m. Bryant (1972) noted similar mean heights of 9.14m, 16.8m and 20.7m for these species respectively.

The following description is based on multiple regression analyses given in Table 4.6. The Sand Martin fed mainly at a medium

Figure 4.3

The mean dry weight of prey items taken (a) by the Swallow and (b) by the Sand Martin in relation to ambient temperature. Data for the nestling diet only from bolus samples. Means ± 1 s.d. are shown. The number of 2 hour periods over which samples were collected is indicated. In (a) significantly larger items are taken at temperatures ≤ 20°C than at or below 14°C ($t = 3.28$, $p < 0.01$). In (b) significantly larger items are taken at temperatures ≥ 17°C than at temperatures below 17°C ($t = 2.45$, $p \leq 0.02$).

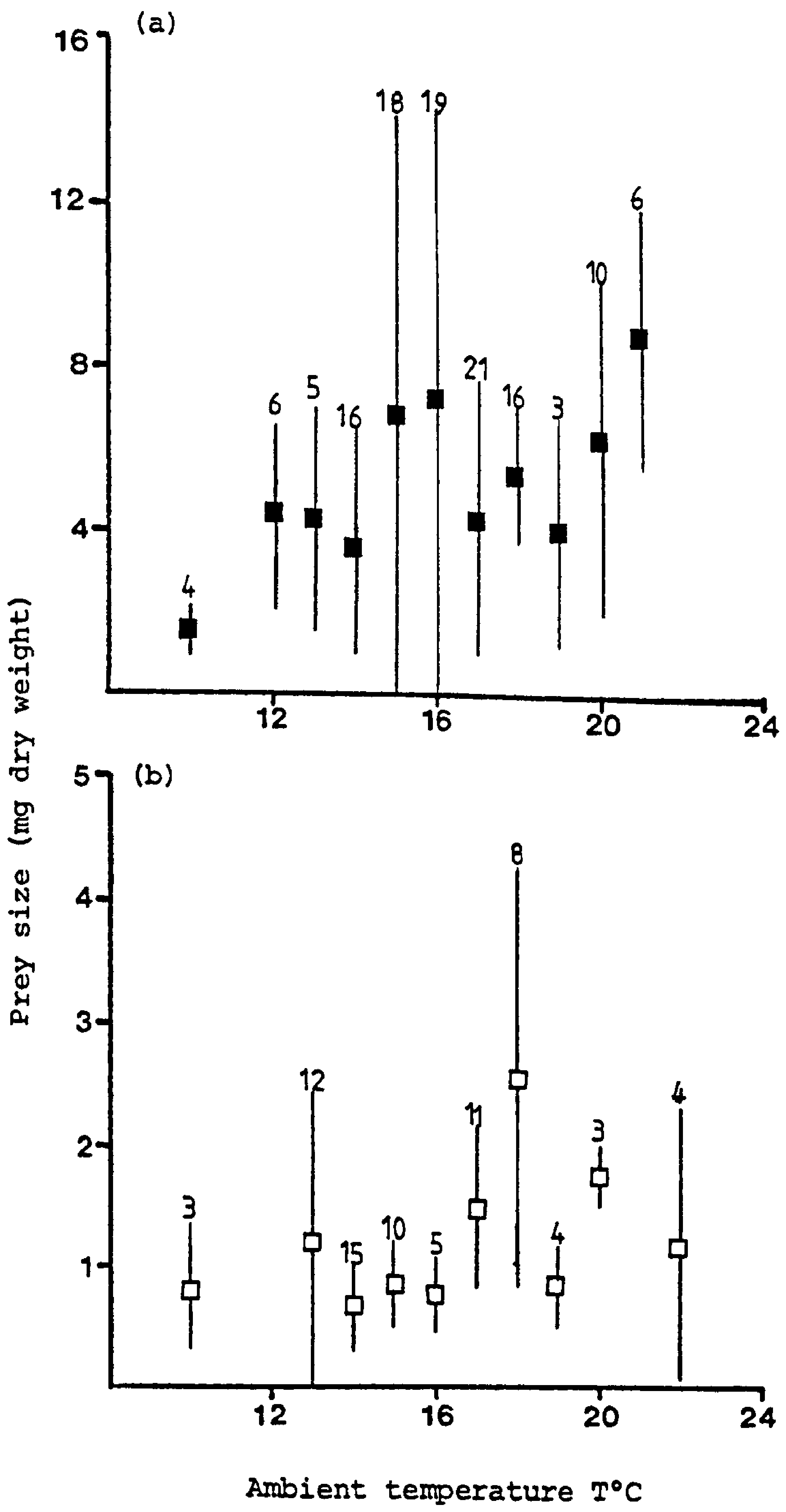

(a)
16
12
8
4
4
6
5
16
18
19
21
16
3
10
6
12
16
20
24
(b)
5
4
3
2
1
3
12
15
10
5
11
8
4
3
4
12
16
20
24
Prey size (mg dry weight)
Ambient temperature T°C

Figure 4.4

The prey size (mg dry weight) taken by the Sand Martin in relation to the prey size available in the suction trap catch (Culicids and chironomids were excluded from the calculation of prey size).

$r = 0.20$, $p < 0.05$

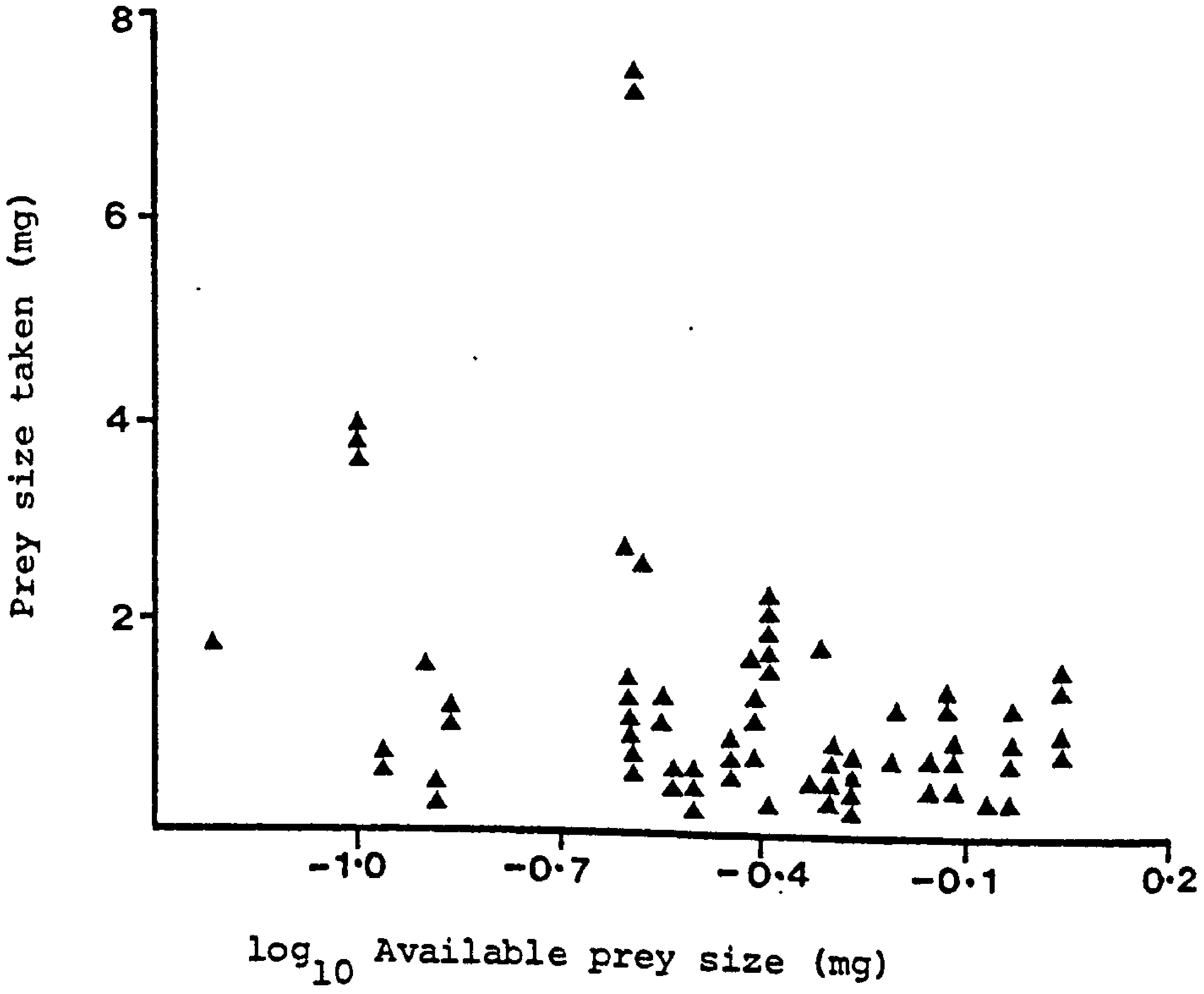

8
6
4
2
Prey size taken (mg)
-1·0
-0·7
-0·4
-0·1
0·2
log$_{10}$ Available prey size (mg)

Figure 4.5

The seasonal variation in the time taken to collect a bolus of food by (a) Swallows and (b) Sand Martins. Means ± 1 s.d. are shown for weekly periods during the season. The numbers of hourly periods over which the data were collected is indicated in (a) late July collection times are significantly higher than those in August ($t = 3.55$, $p < 0.05$).

In (b) there is a significant decrease in collection times during the season ($r = -0.26$, $p < 0.01$).

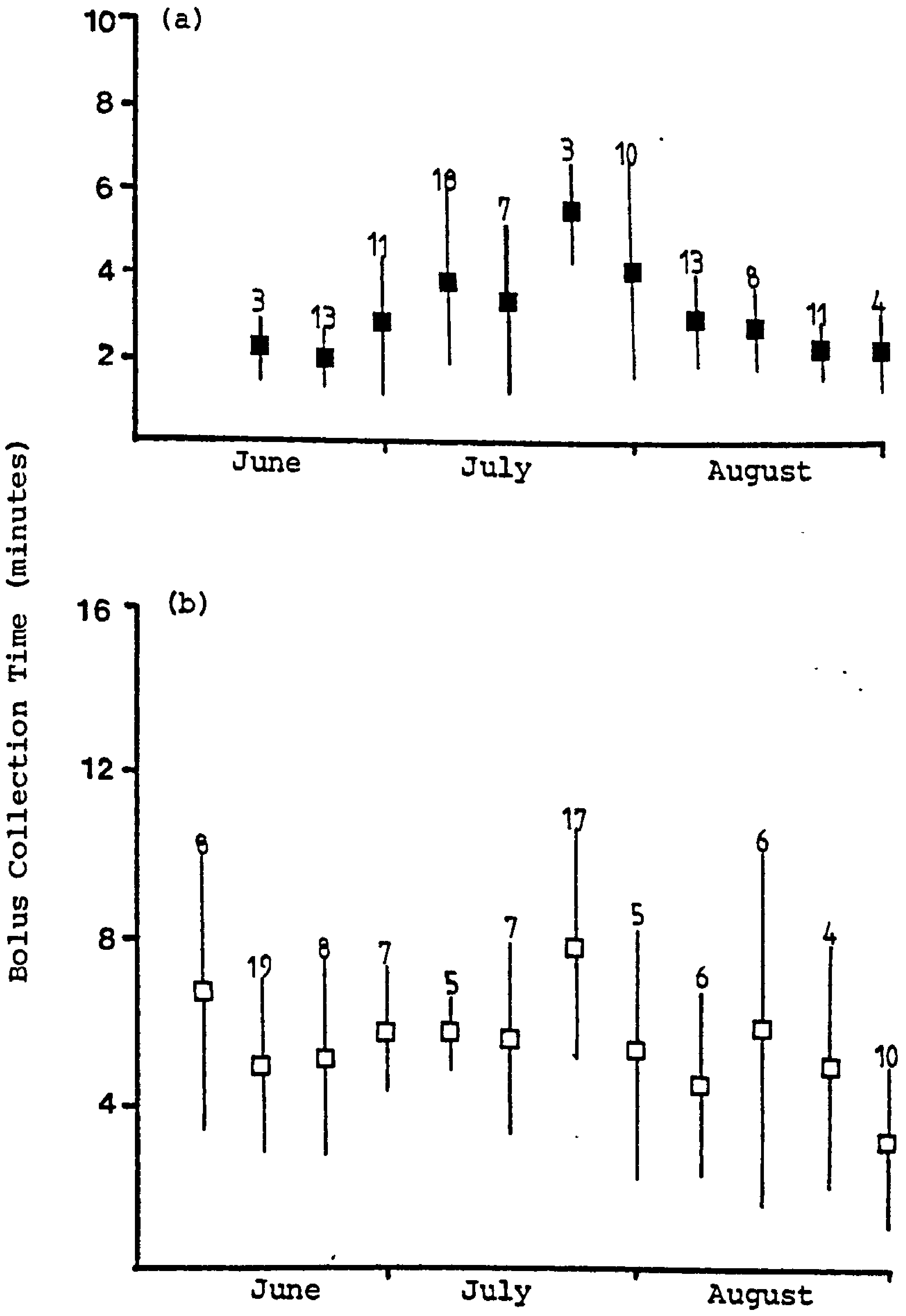

Bolus Collection Time (minutes)
(a)
10
8
6
4
2
3
13
11
18
7
3
10
13
8
11
4
June
July
August
(b)
16
12
8
4
8
19
8
7
5
7
17
5
6
6
4
10
June
July
August

Table 4.4 Bolus collection times (minutes) for Swallows (a) and Sand Martins (b) in good and bad conditions, n = the number of observation periods

	Swallow Collection Time			
(a) Food Supply	Female	Male	t	p
Prey Abundant[1]	1.92 ± 0.74, n = 27	1.96 ± 0.59, n = 27	$t_{male} = 8.01$	<0.001
Prey Scarce[2]	5.72 ± 2.29, n = 23	5.55 ± 1.94, n = 20	$t_{female} = 7.63$	<0.001

	Sand Martin Collection Time			
(b) Weather	Female	Male	t	p
Dry Conditions	4.57 ± 1.98, n = 93	5.09 ± 2.09, n = 89	$t_{male} = 4.57$	<0.001
Heavy Rain	10.64 ± 3.15, n = 12	10.17 ± 3.08, n = 8	$t_{female} = 6.51$	<0.001

[1] $\log_{10}$ (weight of net sample) > 1.5

[2] $\log_{10}$ (weight of net sample) ≤ 0.5

level over open ground. Feeding height was increased when food was abundant (volume of the suction trap catch: $r = 0.36$, $p < 0.001$, $n = 91$) and the available prey size was high. The Swallow generally fed low down, also over open ground. Unlike the Sand Martin, the Swallow fed lower in good conditions when large prey types were abundant (number of large items in the net catch: $r = -0.24$, $p < 0.004$, $n = 120$). Waugh (1978) observed similar behaviour for both species in good feeding conditions. He also noted that Swallows feed more over open water than the other hirundines, especially when food abundance is low. Rain causes a downward shift in the feeding height for both species.

In windy conditions the feeding sites tended to be on the leeward side of shelter belts where insects may accumulate. Different insect taxa may be present according to the height and permeability of the obstruction and the velocity and angle of the wind impinging on it (Lewis 1965, Lewis and Stephenson 1966).

The proportion of flying time spent gliding was greatest for the Sand Martin at high feeding stations, especially in windy conditions. The Swallow used more gliding flight when food abundance and temperatures were low (Table 4.5) whereas the Sand Martin, feeding on small weak flying items used gliding flight in good and bad conditions.

4.6 Distance of Foraging Site

Both the Swallow and the Sand Martin usually flew straight from the nest to the feeding site. This was sometimes a well defined 'patch' such as an isolated tree or a larger area with more indistinct boundaries. Flight during pursuit of insects was less direct and involved rapid turning movements. However, insects may also have been taken en route to the feeding site.

Table 4.5

The proportion of gliding flight used by Swallows (a) and Sand Martins (b) in good and bad conditions and at different feeding stations; n = the number of observation periods

(a)	Swallow Gliding Flight	t	p
Food Abundant[1]	0.07 ± 0.05, n = 50	2.7	<0.01
Food Scarce[2]	0.16 ± 0.19, n = 30		
Minimum Temperature ≥ 12°C	0.15 ± 0.15, n = 22	2.85	<0.01
Minimum Temperature ≤ 6°C	0.37 ± 0.29, n = 17		
High Feeding Station	0.40 ± 0.23, n = 20	6.79	<0.001
Low Feeding Station	0.05 ± 0.03, n = 78		

(b)	Sand Martin Gliding Flight	t	p
Food Abundant[1]	0.14 ± 0.11, n = 26	0.34	n.s.
Food Scarce[2]	0.15 ± 0.08, n = 17		
Minimum Temperature ≥ 12°C	0.15 ± 0.11, n = 11	1.14	n.s.
Minimum Temperature ≤ 6°C	0.09 ± 0.13, n = 10		
High Feeding Station	0.20 ± 0.11, n = 25	6.73	<0.001
Low Feeding Station	0.05 ± 0.02, n = 30		

[1] Suction trap catch ($\log_{10}$ volume + 1) ≥ 1.2

[2] Suction trap catch ($\log_{10}$ volume + 1) ≤ 0.8

The following description is based on multiple regression analyses given in Table 4.10. Swallows chose feeding sites close to the nest when food, especially large items, were abundant. Sand Martins also fed close to the nest in good weather (Table 4.7). In bad weather conditions both parents usually travelled to a nearby stretch of water where aerial insects were still to be found. In windy conditions trees and shelter belts close to the nest site were used. The surrounding topography is hence very important in bad weather when feeding sites are localised.

Table 4.7

The distance (m) of the feeding site from the nest site for Swallows (a) and Sand Martins (b) in good and bad conditions; n = the number of observation periods

(a)	Swallow	t	p
Maximum Daily Temperature ≥ 20°C	147.9 ± 50.1, n = 12	2.03	<0.05
Maximum Daily Temperature ≤ 16°C	203.3 ± 154.7, n = 45		
Large Items Abundant[1]	151.6 ± 64.1, n = 42	3.01	<0.01
Large Items Scarce[2]	257.6 ± 195.0, n = 33		
(b)	**Sand Martin**		
Maximum Daily Temperature ≥ 20°C	110.8 ± 27.9, n = 20	6.54	<0.001
Maximum Daily Temperature ≤ 16°C	501.8 ± 197.1, n = 11		

[1] $\log_{10}$ Number of large items in the suction trap catch (FLIT) ≥ 1.5

[2] FLIT = 0

4.7 Pursuit and Capture of Prey

The following description is based on multiple regression analyses shown in Table 4.10. Pursuit times for the Swallow were long when large, mobile prey items were available. Pursuit times

Table 4.6 Multiple Regression Analyses of Foraging Behaviour

		Dependent Variable	Independent Variable	Standard Partial Regression Coefficient	Cumulative $r^2 \times 100$	n
1.	SWALLOW (female)	Bolus Collection Time (CT)[1]	Food Abundance (NWT)[1]	- 0.60 ***	51	92
			Intensity of Rain (R)	- 0.18 *	53	
2.	SWALLOW (male)	Bolus Collection Time (CT)	Food Abundance (NWT)	- 0.61 ***	46	92
			Distance to Patch (D)	0.18 *	49	
3.	SAND MARTIN (female)	Bolus Collection Time (CT)	Intensity of Rain (R)	- 0.47 ***	35	67
			Distance to Patch (D)	0.23 **	42	
			Available Prey Size (PS3)	- 0.19 *	45	
4.	SAND MARTIN (Male)	Bolus Collection Time (CT)	Distance to Patch (D)	0.32 **	21	67
			Available Prey Size (PS3)	- 0.22 *	27	
			Intensity of Rain (R)	- 0.22 *	31	
5.	SWALLOW	Feeding Height (H)	Temperature (T°)	- 0.37 ***	16	120
6.	SAND MARTIN	Feeding Height (H)	Available Prey Size (PS1)	0.35 ***	16	91
			Wind Strength (W)	- 0.35 ***	26	
7.	SWALLOW	Percent. Gliding (GF)	Temperature (T°)	- 0.41 ***	33	113
			Day (DY)	- 0.55 ***	36	
			Available Prey Size (PS1)	0.39 ***	42	
8.	SAND MARTIN	Percent. Gliding (GF)	Feeding Height (H)	0.49 ***	39	91
			Wind Strength (W)	- 0.28 ***	48	
			Photoperiod (Ph)	0.25 ***	54	

[1] Symbols in parentheses correspond to variables described in Appendix 4.

* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$

were short for weak flying, especially swarming insects which were often taken at high feeding stations close to the nest site. The Sand Martin also had long pursuit times when food was abundant (Table 4.8).

Table 4.8

Pursuit times (secs) of insects for Swallows (a) and Sand Martins (b) in good and bad conditions; n = the number of observation periods

(a)	Swallow	t	p
Large Items Abundant[1]	6.77 ± 1.31, n = 21	5.23	<0.001
Large Items Scarce[2]	5.06 ± 0.98, n = 38		
(b)	Sand Martin		
Food Abundant[3]	5.78 ± 1.57, n = 29	8.07	<0.001
Food Scarce[3]	3.00 ± 0.80, n = 19		

[1] $\log_{10}$ Number of large items in the net (FLIN) ≥ 0.8

[2] FLIN ≤ 0.3

[3] Suction trap catch ($\log_{10}$ volume + 1) ≥ 1.2

[4] Suction trap catch ($\log_{10}$ volume + 1) ≤ 0.8

High degrees of turning in the Sand Martin's flight path were associated with a high speed of flight, especially when the bird was feeding on Ephemeroptera on the local river. The Swallow, on the other hand showed a high degree of turning when gliding and feeding on aggregated, weak flying insects such as aphids.

4.8 Speed of Flight

The maximum range speed (Vmr) of a bird is that speed which allows the individual to travel as far as possible on a given amount of fuel so it is the most economical cruising speed (Appendix 5, Pennycuick 1972). The Sand Martin usually flew at about this speed but the Swallow normally flew faster (Table 4.9). The former, which is the less efficient forager (Section 4.12) is thus more economical of energy than the latter.

Table 4.9

Flight Speeds of Swallows and Sand Martins (direct measurements only)

Species	Vmr	Mean Speed m/s	Range	Study
Swallow	8.40	10.4 ± 2.8 n = 100	5.5 to 18.8	This study
		10.91 ± 1.30 n = 6	10.00 to 13.73	Waugh (1978)
Sand Martin	8.29	8.2 ± 2.7 n = 75	3.5 to 14.2	This study

Details of the multiple regression analyses on speed of flight are given in Table 4.10. Fast speeds of the Sand Martin were associated with low feeding stations especially on calm, wet days. The usual feeding site under such conditions was low over the river where the birds frequently took Ephemeroptera as is shown by food bolus collections. The Swallow also flew fastest at low feeding stations but on windy days. Their speed, however, was mainly determined by the availability of large insects and the weather conditions. Speed of flight was positively correlated with the proportion of large items taken ($r = 0.33$, $p < 0.01$, $n = 79$). The Sand Martin catches smaller items than the Swallow hence it generally flies at a slower speed, using fast flight on special occasions when food is aggregated low over the river.

4.9 Flock Size

Several pairs of Swallows may nest on a single farm, hence they will forage over a common area; nevertheless, they feed singly (or in pairs during the egg laying period). Sand Martins, however, will feed singly, in small or in large flocks (a flock is here

Table 4.10 Multiple Regression Analyses of Foraging Behaviour

		Dependent Variable	Independent Variable	Standard Partial Regression Coefficient	Cumulative $r^2 \times 100$	n
1.	SWALLOW	Distance to Patch (D)[1]	Food Abundance (NNO)[1]	- 0.30 ***	24	118
			Available Prey Size (FLIT)	- 0.26 **	31	
			Intensity of Rain (R)	- 0.23 **	36	
2.	SAND MARTIN	Distance to Patch (D)	Temperature (T°)	- 0.61 ***	37	83
3.	SWALLOW	Pursuit Time (PT)	Feeding Height (H)	- 0.54 ***	34	106
			Available Prey Size (FLIN)	0.24 ***	48	
4.	SAND MARTIN	Pursuit Time (PT)	Food Abundance (Fn)	0.68 ***	48	80
5.	SWALLOW	Turning Rate (TR)	Percent Gliding (GF)	0.40 ***	16	103
6.	SAND MARTIN	Turning Rate (TR)	Flight Speed (Sp)	0.67 ***	45	80
7.	SWALLOW	Speed (Sp)	Cloud Cover (C)	0.69 ***	33	79
			Feeding Height (H)	- 0.57 ***	67	
			Wind Strength (W)	- 0.26 ***	74	
8.	SAND MARTIN	Speed (Sp)	Feeding Height (H)	- 0.47 ***	38	49
			Wind Strength (W)	0.37 **	49	
9.	SAND MARTIN	Flock Size (FS)	Intensity of Rain (R)	- 0.59 ***	61	83
			Distance to Patch (D)	0.43 ***	75	
			Food Abundance (Fn)	- 0.15 **	76	

[1] Symbols in parentheses correspond to variables described in Appendix 4.

* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$

defined as a group of birds each of which is feeding within 2m of its nearest neighbour).

Flock sizes in Sand Martins were large when the food supply was low and the feeding site was far from the nest site (Table 4.10, Figure 4.6). At the study site on bad weather days Sand Martins fed on a certain stretch of the nearby river, suggesting that they had congregated on a comparatively good patch. Flock sizes also decreased from the first brood to the second brood period ($r = 0.32$, $n = 83$, $p = 0.002$).

4.10 Predation

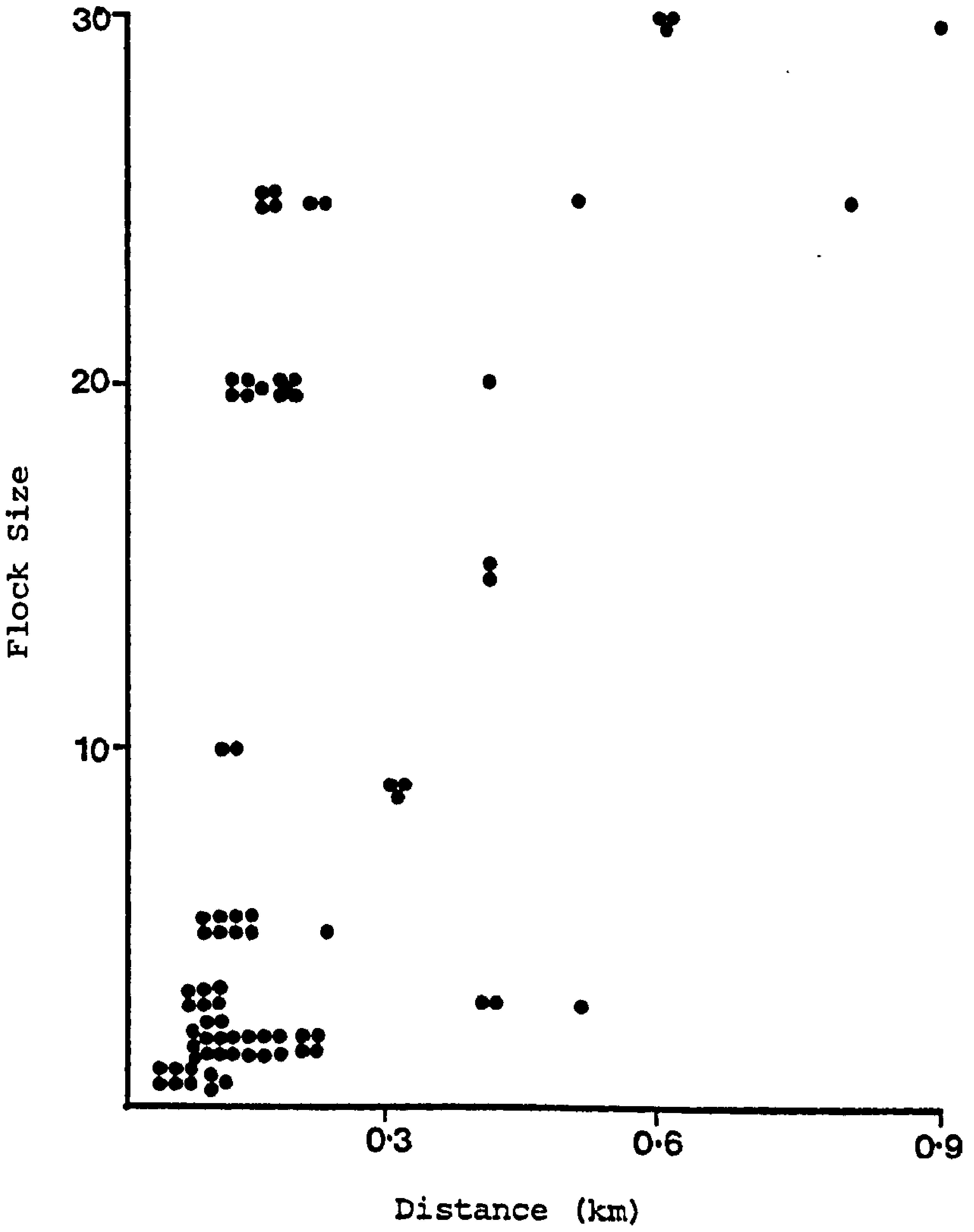
Cats were usually, and Sparrowhawks, *Accipiter nisus*, sometimes, present at the Swallow nest sites. Weasels and Sparrowhawks were frequently seen at the Sand Martin colony. These predators, and also Corvids, gulls and Grey Squirrels, were all mobbed by hirundines.

Sparrowhawks made few capture attempts on Swallows but one juvenile was taken (pers. obs.). Opdam (1979), in a study of Dutch Sparrowhawks, found that Swallows formed 1.3% of the diet. In June 29% of the Swallow prey were juveniles and 47% in July. In May 0.8% of the breeding population of Swallows were taken.

At the Sand Martin colony Sparrowhawks were at times present six or seven times in a day. The average number of capture attempts in July 1977, for example, was 0.28 ± 0.18 per hour. Of 51 observed capture attempts, 11 (21.6%) were successful. A Sparrowhawk was seen to alight at the entrance to burrows on three occasions in attempts to catch nestlings.

Figure 4.6

Flock size of Sand Martins in relation to the distance of the feeding site from the colony.


30
20
10
Flock Size
0·3
0·6
0·9
Distance (km)

4.11.1 Prey Type - Swallow Diet

Diptera were the most important insects in the diet of Swallows (Table 4.11a) comprising 81.3% of the food fed to first broods and 69.4% of that fed to second broods. It was found that 58.1% of the first brood diet consisted of Diptera over 1.5 mg dry weight and 40.8% of the second brood diet was of a similar size. It was evident that choice of prey depended mainly on its size, but there was also some taxonomic selection. Scatophagidae are slow-moving flies which were abundant in the net samples during the first brood period (21.3% of items, Table 4.12) but contributed to only 1.3% of the diet. These flies may have been over represented in the net due to their slow flight, but they would have been equally available to the Swallows. There was little evidence for specialisation on insects other than Diptera. Large moths were caught most often in the late summer in generally poor feeding conditions. These items, however, may have been difficult to handle: escaped moths were sometimes seen below the nest. Lepidopteran larvae were not taken regularly but for four days at the end of June 1979 significant numbers of larvae, including Tortricids and Ypsolopha parenthesella were caught. They formed from 4-16% of the diet each day (10% over the four days). During the whole season 1.2% of the diet was comprised of larvae. This prey item has rarely been recorded in the past. Beal (1918) recorded that 2.39% of the diet was Lepidoptera, mostly adults, but noted that Bank Swallows also take larvae. Thomas (1933-40) listed mainly Diptera and some Lepidoptera fed to nestlings but did not mention larvae, nor did Smith and Newton (1978) in their list of insects. However, Wood (1937) mentioned frequent feeding of a larva, Heterocampa guttwitta. Ypsolopha parenthesella, mainly occurring on oak and birch, hangs down on a thread from a leaf when disturbed and the Swallows were probably feeding on them at such a time. Indeed the birds may have disturbed the larvae by brushing the foliage on which the larvae were feeding (E.C. Pelham-Clinton pers. comm.).

Few Coleoptera and Parasitica were taken. Hemiptera were caught mainly late in the summer. Local swarms may have been common at this time.

Of the Diptera large items (dry weight more than 6.06 mg) were selected more than small prey (less than 1.5 mg dry weight) but were not taken exclusively. During second brood feeding there was a shift towards medium sized Schizophora and Syrphidae. There was, at this time, a significant increase in the relative abundance of very large Schizophora ($p < 0.001$). It may be that very large, fast items are too difficult or energetically expensive for Swallows to pursue so medium sized flies might be a preferred prey type. Large Syrphids, however, would probably be easier to catch than large Schizophora because of their hovering behaviour.

Table 4.11b shows selection indices

$$\frac{\log_{10} \text{percentage occurrence} + 1 \text{ in diet} \times 100}{\log_{10} \text{percentage occurrence} + 1 \text{ in net}}$$

(Bryant 1973) for a variety of taxonomic groups and prey sizes. These indices describe the degree of selection for a prey type in relation to the availability of that prey. Indices greater than 100 indicate selection for that item. Indices less than 100 indicate avoidance of an item. In Figure 4.7 the selection indices are plotted against the mean calorific value of insects in different taxa and size classes. Selection increases with increasing calorific value of the prey but drops for some very large prey such as large Schizophora and

Figure 4.7

Prey size selection by the Swallow.

Selection Indices $$\frac{\log_{10} \text{ percent of taxon } + 1 \text{ in the diet}}{\log_{10} \text{ percent of taxon } + 1 \text{ in the net}} \times 100$$

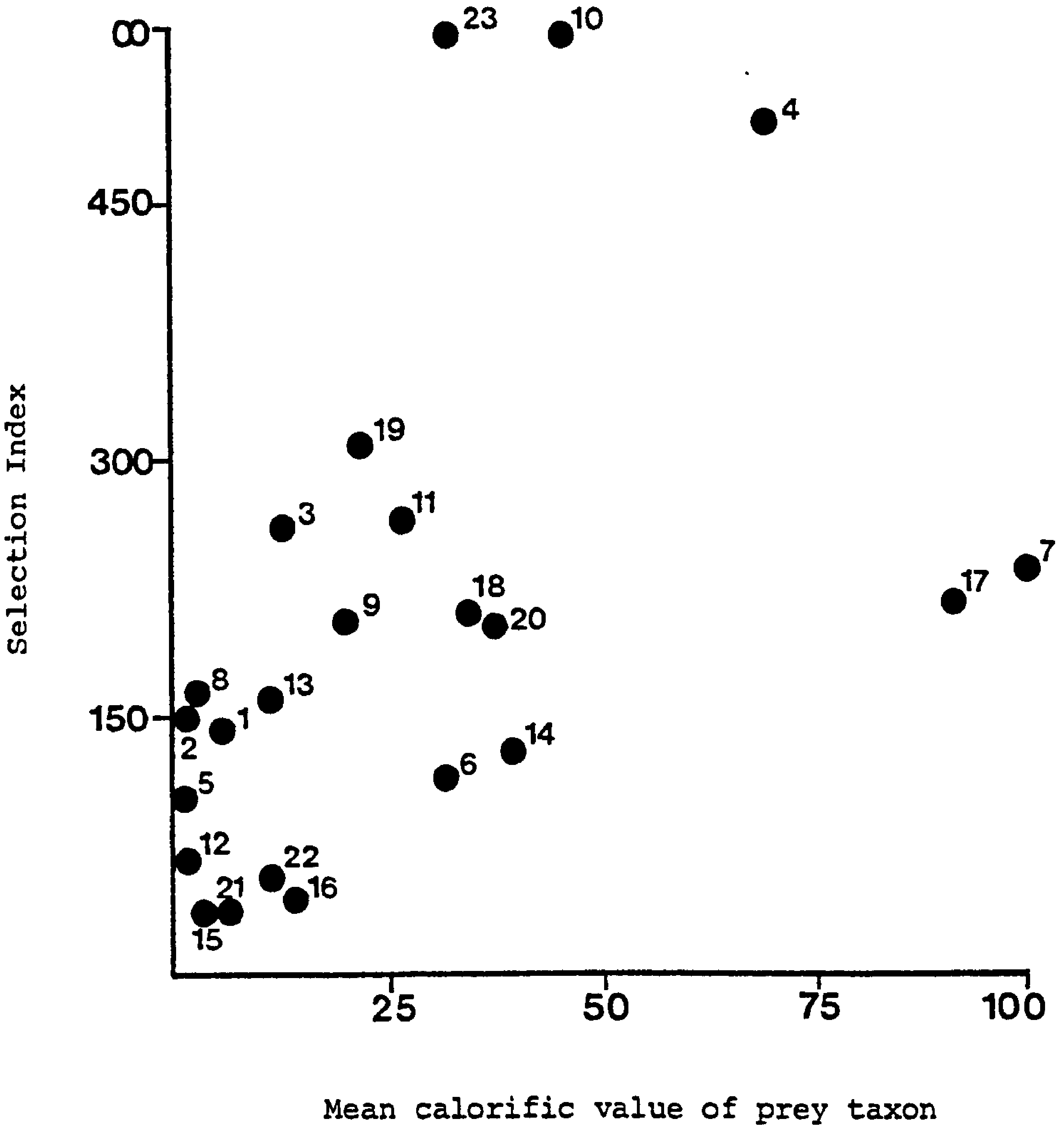
are shown in relation to the mean calorific value of prey taxa.

Small prey : < 1.5 mg dry weight

Medium prey : $\geq 1.5 \leq 6.01$ mg dry weight

Large prey : > 6.01 mg dry weight

1. Ephemeroptera (during 1st brood period)
2. Hemiptera
3. Lepidoptera, medium
4. Lepidoptera, large
5. Nematocera, small
6. Nematocera, medium
7. Nematocera, large
8. Brachycera, small
9. Brachycera, medium
10. Brachycera, large
11. Tabanidae, medium
12. Schizophora, small
13. Schizophera, medium
14. Schizophore, large
15. Hymenoptera, small
16. Hymenoptera, medium
17. Hymenoptera, large
18. Coleoptera
19. Syrphidae, small
20. Syrphidae, medium
21. Syrphidae, large
22. Scatophagidae
23. Lepidopteran larvae



∞
450
300
150
25
50
75
100
Selection Index
Mean calorific value of prey taxon
23
10
4
19
3
11
7
17
18
9
20
8
13
1
2
14
6
5
12
22
21
16
15

Hymenoptera which may have a long pursuit and handling time. In general, however, large items are preferred to small items.

4.11.2 Conspicuousness and Palatability of Prey

Size is probably the most important prey characteristic determining its conspicuousness but colour and shade will also have some effect (Lewis and Taylor 1965). Colour, however, might be less important for aerial feeders, especially Swifts and House Martins, than for birds foraging amongst vegetation. Syrphidae, being brightly coloured and often seen against vegetation, are probably easy for Swallows to detect in spite of their apparent mimicry of bees and wasps.

Sepsidae are unpalatable to Wagtails (Davies 1977a), perhaps because of a resemblance to ants, but both of these groups were taken by hirundines. Bees and wasps are infrequently taken, probably due to the possibility of the bird being stung. Flycatchers take wasps, removing the sting before feeding them to the nestlings (Davies 1977b). Most of those taken by hirundines are non-stinging drones (Lacey 1910, Stemmler-Morath 1932, Grant 1945) which fly late in the summer. Bees may provide an alternative to large Diptera early in the morning or when it is cool, since they are able to be active at lower temperatures than Diptera (Davies 1977b). In the present study they formed only 0.1% of the items taken.

4.11.3 Prey Type - Sand Martin Diet

Ephemeroptera comprised more than 30% of the diet of Sand Martins (Table 4.13a) at the study colony. Diptera, especially small Nematocera, and Hemiptera made up the other most important groups in the diet. Waugh (1978) found that only 1.05% of the diet (obtained from faecal samples) consisted of Ephemoroptera, acalypterate

Table 4.11a Mean percentage occurrence of insect taxa in Swallow food boluses for the months of June to August in 1978 and 1979

Taxon	Prey Size[1]						
	Small		Medium		Very Large		All Sizes
	1st brood	2nd brood	1st brood	2nd brood	1st brood	2nd brood	(1st/2nd brood)
Ephemeroptera/ Neuroptera/ Trichoptera	0.14	0.18	0.14	1.06	0.05	0.08	0.92
Hemiptera/ Pscocoptera	9.86	25.26	0.42	0.53	-	-	19.13
Lepidoptera (adults)	-	-	0.47	0.21	0.23	1.70	1.39
Lepidoptera (larvae)	-	-	2.72	-	-	-	1.20
Nematocera	12.92	15.65	0.33	0.03	0.38	1.20	15.48
Brachycera	4.74	3.81	10.05	13.88	0.23	0.18	16.65
Tabanidae	-	-	0.23	0.03	6.67	0.11	3.04
Syrphidae	-	0.07	3.90	5.02	6.76	1.94	8.59
Scatophagidae	-	-	0.70	0.14	1.74	0.28	1.29
Schizophora	5.59	9.01	17.05	14.06	12.59	4.38	30.75
Hymenoptera	0.94	0.28	0.28	0.14	0.09	0.25	0.94
Coleoptera	0.52	0.46	0.23	0.71	0.05	-	1.01

[1] Small prey - < 1.5 mg dry weight
Medium prey - $\geq 1.5 \leq 6.01$ mg dry weight
Very large prey - > 6.01 mg dry weight

n (1st broods) = 2129 items
n (2nd broods) = 2831 items

Table 4.11b Selection Indices[1] of insect taxa in Swallow food boluses

Taxon	Prey Size						
	Small		Medium		Very Large		All sizes
	1st brood	2nd brood	1st brood	2nd brood	1st brood	2nd brood	1st and 2nd broods
Ephemeroptera/ Neuroptera/ Trichoptera	142.3	∞	∞	∞	∞	∞	625.1***
Hemiptera/ Pscoptera	156.3	144.4***	∞	∞	-	-	178.0***
Lepidoptera (adults)	-	-	259.6	-	∞	499.5***	555.0***
Lepidoptera (larvae)	-	-	1075.0***	-	-	-	827.3***
Nematocera	129.0***	73.4***	233.3*	5.8***	263.5*	266.2***	105.6
Brachycera	85.61*	248.8***	117.7***	289.7***	∞	83.2	113.9***
Tabanidae	-	-	269.0	∞	5224.2***	∞	1464.9***
Syrphidae	-	34.0	110.7	492.3***	192.4***	212.8***	132.6***
Scatophagidae	-	-	18.9***	∞	53.2***	∞	56.1***
Schizophora	68.2***	67.9***	87.6***	232.2***	171.0***	88.2***	90.7***
Hymenoptera	64.4**	14.0***	39.11**	15.6***	219.7	∞	45.7***
Coleoptera	544.1	190.3*	51.1	∞	63.4	-	150.5

[1] Selection index = $\frac{\log_{10} \text{(percentage occurrence of taxon + 1 in diet × 100)}}{\log_{10} \text{(percentage occurrence of taxon + 1 in net)}}$

Asterisks indicate the probability of the index being significantly greater or less than 100:

$*p < 0.05$, $**p < 0.01$, $***p < 0.001$. See text for further explanation.

Table 4.12 Percentage occurrence of insect taxa in net catches for the months of June to August in 1978 and 1979

Taxon	Available Prey Size[1]						
	Small		Medium		Very Large		All Sizes
	1st brood	2nd brood	1st brood	2nd brood	1st brood	2nd brood	(1st and 2nd broods)
Ephemeroptera/ Neuroptera/ Trichoptera	0.13	-	-	-	-	-	0.11
Hemiptera/ Psocoptera	3.60	8.61	-	-	-	-	4.40
Lepidoptera (adults)	-	-	0.16	-	-	0.22	0.17
Lepidoptera (larvae)	-	-	0.13	-	-	-	0.11
Nematocera	6.70	45.05	0.13	0.66	0.13	0.44	13.20
Brachycera	6.70	0.88	6.70	1.54	-	0.22	11.44
Tabanidae	-	-	0.08	-	0.04	-	0.10
Syrphidae	-	0.22	3.20	0.44	1.90	0.66	4.50
Scatophagidae	-	-	15.6	-	5.65	-	3.38
Schizophora	14.90	28.70	27.2	2.21	3.60	5.74	44.26
Hymenoptera	1.80	4.86	0.88	1.32	0.04	-	3.27
Coleoptera	0.08	0.22	0.50	-	0.08	-	0.59

[1] prey size as in Table 4.11

n = 2391 items (1st brood)

n = 453 items (2nd brood)

Schizophora being the most important items. Beal (1918) also noted that Diptera were an important part of the diet (26.63%) with only a few percent comprised of Odonata, Ephemeroptera and similar insects. Stoner (1936) found that Diptera formed 45.7% of the food present in nestling Bank Swallows in June, decreasing to 19.7% in July while Coleoptera increased from 21.4 to 38.8% over this period. It is likely, however, that soft bodied insects such as Ephemeroptera are under represented in faecal samples and possibly also in gizzards (as in Beal 1918 and Stoner 1936), since in the present study faecal samples revealed only 4% of Ephemeroptera in the diet.

The majority of the items taken were in the range 0.4 to 1.3 mg dry weight. Most of the larger prey caught were weak flying Ephemeroptera but a few more mobile items such as Calypterates and Tabanids were also taken.

Selection indices are shown in Table 4.13b and are plotted against the mean calorific value of different taxa and size classes in Figure 4.8. Very small items were avoided but, unlike the Swallow, the Sand Martin did not prefer large prey items. Selection was high for some medium/small, presumably swarming, insects such as Nematocera. Items such as large moths, Hymenoptera and Diptera were avoided. Selection was high for Ephemeroptera but the availability of this taxon was not adequately reflected by the suction trap: this prey type does not occur far from water and were evidently available to the Sand Martin colony.

Figure 4.8

Prey size selection by the Sand Martin.

Selection Indices $$\frac{\log_{10} \text{percent of taxon} + 1 \text{ in the diet}}{\log_{10} \text{percent of taxon} + 1 \text{ in the net}} \times 100$$

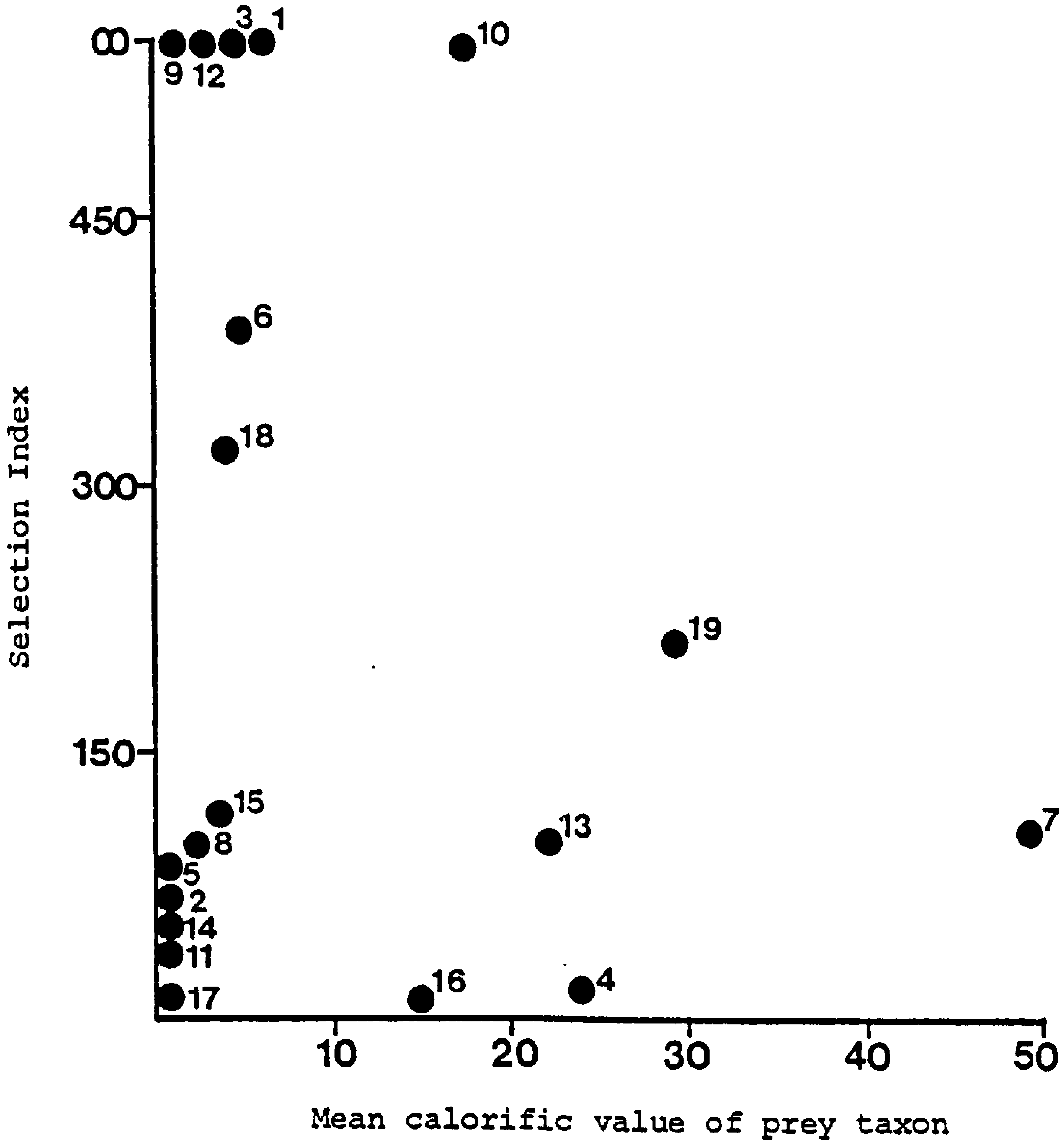
are shown in relation to the mean calorific value of prey taxa.

Small prey : < 0.32 mg dry weight

Medium prey : $\geq 0.32 \leq 1.26$ mg dry weight

Large prey : > 1.26 mg dry weight

1. Ephemeroptera
2. Hemiptera, small
3. Hemiptera, medium
4. Lepidoptera
5. Nematocera, small
6. Nematocera, medium
7. Nematocera, large
8. Brachycera, small
9. Brachycera, medium
10. Brachycera, large
11. Schizophera, small
12. Schizophors, medium
13. Schizophora, large
14. Hymenoptera, amsll
15. Hymenoptera, medium
16. Hymenoptera, large
17. Coleoptera, small
18. Coleoptera, medium
19. Coleoptera, large


∞
450
300
150
Selection Index
10
20
30
40
50
Mean calorific value of prey taxon
1
2
3
4
5
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7
8
9
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11
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17
18
19

Table 4.13a Mean percentage occurrence of insect taxa in Sand Martin food boluses for the months of May to August in 1978 and 1979

Taxon	Prey Size[1]						
	Small		Medium		Very Large		All Sizes
	1st brood	2nd brood	1st brood	2nd brood	1st brood	2nd brood	1st and 2nd broods
Ephemeroptera[2]/ Neuroptera/ Trichoptera	0.82	-	25.07	28.17	10.16	4.15	34.40
Hemiptera/ Pscoptera	9.43	17.03	16.10	9.82	0.04	0.31	26.27
Lepidoptera (adults)	-	-	-	-	0.02	0.11	0.06
Nematocera	18.93	10.10	6.24	5.11	0.80	0.34	21.33
Brachycera	0.75	0.87	1.00	3.62	0.89	0.70	3.76
Scatophagidae	-	-	-	-	0.02	0.14	0.07
Schizophora	0.66	1.63	5.00	10.04	2.55	4.85	11.88
Hymenoptera	0.38	1.29	0.24	0.11	0.07	0.22	1.10
Coleoptera	0.04	0.05	0.53	0.84	0.20	0.25	0.93
Arachnida	-	-	-	0.05	-	0.15	0.09

[1] small prey - < 0.32 mg dry weight
medium prey - ≥ 0.32 ≤ 1.26 mg dry weight
large prey - > 1.26 mg dry weight
n (1st brood) = 4516 items
n (2nd brood) = 3465 items

[2] Ephemeroptera was the most important taxon in this group forming 97% of the items.

Table 4.13b Selection indices[1] of insect taxa in Sand Martin food boluses

Taxon	Prey Size						
	Small		Medium		Very Large		All Sizes
	1st brood	2nd brood	1st brood	2nd brood	1st brood	2nd brood	1st and 2nd brood
Ephemeroptera/ Trichoptera/ Neuroptera	∞		∞	5788.9***	∞	∞	12066.5***
Hemiptera/ Psocoptera	64.21***	71.81***	∞	1517.68***	∞	∞	85.24***
Lepidoptera	-	-	-	-	15.11*	14.54**	11.78***
Nematocera	80.96***	86.77***	381.58***	380.05***	136.13*	66.78	93.10
Brachycera	63.03***	115.42	201.74***	2626.43***	∞	∞	192.40***
Scatophagidae	-	-	-	-	∞	∞	∞
Schizophora	24.57***	46.09***	749.64***	700.44***	83.02***	114.30***	102.81
Hymenoptera	24.88***	33.85***	164.17	79.65	4.57***	13.28***	30.35***
Coleoptera	3.68***	6.80***	60.48***	584.29***	∞	213.82***	58.45**
Arachnida	-	-	-	∞	-	∞	58.06

[1] Selection Index = $\frac{\log_{10} (N_B + 1) \times 100}{\log_{10} (N_S + 1)}$ where N_B and N_S are the percentage occurrences of any taxon in the boluses and suction trap respectively.

Asterisks indicate the probability of the selection index being significantly greater or less than 100.

*p < 0.05, **p < 0.01, ***p < 0.001. See text for further explanation.

Table 4.14 Percentage occurrence of insect taxa in suction trap catches for the months May to August in 1978 and 1979

Taxon	Available Prey Size[1]						
	Small		Medium		Very Large		All Sizes
	1st brood	2nd brood	1st brood	2nd brood	1st brood	2nd brood	1st and 2nd broods
Ephemeroptera/ Neuroptera/ Trichoptera	-	-	-	0.06	-	-	0.03
Hemiptora/ Psocoptera	37.53	55.12	-	0.17	-	-	47.34
Lepidoptera (adults)	-	-	-	-	0.14	1.05	0.64
Nematocera	39.29	15.02	0.68	0.61	0.54	0.55	27.11
Brachycera	1.43	0.72	0.41	0.06	-	-	1.25
Scatophagidae	-	-	-	-	-	-	-
Schizophora	6.87	7.15	0.27	0.39	3.60	3.69	11.01
Hymenoptera	2.65	10.56	0.14	-	3.40	3.47	10.52
Coleoptera	1.90	1.05	1.02	0.11	-	0.11	2.08
Arachnida	0.14	0.17	-	-	-	-	0.16

[1] Prey size as in Table 4.13

n (1st brood) = 1471 items

n (2nd brood) = 1818 items

Culicidae and chironomidae (42.0% of the catches) were excluded from the table (this does not affect the relative degree of selection on different taxa shown in Figure 4.8).

4.11.4 Prey Abundance and Quality

The Swallow responded to an improvement in feeding conditions by increasing its foraging rate (the rate of energy gain in assimilable kcal min^{-1}).

There was a positive correlation between the foraging rate and four characteristics of the food supply (from net samples) :

(a) prey size $r = 0.32^{***}$, $n = 91$

(b) the number of large items in the net $r = 0.51^{***}$, $n = 91$

(c) the weight of prey $r = 0.50^{***}$, $n = 91$

and (d) the number of prey items $r = 0.29^{**}$, $n = 91$.

The correlation was least good with 'number of items' since it is at times possible to obtain many very small items in the net in bad weather and at other times there are just a few large items in the sample. The latter case may provide better feeding conditions despite the lower number of prey (Bryant 1973).

The importance of prey quality rather than prey quantity is supported by Figure 4.9a which shows that as the number of large items (≥ 1.5 mg dry weight) in the net increased, a greater proportion of large items was incorporated into the diet. The proportion of large items plateaus at high abundances of such prey at a little less than 100% indicating that small items were still being caught. The number of small items (< 1.5 mg dry weight) in the net had no effect on the number taken by the Swallow in accordance with the prediction of optimal foraging theory (Figure 4.9b). Similar results on the inclusion of proportionately more large prey in the diet when their abundance increases have been obtained for the Redshank, *Tringa totanus* (Goss Custard 1977a) and the Spotted Flycatcher, *Muscicapa striata*, (Davies 1977b).

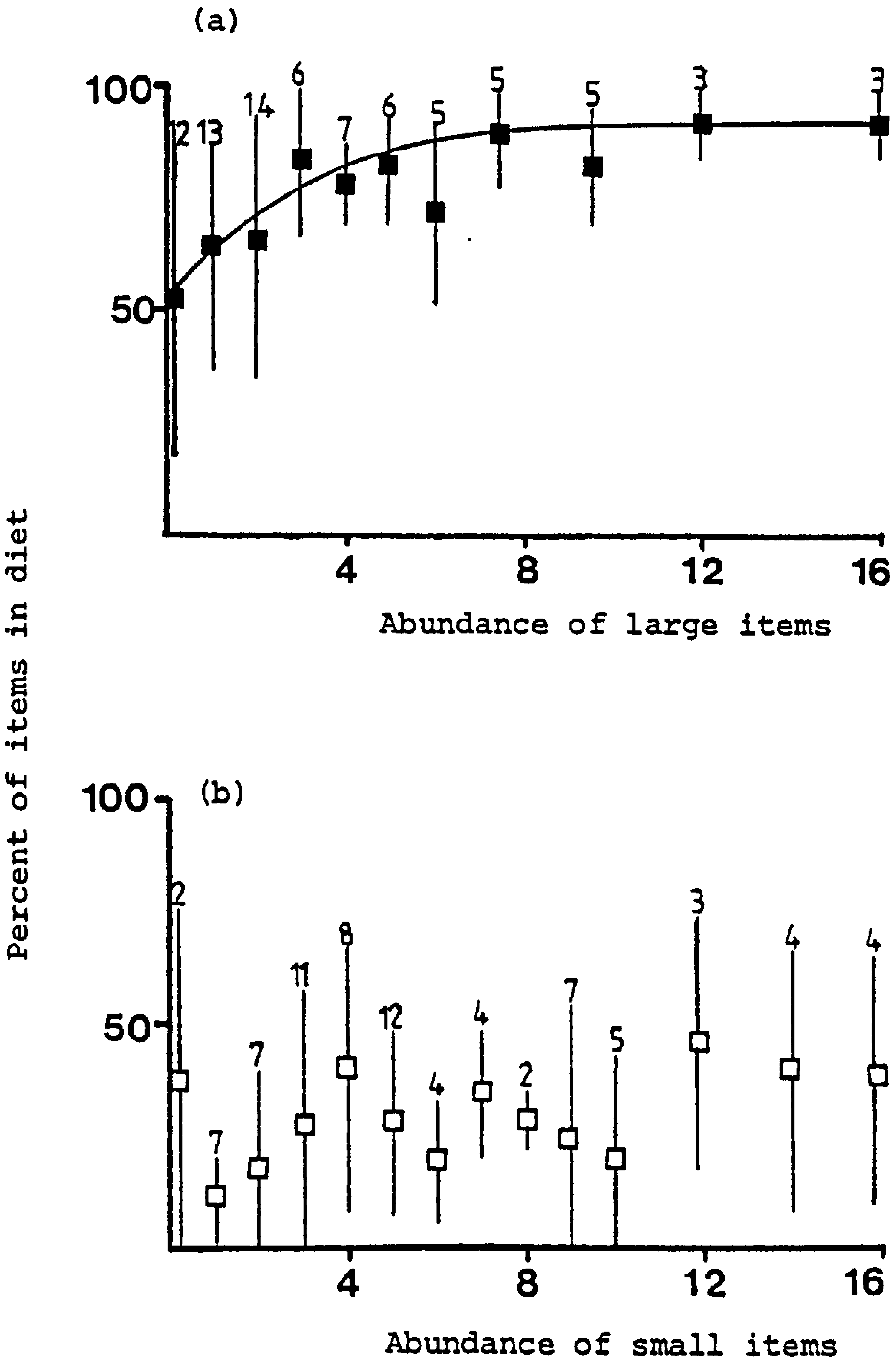
Figure 4.9

(a) The probability of a large item (≥ 1.5 mg dry weight) being included in the Swallow's diet depends on its absolute abundance in the net catch.

(b) The probability of a small item (< 1.5 mg dry weight) being included in the Swallow's diet does not depend on its absolute abundance in the net catch. Means ± 1 s.d. are shown. The number of 2 hour periods over which the data were collected is indicated.

The curve was drawn by eye.

(a) $r = 0.32$, $p < 0.001$; (b) no significant correlation

(a)
100
50
12
13
14
6
7
6
5
5
5
3
3
4
8
12
16
Abundance of large items
Percent of items in diet
100
(b)
50
2
7
7
11
8
12
4
4
2
7
5
3
4
4
4
8
12
16
Abundance of small items

Additional support for the effect of prey quality on feeding conditions is seen from an analysis of selection indices (see above). Large items were generally heavily selected for when they were rare in the environment (Figure 4.10a, b); selection decreased as they became absolutely or relatively more abundant to a selection index of about 100 at 30% relative abundance. Small items, however, were not selected for and were sometimes avoided i.e. their selection indices were around 100 or less (Figure 4.10c, d). When they were very scarce the inclusion of just a few in the diet sometimes led to high selection indices but this had a negligible effect on the overall pattern of selection.

In an attempt to assess the effects of relative and absolute abundance on prey selection the data on Swallow diet obtained in this study were examined and compared with predictions of optimal foraging theory.

Since the absolute abundance of large items affected prey selection the effects of relative abundance were measured while absolute abundance was kept constant.

The data were divided into three groups: (a) high abundance samples where there were ≥ 10 items per 50 sweeps of the net (the median number of samples); (b) medium abundance where there were < 10 ≥ 4 items per 50 sweeps of the net; (c) low abundance where there were < 10 items per 50 sweeps of the net and the foraging rates of both sexes were ≤ 0.06 kcal min^{-1} excluding travel time. At this foraging rate the parents would experience difficulty in feeding adequately a brood of five nestlings. Hence at this level of abundance food can be assumed to be scarce for feeding Swallows.

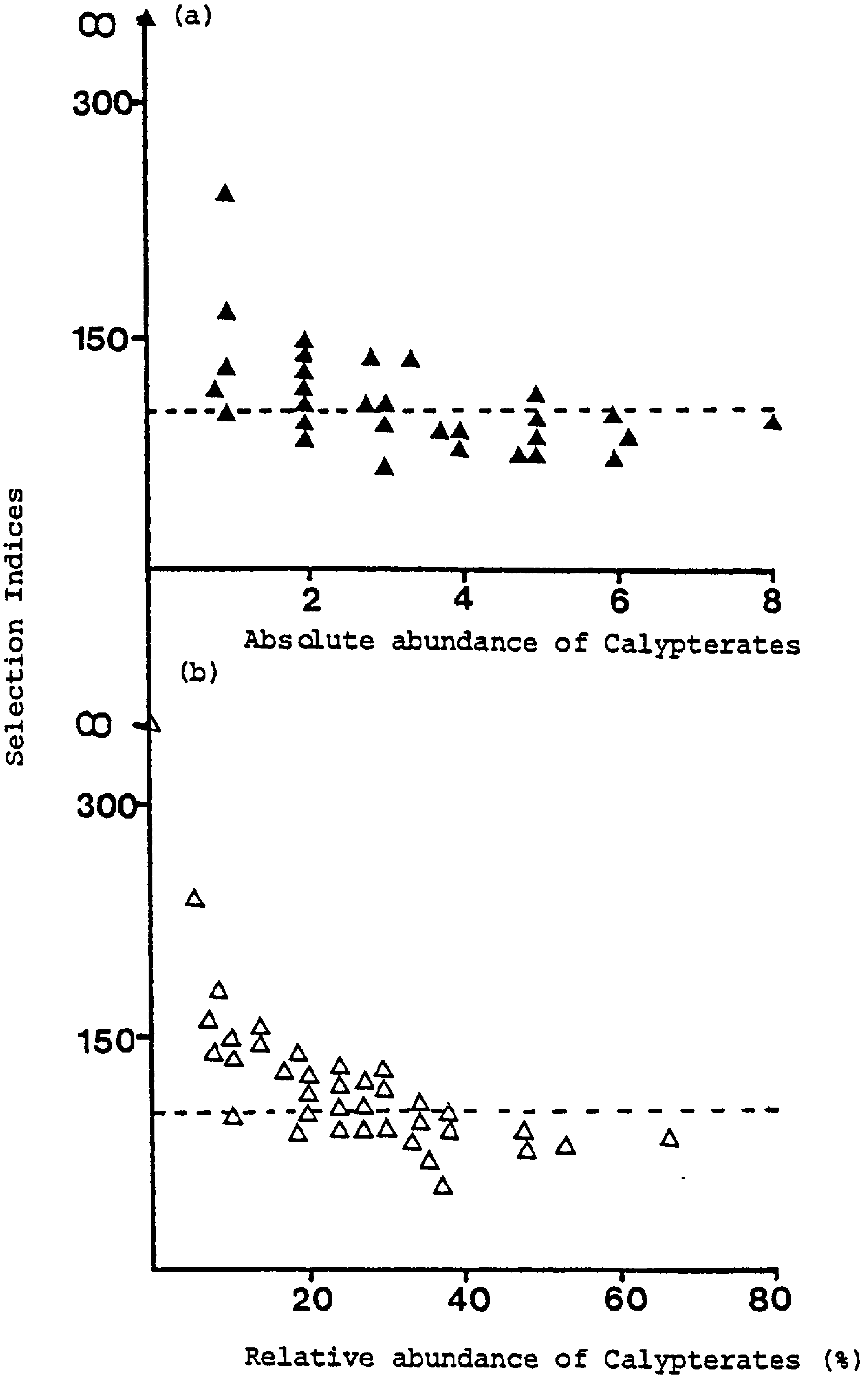
Figure 4.10

Dependence of selection indices

$$\frac{\log_{10} \text{percentage of prey taxon} + 1 \text{ in diet}}{\log_{10} \text{percentage of prey taxon} + 1 \text{ in net}} \times 100$$

on (a) the absolute abundance and (b) the relative abundance of large Calypterates (preferred prey), and on (c) the absolute abundance and (d) the relative abundance of small Acalypterates (non-preferred prey). Dashed lines indicate the value of the selection index (100) at which there is no selection either for or against the prey.

(Large prey ≥ 1.5 mg in weight, small prey < 1.5 mg in weight)


(a)
∞
300
150
2
4
6
8
Absolute abundance of Calypterates
Selection Indices
(b)
∞
300
150
20
40
60
80
Relative abundance of Calypterates (%)

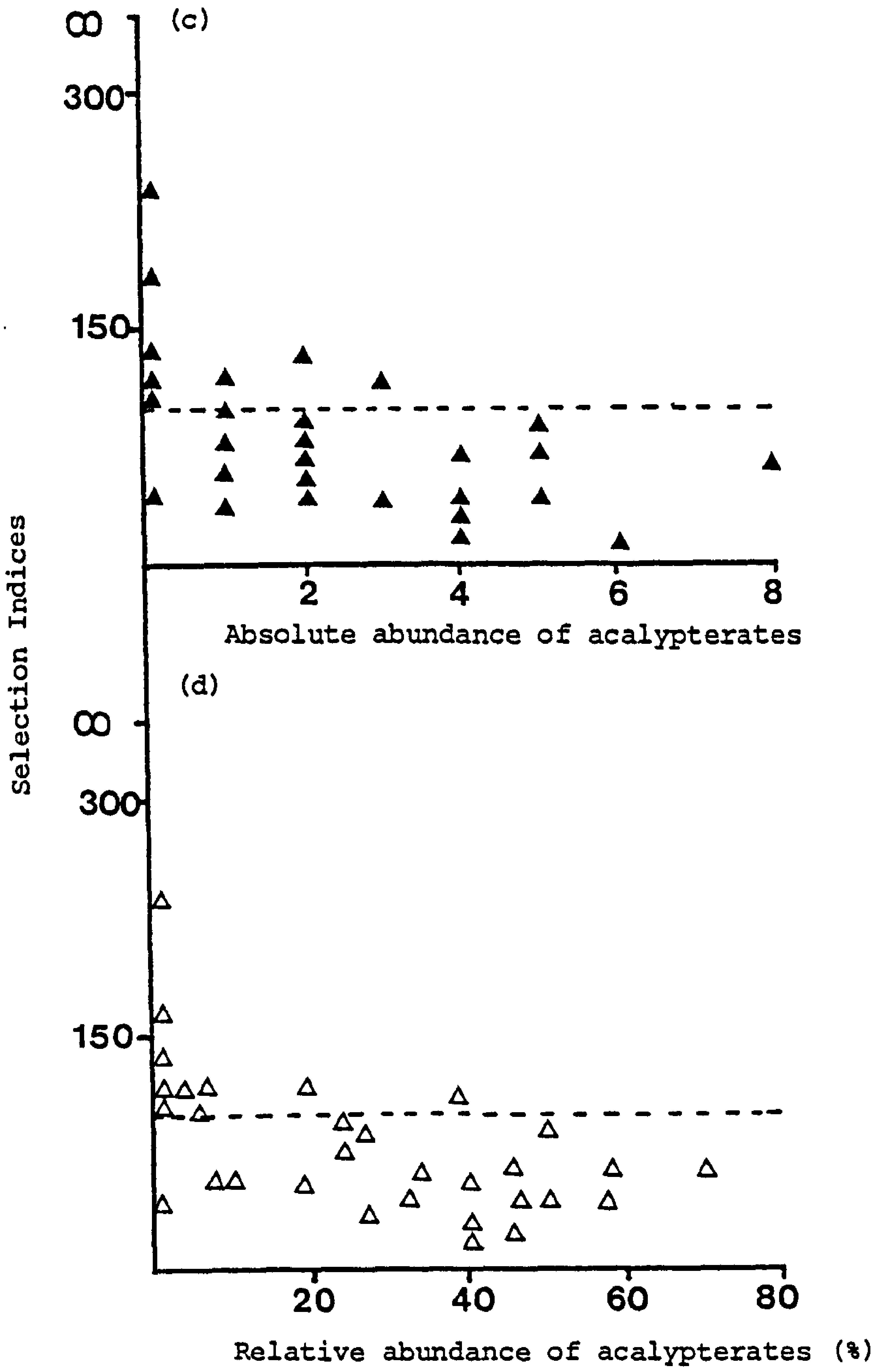


Figure 4.10 c, d

In previous studies (e.g. Werner and Hall 1974, Krebs et al 1978) the predator has been provided with high and low densities of food without regard to whether these densities were experienced as abundant or scarce by the predator relative to encounter rates in the wild.

In addition to the classification of the data by the number of items in the net they were also grouped according to weight in a second analysis: (a) high abundance samples when the weight of the net sample was $\geq$ 16.22 mg dry weight (the median of the samples); (b) medium abundance when there were $<$ 16.22 mg in the net and the foraging rate was $>$ 0.06 kcal min^{-1}; (c) low abundance when there were $<$ 16.22 mg in the net and the foraging rate was $\leq$ 0.06 kcal min^{-1}. This method of determining abundance, by weight instead of by number, has not been previously used. However, the correlation between foraging rate and food weight was better than that for foraging rate and prey numbers suggesting that the Swallow was responding to the weight of prey rather than to numbers.

A third classification of the data was tried combining weights and numbers: (a) high abundance when there were $\geq$ 16.22 mg and $\geq$ 10 items in the net; (b) medium abundance when there were $<$ 16.22 mg and $<$ 10 items in the net; (c) low abundance when there were $<$ 16.22 mg and $<$ 10 items in the net and foraging rates were $\leq$ 0.06 kcal min^{-1}. For all high and medium abundances the foraging rates were $>$ 0.06 kcal min^{-1}.

An arcsin transformation was made on the data. The diets were compared when small items were relatively abundant or scarce in the net and were compared with the diet predicted from optimal foraging theory: "When food is abundant only the preferred, large items should be taken; when food is scarce non preferred small items should be included in the diet in the proportion in which they are encountered". For each abundance two or three classes were made (depending on the sample size):

(1) relative abundance of small items in the net = 75 to 100%;

(2) relative abundance of small items = 50 to 75%;

(3) relative abundance of small items is less than 50%.

Classes 1 and 2 were combined if the sample size was small. There was only one class (Class 1) when food was scarce.

The results are shown in Figure 4.11 and Table 4.15:

1. When food was abundant, in terms of weight and/or numbers, the Swallow took significantly more small items when they were relatively common than when they were relatively scarce. Significantly more small items were taken than expected from optimal foraging theory except when numbers of small items were relatively scarce in the analysis by numbers.

2. When food was at a medium abundance the Swallow only took significantly more small items when they were relatively common if the analysis was based on weight or weight and numbers of prey. Again, significantly more small items were taken than expected except when small items were relatively scarce in the analysis by weight.

3. When food was scarce small items were always relatively more abundant than large items. Significantly fewer small items were taken than expected. Hence large items were still being selected for.

The important points to emerge from this analysis are (1) Swallows

Figure 4.11

A comparison of the size of prey taken by the Swallow with the size of prey in net catches and with the diet expected from optimal foraging theory. The percentages have been transformed (arcsin).

Open columns = the ratio of small to large prey encountered

Light shading = the ratio of small to large prey expected in the diet

Dark shading = the ratio of small to large prey actually taken by the Swallow.

s = small prey (< 1.5 mg dry weight)

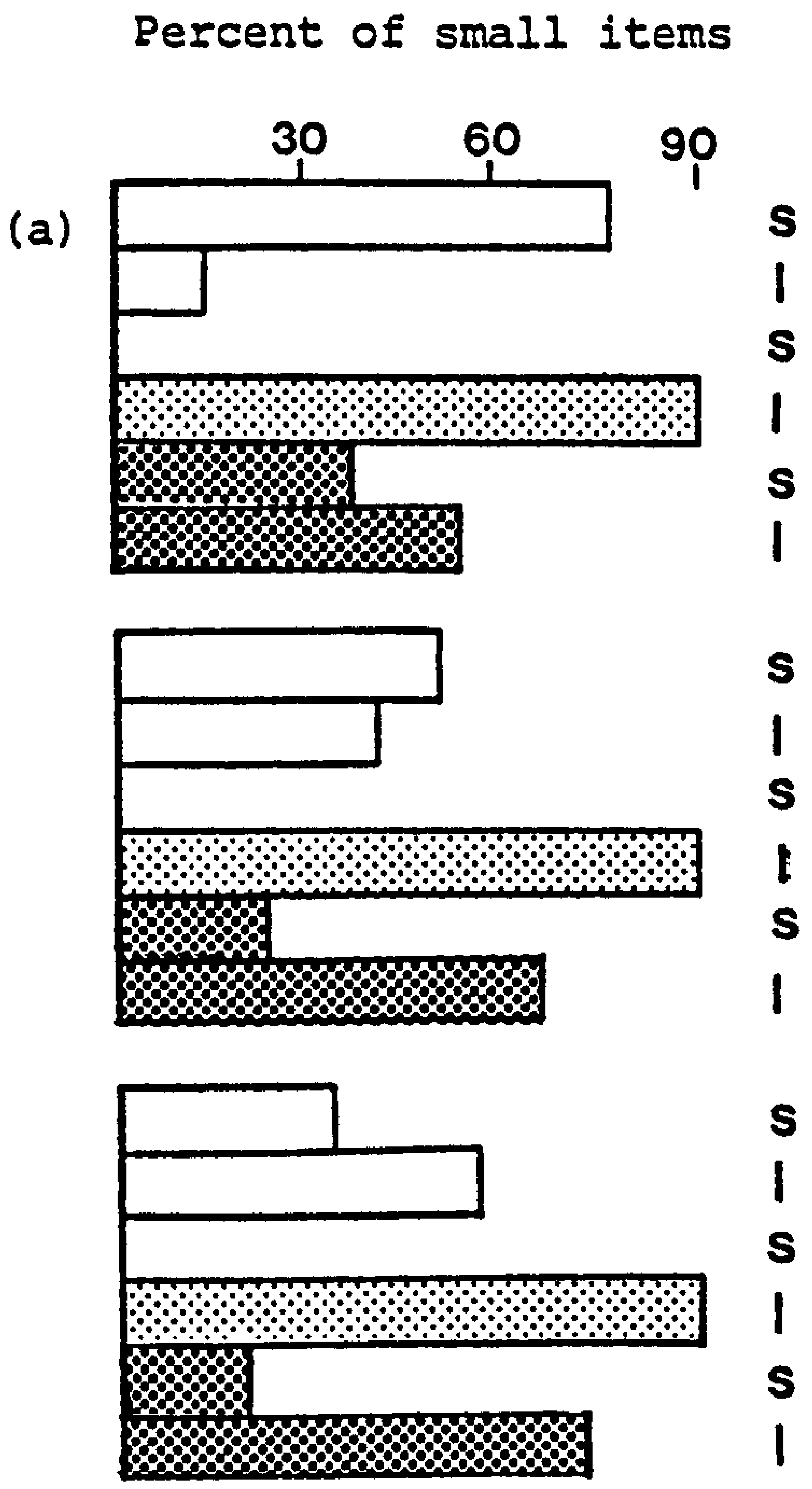
l = large prey (≥ 1.5 mg dry weight)

(a) The diet when food is very abundant

(b) The diet when food is at a medium abundance

(c) The diet when food is scarce

Abundance is in terms of numbers of prey. Analyses of diets when food abundance is measured in terms of weight of prey or a combination of numbers and weight are shown in Table 4.15. Further explanation is given in the text.

Percent of small items
30
60
90
(a)
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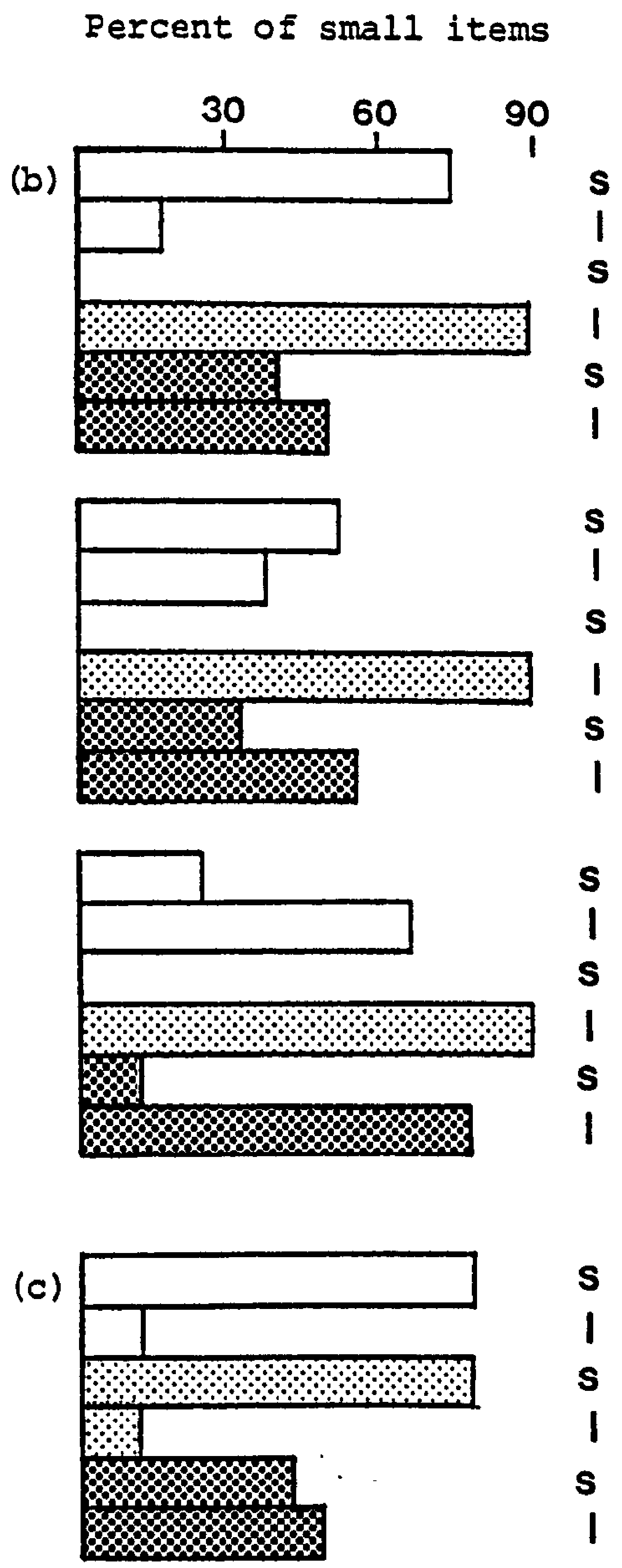


Figure 4.11 b, c

Table 4.15 Analysis of prey size selection by the Swallow. (See text for explanation).

		Mean relative abundance of items <1.5 mg dry weight		Comparison of classes			Difference from expected diet	
		In the net	In the diet	t-test			χ^2-test	
1. Level of Food Abundance : HIGH								
(a) Analysis by numbers								
Class 1	n = 16	76.36 ± 8.54	36.71 ± 23.47	$t_{1,2}$	1.86	n.s.	263.81	<0.001
Class 2	n = 11	50.05 ± 4.23	23.20 ± 13.96	$t_{2,3}$	1.12	n.s.	20.12	<0.05
Class 3	n = 15	32.76 ± 7.22	17.56 ± 11.32	$t_{1,3}$	2.92	<0.01	16.45	n.s.
(b) Analysis by weight								
Classes 1 & 2	n = 22	54.31 ± 8.36	32.05 ± 15.09	$t_{1,2,3}$	2.58	<0.02	104.23	<0.001
Class 3	n = 23	32.59 ± 6.31	21.02 ± 13.56				46.9	<0.01
(c) Analysis by numbers and weight								
Classes 1 & 2	n = 13	54.95 ± 11.53	27.92 ± 13.11	$t_{1,2,3}$	2.22	<0.05	59.1	<0.001
Class 3	n = 15	32.36 ± 7.31	17.56 ± 11.32					

2./

Table 4.15 (continued)

		Mean relative abundance of items <1.5 mg dry weight		Comparison of classes			Difference from expected diet	
		In the net	In the diet	t-test			χ^2-test	
2. Level of Food Abundance : MEDIUM								
(a) Analysis by numbers								
Class 1	n = 9	74.33 ± 11.39	40.57 ± 16.66	$t_{1,2}$	0.25	n.s.	131.47	<0.001
Class 2	n = 15	52.52 ± 3.30	38.83 ± 16.82	$t_{2,3}$	0.07	n.s.	60.51	<0.001
Class 3	n = 7	32.16 ± 10.70	25.26 ± 17.41	$t_{1,3}$	1.78	n.s.	17.03	<0.02
(b) Analysis by weight								
Class 1	n = 19	75.81 ± 10.37	30.64 ± 18.59	$t_{1,2}$	0.22	n.s.	399.19	<0.001
Class 2	n = 6	52.80 ± 2.00	32.83 ± 22.29	$t_{2,3}$	2.13	n.s.	150.46	<0.001
Class 3	n = 7	23.39 ± 15.02	11.21 ± 10.27	$t_{1,3}$	3.37	<0.01	1.16	n.s.
(c) Analysis by numbers and weight								
Classes 1 & 2	n = 12	66.18 ± 12.33	39.39 ± 15.38	$t_{1,2,3}$	6.50	<0.001	344.62	<0.001
Class 3	n = 2	29.05	9.65 ± 1.55				0.90	n.s.
3. Level of Food Abundance: SCARCE								
(a) Analysis by numbers								
Class 1	n = 9	77.60 ± 15.63	40.89 ± 23.94				45.32	<0.001
(b) Analysis by weight								
Class 1	n = 13	80.50 ± 11.35	46.12 ± 24.50				45.59	<0.001
(c) Analysis by weight and numbers								
	n = 9	80.19 ± 9.08	41.78 ± 27.35				39.19	<0.001

responded to both increase in numbers and in weight of prey but at medium densities weight seems to be more important; (2) small items were taken significantly more than expected even at high food densities; (3) large items were still selected for at low food densities; (4) as small items became relatively more abundant at a constant absolute abundance significantly more of these items were taken.

4.11.5 The Adults' Diet

The mean size of prey ingested by the adult Swallow and Sand Martin is smaller than that fed to their respective nestlings; it is also smaller than that taken by the adults prior to the clutch hatching (Waugh 1978). Studies on Great Tits *Parus major* (Royama 1970) and the Blue Gray Gnatcatcher *Polioptila caerulea* (Root 1967) have also shown that adults feed larger items to their nestlings than they ingest themselves. Root (1967) suggested that it required less energy to catch a small item than it would to catch a large one hence the adult could conserve energy by feeding itself on small prey.

In the present study an investigation was made into the diet of adult Swallows and Sand Martins which were egg laying or were in the early stages of incubation. The diet was sampled from faecal samples and gizzard contents.

Both species concentrated on Bibionids, Coleoptera and Schizophora (Table 4.16). Large Schizophora ($\geq$ 1.5 mg) were more important to the Swallow (21% of Schizophora taken) than to the Sand Martin (3.5%). Data from Bryant (1975) for the House Martin are included in Table 4.16 for comparison. The House Martin is more reliant on aphids

Table 4.16 Percentage occurrence of taxa in egg layer's diet

	Coleoptera	Aphidoidea	Bibionidae	Brachycera	Schizophora	Parasitica	Ephemeroptera
Swallow	26.07	0.47	15.64	1.42	52.13	0.95	1.42
Sand Martin	26.74	10.07	14.93	12.15	15.63	1.74	8.68
House Martin[1]	2.80	45.8	4.00	5.20	10.10	6.50	2.50

[1] Bryant (1975) from Southern England

Table 4.17 Prey size taken during egg laying

	Mean Prey Weight (mg)	Mean Prey Wing Length (mm)	n
Swallow	2.59 ± 2.37	5.45 ± 1.83	211
Sand Martin	1.15 ± 0.94	4.90 ± 1.73	288
House Martin[1]	0.49 ± 0.01	3.66 ± 0.65	255

[1] Bryant (unpubl. data)

than are the other hirundines at this stage of the season at least in Southern Britain.

As with the nestling diet there is a difference in the size of prey taken by the three hirundines (Table 4.17).

The mean prey size ingested by the Swallow at this stage was less than that fed to the nestlings ($t = 18.8$, $p < 0.001$). The prey sizes of the egg laying adult and nestling Sand Martin were more similar ($t = 1.92$ n.s.).

4.12 Foraging Rates and Efficiencies

The mean foraging rates (rate of assimilable energy gain) of Swallows and Sand Martins (calculated from bolus weights and bolus collection times) are given in Table 4.18. The distributions are skewed towards the lower values giving median values of 0.18 and 0.15 assimilable kcal min^{-1} (0.175 kJ and 0.63 kJ) for female and male Swallows and values of 0.06 and 0.04 assimilable kcal min^{-1} (0.25 kJ and 0.17 kJ) for Sand Martins (Figure 4.12). Swallows show a wider range of foraging rates than Sand Martins and a more even spread over that range.

A considerable part of the daily energy expenditure of a hirundine during the nestling rearing stage is spent on collecting food, so it is reasonable to assume that the parent will try to maximise its foraging efficiency (defined as

$$\frac{\text{assimilable food energy collected}}{\text{energy expended during its collection}}),$$

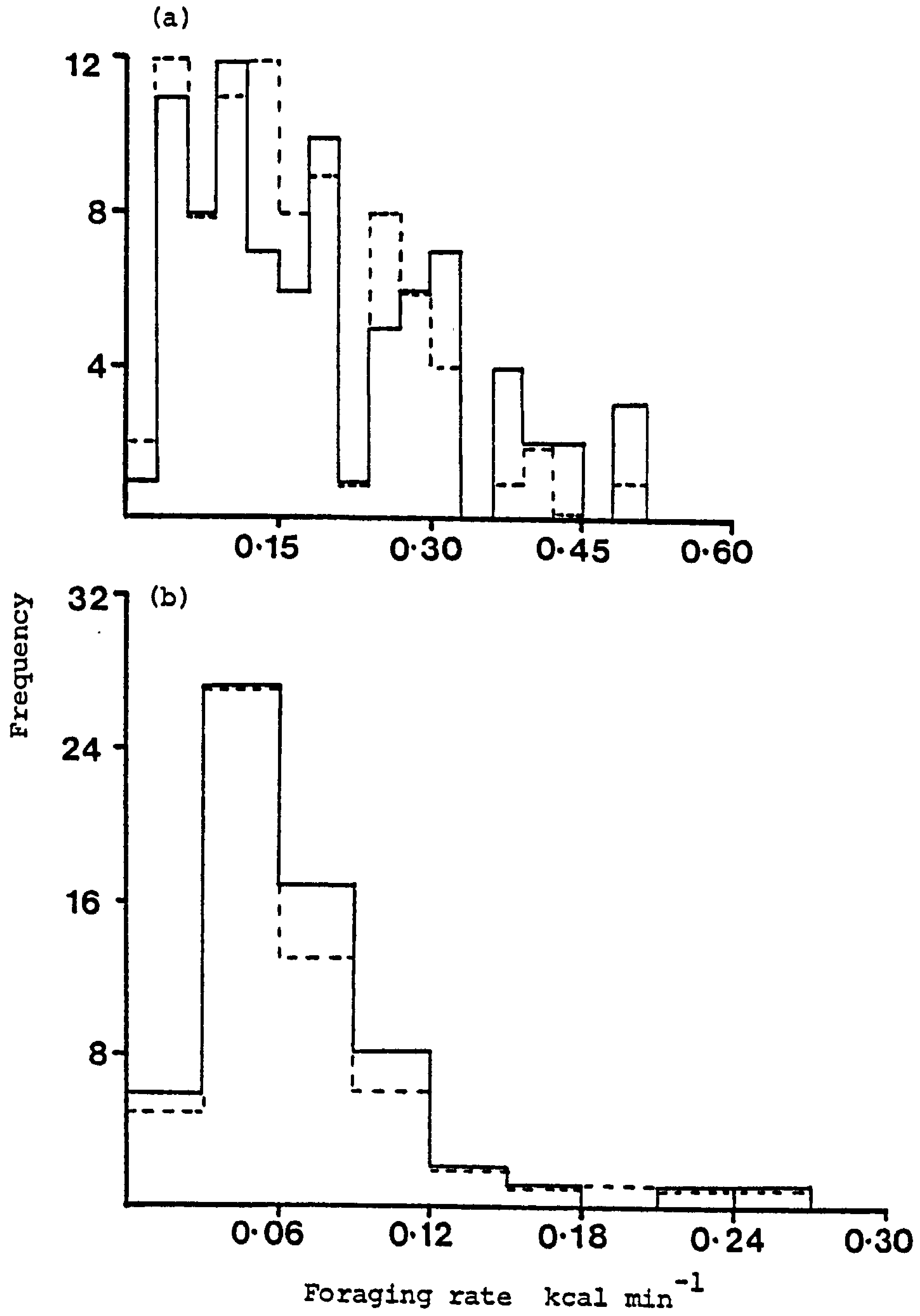
Table 4.18 shows the mean foraging efficiencies of Swallows and Sand Martins. These were calculated for 3h periods using 70% assimilation efficiency. Foraging efficiencies > 1 indicate a net gain of energy. Foraging efficiencies of less than 1 (i.e. a net loss of

Figure 4.12

The frequency distribution of foraging rates (intake rate of metabolisable energy in kcal min^{-1}) of (a) Swallows and (b) Sand Martins. The foraging rates exclude the time spent travelling between the nest site and feeding site.

Solid line = female foraging rates

Dashed line = male foraging rates


(a)
12
8
4
0·15
0·30
0·45
0·60
Frequency
32
(b)
24
16
8
0·06
0·12
0·18
0·24
0·30
Foraging rate kcal min^{-1}

energy) could not be sustained for long, but occurred on five occasions with Sand Martins and twice with Swallows either in very heavy rain or when the parents had small broods of two or three. It is possible in these cases that part of the time spent away from the nest was not used for collecting food for the nestlings leading to an under-estimate for the foraging efficiency. Some very high values were recorded, due to very good feeding conditions but were not sustained for long.

These values are comparable to those of other birds such as the Dickcissel, Spiza americana, at 12.8 and tropical hummingbirds at 3.8 to 22.2, although the hummingbird, Eugenes fulgens, had values of 7.0 to 70.0 (Lawton 1973, Table II). Waugh (1978) found values for Swallows of 5.39 to 22.14 with a mean of 10.24 (assuming an assimilation efficiency of 100%).

The Sand Martin had a generally lower efficiency than the Swallow although the lowest value for the latter was less than the lowest for the Martin. Males also tended to have lower values than females.

Daily foraging efficiencies for the hirundines are more similar than the above values suggest. The daily foraging efficiency for House Martins is from 1 to 3 (D.M. Bryant pers. comm.). These values were directly obtained from D_2O^{18} measured metabolic rates. Values for Swallows and Sand Martins were calculated from mean foraging rates and time budgets to obtain a comparison with the House Martin.

Sand Martins had a daily foraging efficiency of 1.5; it was higher for second broods (2); the maximum attained was 3.5 for a

Table 4.18

Foraging rates (intake rate of assimilable energy) and foraging efficiencies $\frac{\text{(assimilable food energy collected)}}{\text{(energy expended during its collection)}}$ of Swallows and Sand Martins. Ranges and the mean ± 1 s.d. are given for values including and excluding the travel time from nest site to feeding site.

	Foraging Rate (assimilable kcal min^{-1})	
	Including travel time[1]	Excluding travel time[1]
Swallow female	0.010 - 0.380 0.149 ± 0.089	0.011 - 0.515 0.198 ± 0.130
Swallow male	0.010 - 0.351 0.134 ± 0.077	0.011 - 0.504 0.169 ± 0.105
Sand Martin female	0.017 - 0.185 0.053 ± 0.034	0.018 - 0.247 0.062 ± 0.044
Sand Martin male	0.016 - 0.158 0.049 ± 0.031	0.017 - 0.217 0.057 ± 0.040

	Foraging Efficiency	
	Including travel time[1]	Excluding travel time[1]
Swallow female	0.433 - 16.385 6.257 ± 3.836	0.488 - 22.207 8.314 ± 5.625
Swallow male	0.433 - 15.302 5.707 ± 3.404	0.488 - 21.764 7.228 ± 4.584
Sand Martin female	0.664 - 7.100 2.043 ± 1.284	0.695 - 9.478 2.382 ± 1.694
Sand Martin male	0.626 - 6.066 1.881 ± 1.169	0.645 - 8.317 2.177 ± 1.549

[1] Travel time is the time taken to go between the nest site and feeding site; it does not include time spent travelling between patches.

female feeding a second brood. Swallows had slightly higher daily foraging efficiencies (3 for first broods) but they could theoretically reach high values of 5 or 6 when feeding conditions are very good (4 or more large items per 50 sweeps of the net).

The following description is based on multiple regression analyses shown in Table 4.20. The foraging rates and efficiencies of Swallows and Sand Martins were very much influenced by feeding conditions as exemplified by variables such as ambient temperature, rainfall, cloud cover and especially available prey size in the suction trap (Sand Martin) or the number of large items in the net (Swallow), Figures 4.13 to 4.15 and Table 4.19. The rates and efficiencies increased as more large items were included in the diet, although this was also associated with an increase in the parents' energy expenditure due to faster speeds and more flapping flight. The size of prey caught, however, outweighed this disadvantage, especially for the Swallow. The foraging rate of the Sand Martin peaked at medium speeds of 7-10 ms^{-1} as it is adapted to take smaller, slower items than the Swallow.

Although foraging rates and efficiencies increased with the proportion of large items captured they peaked at around the average prey size and decreased when very large items such as moths were taken perhaps because of long search and handling times and the difficulty of dealing with more than two or three of such items at a time (Figure 4.16). In addition large items sometimes escaped from the parent.

Figure 4.13

Foraging rates (rate of assimilable energy intake, kcal min^{-1}) of Swallows in relation to (a) food abundance measured by net catches and (b) the number of prey $\geq$ 1.5 mg dry weight in the net catch.

(a) $r = 0.29$, $p < 0.003$

(b) $r = 0.51$, $p < 0.001$

Each point represents the foraging rate calculated over a 2 hour period from the mean food bolus size and the mean bolus collection time. Time spent travelling to and from the feeding site is excluded.

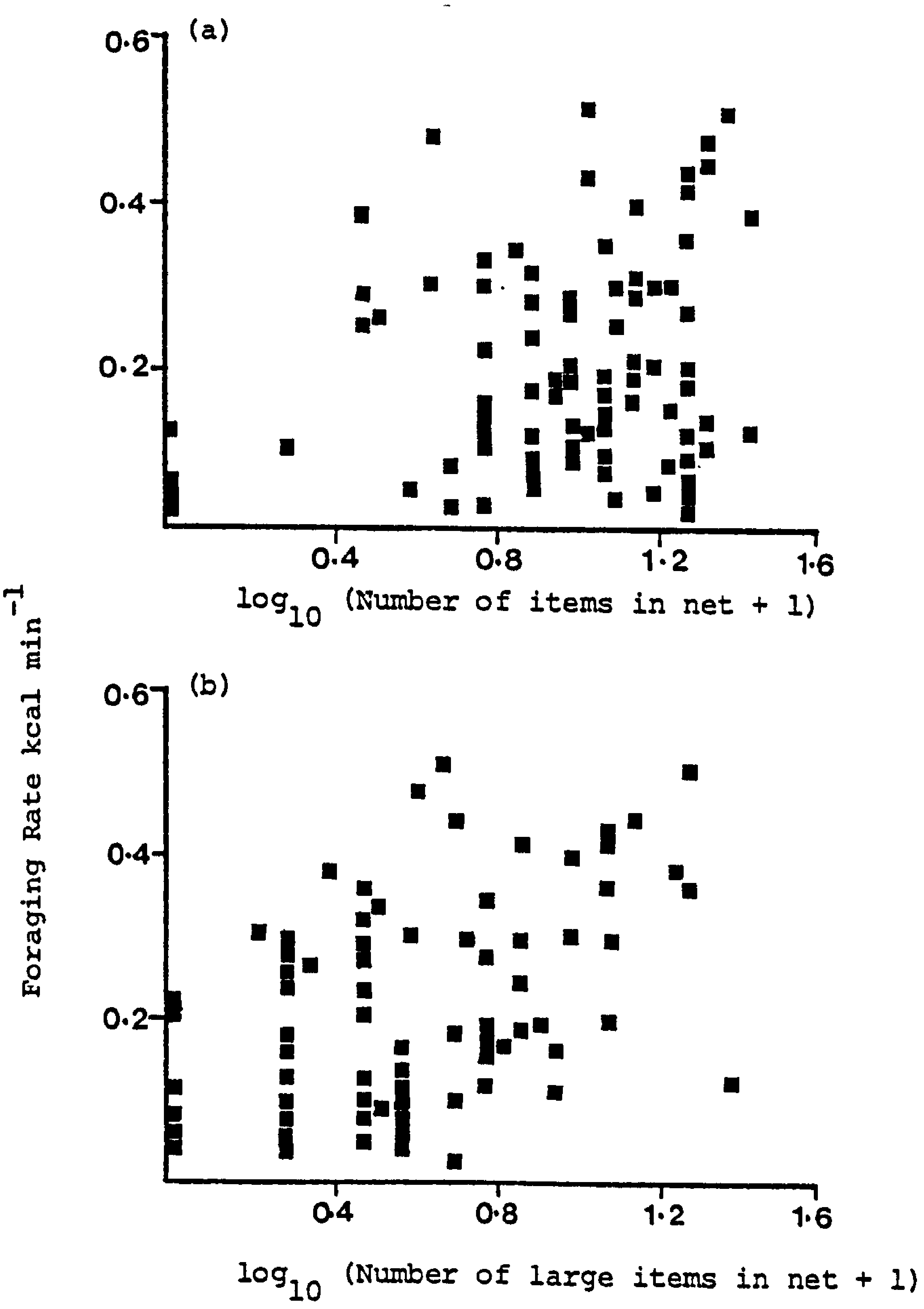

(a)
0·6
0·4
0·2
0·4
0·8
1·2
1·6
log$_{10}$ (Number of items in net + 1)
Foraging Rate kcal min^{-1}
(b)
0·6
0·4
0·2
0·4
0·8
1·2
1·6
log$_{10}$ (Number of large items in net + 1)

Figure 4.14

The foraging rate (rate of assimilable energy intake, kcal min^{-1}) of Sand Martins in relation to (a) food abundance as shown by the suction trap catch and (b) the mean prey size (mg dry weight) excluding culicids, chironomids, and aphids in the suction trap catch.

(a) $r = 0.25$, $p = 0.024$

(b) $r = 0.46$, $p < 0.001$

Foraging rates calculated as for Figure 4.13.

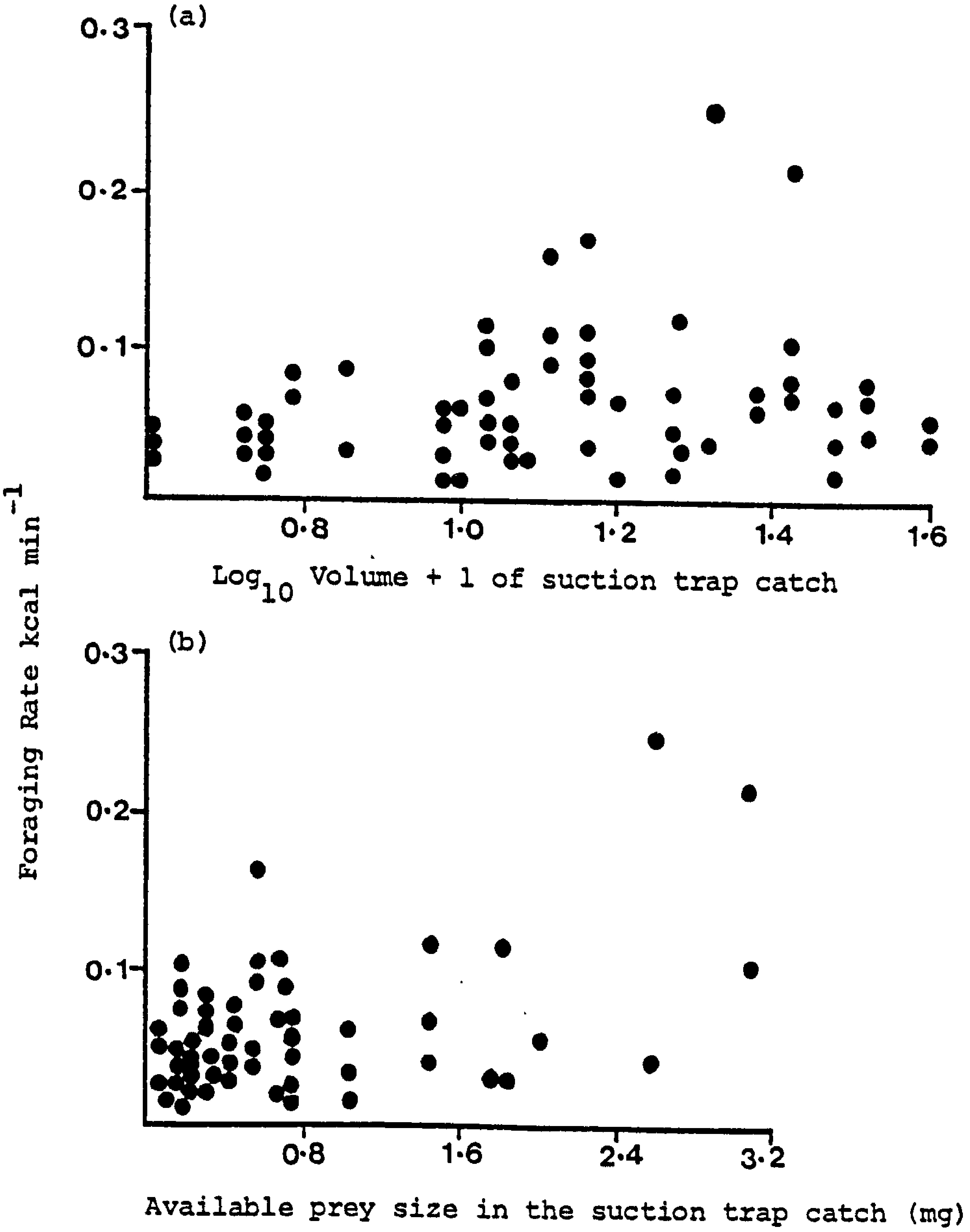

(a)
0·3
0·2
0·1
0·8
1·0
1·2
1·4
1·6
Log10 Volume + 1 of suction trap catch
Foraging Rate kcal min-1
(b)
0·3
0·2
0·1
0·8
1·6
2·4
3·2
Available prey size in the suction trap catch (mg)

Figure 4.15

Foraging rates (rate of assimilable energy intake kcal min^{-1}) of (a) Swallows and (b) Sand Martins in relation to the ambient temperature.

(a) $r = 0.37, p < 0.001$

(b) $r = 0.36, p < 0.002$

Foraging rates calculated as for Figure 4.13.

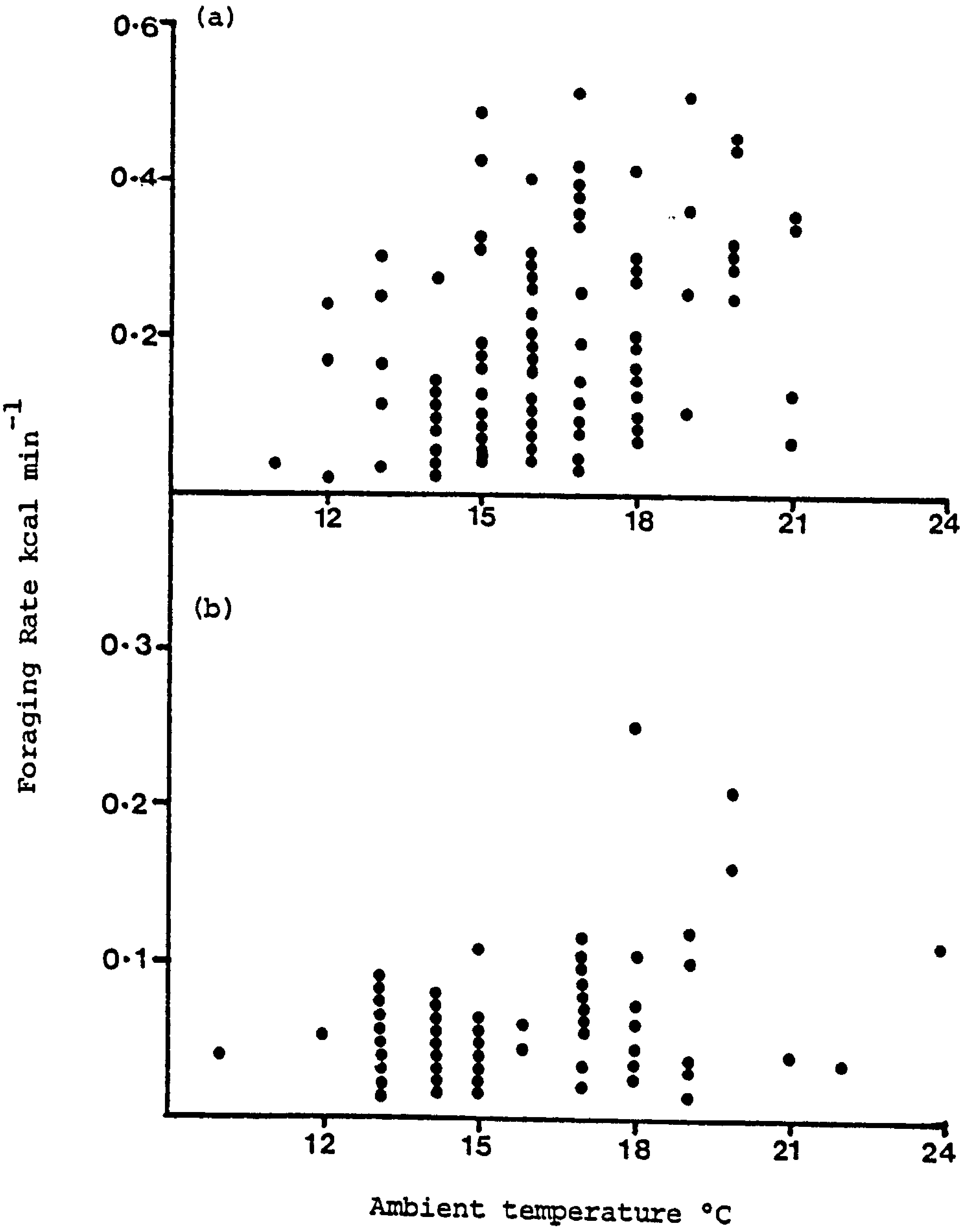

(a)
0·6
0·4
0·2
12
15
18
21
24
(b)
0·3
0·2
0·1
12
15
18
21
24
Foraging Rate kcal min^{-1}
Ambient temperature °C

Figure 4.16

The foraging efficiency (Energy gain/Energy expended) of (a) Swallows and (b) Sand Martins in relation to the mean dry weight of prey taken. Means ± 1 s.d. are sh~~wo~~own for each size class of prey. Horizontal lines indicate the range of prey weights for which the efficiencies were calculated. In (a) prey weighing 26 to 34 mg were grouped together. In (b) prey weighing 4 to 7 mg were grouped together. The number of 2h periods over which the data were collected is indicated. The extreme data points are all significantly less than the maximum value at the 5% level.

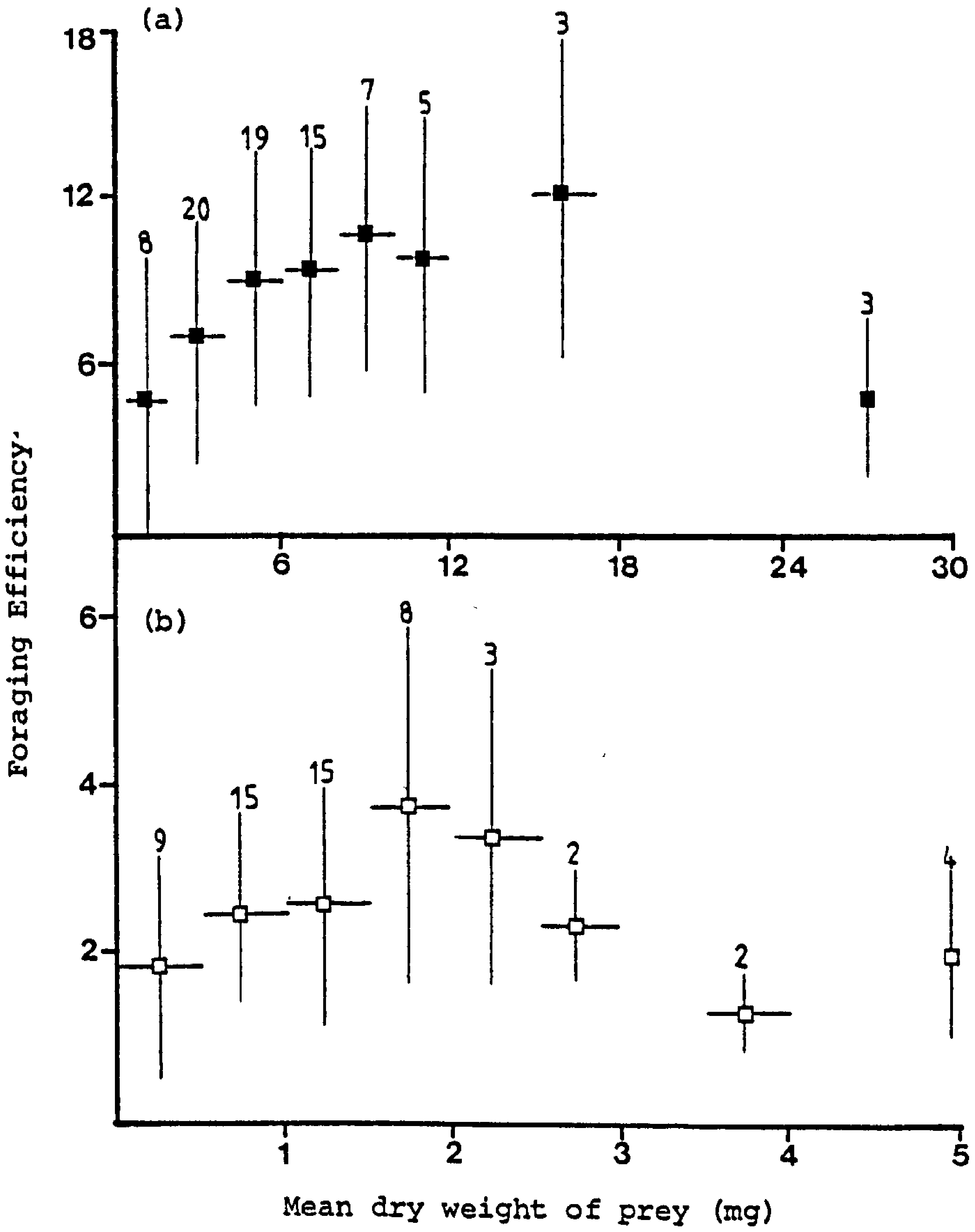

(a)
18
12
6
8
20
19
15
7
5
3
3
6
12
18
24
30
Foraging Efficiency
(b)
6
4
2
9
15
15
8
3
2
2
4
1
2
3
4
5
Mean dry weight of prey (mg)

Table 4.19

Foraging rates (FOR) and foraging efficiencies (FE) of Swallows (a) and Sand Martins (b) in good and bad feeding conditions; n = the number of observation periods (the mean ± 1 s.d. for the female only are shown).

(a)	Swallow Foraging Rate		t	p
Large Items Abundant[1]	0.41 ± 0.12	n = 18	8.70	<0.001
Large Items Scarce[2]	0.05 ± 0.03	n = 11		

	Swallow Foraging Efficiency		t	p
Large Items Abundant[1]	13.40 ± 5.16	n = 18	7.38	<0.001
Large Items Scarce[2]	2.94 ± 2.41	n = 11		

(b)	Sand Martin Foraging Rate		t	p
High Prey Size[3]	0.10 ± 0.07	n = 10	2.66	<0.02
Low Prey Size[4]	0.04 ± 0.02	n = 22		

	Sand Martin Foraging Efficiency		t	p
High Prey Size[3]	3.92 ± 2.86	n = 10	2.47	<0.02
Low Prey Size[4]	1.66 ± 0.61	n = 22		

[1] $\log_{10}$ Number of large items in the net (FLIN) ≥ 0.8

[2] FLIN = 0

[3] Available prey size in the suction trap (PS3) ≥ 1.3

[4] PS3 ≤ 0.2

Table 4.20 Multiple Regression Analyses of Foraging Rates and Efficiencies

		Dependent Variable	Independent Variable	Standard Partial Regression Coefficient	Cumulative $r^2 \times 100$	n
1.	SWALLOW (female)	Foraging Rate (FOR)[1]	Speed (Sp)[1]	0.49 ***	30	74
			Temperature (T°)	0.27 **	37	
2.	SWALLOW (male)	Foraging Rate (FOR)	Speed (Sp)	0.41 ***	33	74
3.	SWALLOW (female)	Foraging Efficiency (FE)	Available Prey Size (FLIN)	0.47 ***	26	74
			Time (TM±)	- 0.21 *	30	
4.	SWALLOW (male)	Foraging Efficiency (FE)	Available Prey Size (FLIN)	0.31 **	24	74
			Time (TM±)	- 0.28 **	31	
			Rainfall (Rain)	- 0.29 **	38	
5.	SAND MARTIN (female)	Foraging Rate (FOR)	Available Prey Size (PS3)	0.38 **	21	62
6.	SAND MARTIN (male)	Foraging Rate (FOR)	Prey Size Taken (PLI)	0.38 **	13	62
			Percent. Gliding (GF)	- 0.46 ***	27	
			Cloud Cover (C)	0.34 **	37	
7.	SAND MARTIN (female)	Foraging Efficiency (FE)	Cloud Cover (C)	0.44 ***	13	62
			Percent. Gliding (GF)	- 0.38 **	25	
			Prey Size Taken (PLI)	0.35 **	37	
8.	SAND MARTIN (male)	Foraging Efficiency	Prey Size Taken (PLI)	0.37 **	13	62
			Percent. Gliding (GF)	- 0.37 **	21	
			Cloud Cover (C)	0.32 **	31	

[1] Symbols in parentheses correspond to variables described in Appendix 4

* $p < 0.05$
** $p < 0.01$
*** $p < 0.001$

4.13 Prey Selection and Flight Costs

The mean sizes of small (< 1.5 mg dry weight) and large (≥ 1.5 mg dry weight) prey taken by the Swallow were 1.06 mg and 6.61 mg dry weight respectively. Large items required more energy to be expended in their capture than small items for two reasons: (a) faster, flapping flight was used and (b) they took longer to catch. The speed(s) of the Swallow increased as more large prey (PLI) were taken: $\log_{10} s = 0.19PLI + 0.67$, $r = 0.40$, $n = 79$, $p < 0.001$. The capture rate (CR) of prey increased as the prey size taken (PS) decreased: $\log_{10} CR = 1.29 - 0.58 \log_{10} PS$, $r = 0.50$, $n = 92$, $p < 0.001$. The high calorific value of large items is thus offset to some extent by high flight costs. Nevertheless, large items are still more profitable than small ones. The energy gained from a prey item less the energy cost of catching it is 32.9 calories (137.7J) for large prey but is only 5.3 calories (22.2J) for a small item.

The relative costs and gains of feeding on different proportions of large and small items are shown in Table 4.21 (and see Figure 4.17). Because of the high costs and low capture rates of feeding on large items and the cost of travelling far from the nest the ratio of gains to costs when the bird is feeding on large or small items are very similar.

If a Swallow is feeding only on large items it takes a maximum of 15 per bolus. The inclusion of a few small items slightly decreases the foraging rate but slightly increases the foraging efficiency. If the Swallow captured more large items per foraging trip it would increase its efficiency and energy intake rate but it would also increase the length of the trip. Capturing a high

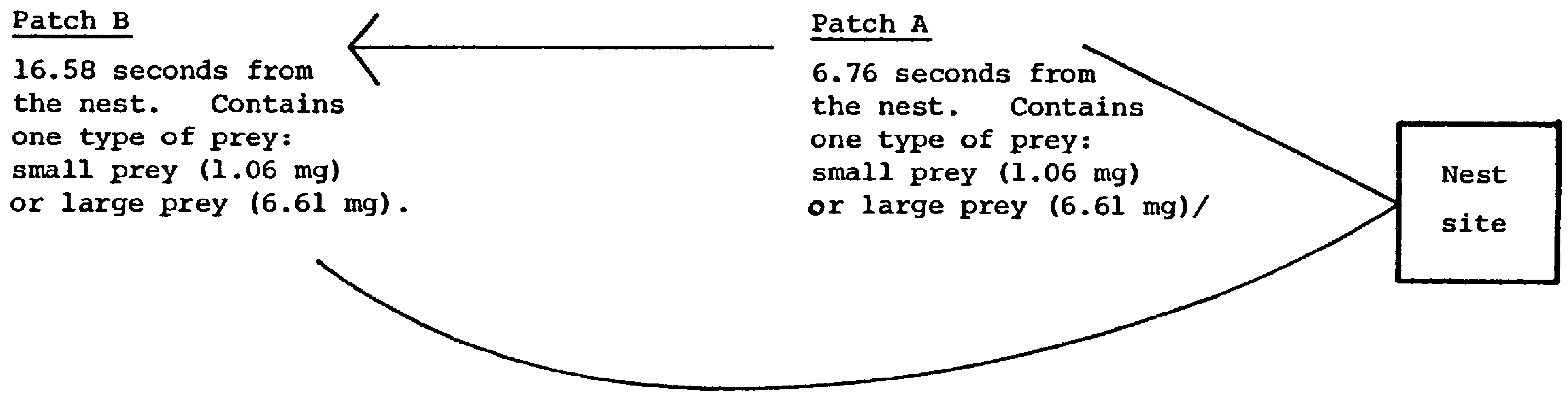

Patch B
16.58 seconds from
the nest. Contains
one type of prey:
small prey (1.06 mg)
or large prey (6.61 mg).
Patch A
6.76 seconds from
the nest. Contains
one type of prey:
small prey (1.06 mg)
or large prey (6.61 mg)/
Nest
site

Figure 4.17

Legend to Table 4.21

Patch A is 6.75 seconds from the nest and Patch B is 16.58 sec. from the nest.

S = small prey (1.06 mg dry weight) and these are taken in Patch A except in 1. See equations in text for the capture rate.

L = large prey (6.61 mg dry weight) and these are taken in Patch B except in 1. See equations in text for the capture rate.

The Swallow flies straight to a patch (flight cost = 0.0732 kcal $g^{-1}h^{-1}$); flies fast (11.22 ms^{-1}) to catch large prey and slowly (4.68 ms^{-1}) to catch small items (see equations in text). The cost of chasing large prey is assumed to be the mean flight cost of 0.0732 kcal $g^{-1}h^{-1}$ and the cost of chasing small prey is proportionately less at 0.0305 kcal $g^{-1}h^{-1}$.

A value of 70% assimilation efficiency is assumed for the calculations of foraging efficiency ($\frac{\text{Gains}}{\text{Costs}} \times 0.7$) and foraging rate ($\frac{\text{Gains}}{\text{Time}} \times 0.7$).

On average a bolus contains 15 large and 3 small items; in poor conditions it contains 11 large and 40 small items. The maximum number of large items in a bolus is 15. A comparison is given in the table of costs and gains if 18 large items instead of a mixture of 18 large and small items are taken.

In 3. and 4. capture rates are increased by 10%. In 5. and 6. costs are increased by 10%. When the cost of catching large items is increased the cost of travelling to a patch is also increased.

Table 4.21

Prey size selection : Costs and Benefits

Feeding Behaviour		Costs (kcal)	Gains (kcal)	Time (mins)	Gains / Costs × 0.7	Gains / Time × 0.7
1. Feeding for 1 min at						
	A on S	0.0148	0.1101	1.11	5.21	0.07
	A on L	0.0284	0.2392	1.11	5.89	0.15
	B on S	0.0225	0.1101	1.28	3.42	0.06
	B on L	0.0360	0.2392	1.28	4.65	0.13
2. Bolus consists of:						
	15L + 3S	0.0672	0.5628	2.72	5.87	0.15
	15L	0.0657	0.5453	2.37	5.81	0.16
	18L	0.0763	0.6544	3.01	6.01	0.17
	11L + 40S	0.0722	0.6331	4.07	6.15	0.11
3. Bolus consists of:						
(and capture	15L + 3S	0.0680	0.5628	2.42	5.88	0.16
rate of S is	18L	0.0763	0.6544	3.01	6.01	0.17
CR + 10%)	11L + 40S	0.0702	0.6331	3.60	6.31	0.12
4. Bolus consists of:						
(and capture	15L + 3S	0.0623	0.5628	2.49	6.32	0.16
rate of L &	18L	0.0705	0.6544	2.76	6.50	0.17
S is	11L + 40S	0.0701	0.6331	3.45	6.32	0.13
CR + 10%)						
5. Bolus consists of:						
(and costs of	15L + 3S	0.0673	0.5628	2.72	5.85	0.15
catching S	18L	0.0763	0.6544	3.01	6.01	0.17
are costs +	11L + 40S	0.0740	0.6331	4.07	5.99	0.11
10%)						
6. Bolus consists of:						
(and costs	15L + 3S	0.0739	0.5628	2.72	5.33	0.15
of catching	18L	0.0839	0.6554	3.01	5.46	0.17
L & S are	11L + 40S	0.0792	0.6331	4.07	5.60	0.11
costs + 10%)						

proportion of small items further increases the efficiency but decreases the foraging rate.

Increasing capture rates by 10% decreases costs by a few percent; increasing flight costs has a little more effect on foraging efficiency but the relative value of including more small items remains the same.

4.14 Food Delivery to the Nest - Brood Size and Seasonal Effects

The feeding rate observations showed that the parent bird, especially the male, increased the number of visits made to large broods and to second broods. Since brood size did not affect food bolus size or composition (Waugh 1978, this study) this resulted in a larger quantity of food being delivered to large Swallow broods (Table 4.22) although still not sufficient to maintain the quantity delivered to each nestling (Section 3.7). The increase in feeding rate to second broods was accompanied by a decrease in the size of the bolus so the average food quantity delivered to the nest did not change markedly.

Table 4.22

Swallow and Sand Martin feeding rates

Brood	Feeding Rate	Food delivered (kcal h^{-1})	Nest days
Swallow			
Brood of 7	38.68	15.61	5
1st brood of 5	26.48	12.06	7
2nd brood of 5	32.30	11.47	12
Sand Martin			
Brood of 7	26.17	8.66	3
1st brood of 5	20.50	7.26	5
2nd brood of 5	29.27	9.12	4

The food delivered per hour was calculated from mean hourly feeding rates and mean bolus sizes.

The seasonal decrease in bolus size may be due to a change in the parent's foraging behaviour. It is possible that the time taken to search for, pursue and catch the prey was longer during the late part of the season since available prey items tend to be large and mobile then. The distance travelled to the feeding site was shorter late in the season (Section 3.10.2); it might therefore be economical to bring in a small bolus of food (Orians and Pearson 1979).

CHAPTER 5

5. DISCUSSION

5.1 Time and Energy Budgets

The daily energy requirements of homeotherms have been measured by various methods such as heart rate telemetry, the D_2O^{18} technique, time budget analysis and the measurement of food intake. These methods, used on a variety of birds, (Table 5.1) have shown that non-breeding individuals have a low daily energy budget (DEB) of about 1.5 to 3 × BMR while breeding birds increase their expenditure of energy to 3 to 6 × BMR. It was shown in section 3.11 that the British hirundines during the breeding season have a DEB ranging from 2.6 to 4.9 × BMR, which is in general agreement with the results of studies on other birds shown in Table 5.1. The methods of time budget analysis and direct measurement gave similar results for the DEB.

The daily energy budget varies with the stage of the breeding season: the DEB was highest during nestling rearing in this study. Withers (1977) considered that nest construction was the most energy demanding stage for the Cliff Swallow, Petrochelidon pyrrhonota. However, he did not take into account possible differences in flight costs at different stages. Also many pairs of Swallows repair and reuse old nests rather than build a new one, hence energy costs generally remain low.

The energy cost of incubation has been much discussed recently, since it has not been clear if the normal heat loss from the parent is sufficient to incubate the eggs (King 1973). Mertens (1978) found that the energy costs for a Great Tit while on eggs in a nest-box were 1.5 × BMR although, after more recent work, he believes costs may be higher (Mertens, in press). Walsberg and King (1978) estimated that an incubating White-crowned Sparrow *Zonotrichia leucophrys*, expends 15% less energy than a bird perching outside the nest. Biebach (1979) found that incubating and non-incubating Starlings, *Sturnus vulgaris*, had the same metabolic rate at 12-20°C. At lower temperatures the former group had metabolic rates 25-30% higher than the latter birds. Bryant and Westerterp (in press) using the D_2O^{18} technique to measure metabolism directly, obtained values of 2.72 × BMR for female and 2.93 × BMR for male House Martins for whole day metabolism during incubation, compared with 2.66 × BMR for non-breeding birds. Bryant and Gardiner (1979) showed that incubating House Martins have a metabolic rate 16% greater than a bird resting in a nestbox.

Recent evidence thus suggests that incubation is not very demanding of energy. The calculated energy budgets of Swallows and Sand Martins in this study, using measured values for variables in Kendeigh's (1963) equation (Appendix 5), support this view. The female Swallow during incubation had a DEB of 2.71 × BMR, similar to the House Martin value. While on the eggs her metabolic rate was 1.53 × BMR (23% lower than the metabolic rate of a bird perching outside). The incubating Sand Martin had a slightly higher DEB (3.23 × BMR for the female and 4.32 × BMR for the male) because of the higher flight costs. While on the eggs, however, the metabolic rate was also only 1.55 × BMR. Although Kendeigh's (1963) equation is very sensitive to temperature changes and cooling rates, if such measurements are made in the field for the species concerned (as was the case in this study - section 3.5 and Appendix 5) it can give a satisfactory estimate of the energetic requirements of incubation.

Table 5.1 Daily Energy Budgets (DEB), as Multiples of BMR, in a Variety of Avian Species

Species	Activity	Methodology	DEB (×BMR)	Source
H. rustica	Non breeding	Flight costs from i O_2 consumption	2.0 - 2.6	Keskpaik 1968
D. urbica	Daily existence	ii weight loss iii heat loss estimates iv theoretical model		
H. rustica	Breeding	D_2O^{18}, Time Budget	2.73 - 3.52	This study
R. riparia	Breeding	D_2O^{18}, Time Budget	2.77 - 4.99	This study
D. urbica	Breeding	D_2O^{18}	2.66 - 3.59	Bryant and Westerterp, in press
Petrochelidon pyrrhonota	Breeding	Time Budget	2.92 - 3.67	Withers 1977
Progne subis	Feeding Nestlings	D_2O^{18}	2.14 - 3.31	Utter and Lefebvre 1973
Spiza americana	Territorial male	Time Budget	1.41	Schwartz and Zimmerman 1971
Mimus polyglottus	Not feeding young	D_2O^{18}	1.7 - 2.1	Utter 1971
" "	Feeding young	D_2O^{18}	2.7 - 2.0	Utter 1971
Calypte anna	Immediate Postbreeding	O_2 consumption, Time Budget	3.5 - 4.7	Pearson 1954
Anas rubripes	Non-breeding	Heart rate, Time Budget	1.5 - 2.0	Wooley and Owen 1978
Oxyura maccoa	Incubating	Time Budget	2.94	Siegfried et al. 1976
Branta leucopsis	Over wintering	Food Intake	2.2	Ebbinge, Canters and Drent 1975
Strigidae spp.	Breeding	Pellet analysis	3.1 - 6.1	Graber 1962

Energy expenditures of different species during nestling feeding (as multiples of BMR) do not differ greatly despite differences in foraging method. The low-cost flight of hirundines (section 3.10) is obviously important in keeping overall costs low since they spend much of the day flying whereas the Mockingbird, *Mimus polyglottus*, with a similar DEB (Table 5.1) forages for insects primarily on the ground with occasional short flights (Utter 1971).

The proportion of time spent feeding by hirundines is similar to that reported for other species: 50-55% of the daylight hours for the Verdin (Austin 1978) in the summer, 50% for the Long-billed Marsh Wren (Verner 1965) and the Brewer's Blackbird (Verbeek 1964) and 47-67% for the Purple Martin (Utter and Lefebvre 1973). However, some species forage for considerably less time, e.g. 10% for hummingbirds (Pearson 1954, Wolf and Hainsworth 1971) and 17-21% for the male Dickcissel, *Spiza americana*, (Schartz and Zimmerman 1971) perhaps due to such factors as the calorific value, digestibility and spatial density of their food. Foraging time is reduced to about 20-40% of the day during incubation (e.g. Siegfried et al 1976, Withers 1977, Walsberg and King 1978, Bryant and Westerterp, in press, this study). In some conditions foraging time may be increased: Verdins spend 80-90% of the day foraging in September when the weather is cool (Austin 1978).

5.2.1 The Timing of Egg Laying

It was shown in section 4 that the Swallow and Sand Martin differ in their diet and in the rate at which they are able to collect food. These differences can provide an insight into the timing and level of each breeding effort in these hirundines since food abundance and quality are likely to be important in limiting the earliness of laying and brood size. However, other factors (such as photoperiod, ambient temperature, the size and age of the female and the habitat) have also been implicated (Perrins 1979).

In temperate regions the proximate stimulus ~~to~~ for breeding is usually the photoperiod (Marshall 1961) with temperature being important in determining the precise date (Löhrl 1957, Perrins 1965). This may well be the case for many passerines in which laying by birds of different ages occurs within a few days (Snow 1958, von Haartman 1967, Perrins 1970) but photoperiod alone cannot explain why hirundines lay over several weeks and may shift between years (Bryant 1975).

Ambient temperature could influence laying dates directly by changing the availability of food (this effect is discussed below) or indirectly by affecting the quantity of food required for daily maintenance (Perrins 1979). For example, O'Connor (1978) found that those Great Tit nestboxes in which females laid early provided better insulation against low ambient temperatures than nestboxes in which birds bred late. Daily energy requirements may be reduced in a warm nestbox so gonad and subsequently egg development could start earlier. The Sand Martin may well benefit from the constant temperature and insulation of the burrow (Section 3.5.3) but if this effect was very important one would also expect the House Martin to lay before the Swallow since it has an enclosed and, therefore, better insulated nest.

The size of the bird affects laying dates in titmice - small species lay, in order of body size, before the larger Great Tit (Dunn 1976) and small female Great Tits lay before large individuals

(Jones 1973). A small bird may need less food than a large one hence may start laying at a lower level of food abundance. However, the present study has shown that the Sand Martin has a daily energy budget as high as that of the larger Swallow (Table 3.27). In addition, the House Martin, although similar in size to the Swallow, is the last of the hirundines to lay. So size has little, if any, effect on laying dates in these birds. The age of the female, however, does have an effect since older individuals generally start to lay early (Bryant 1975, 1979).

Laying dates in birds also differ between geographical areas and habitats. For example, hirundines lay several days earlier in southern than in northern Britain (section 3.4.3) and Great Tits lay earlier in gardens than in nearby woodland (Perrins 1979). This effect is probably due to differences in climate and food supply both over large areas and between habitats.

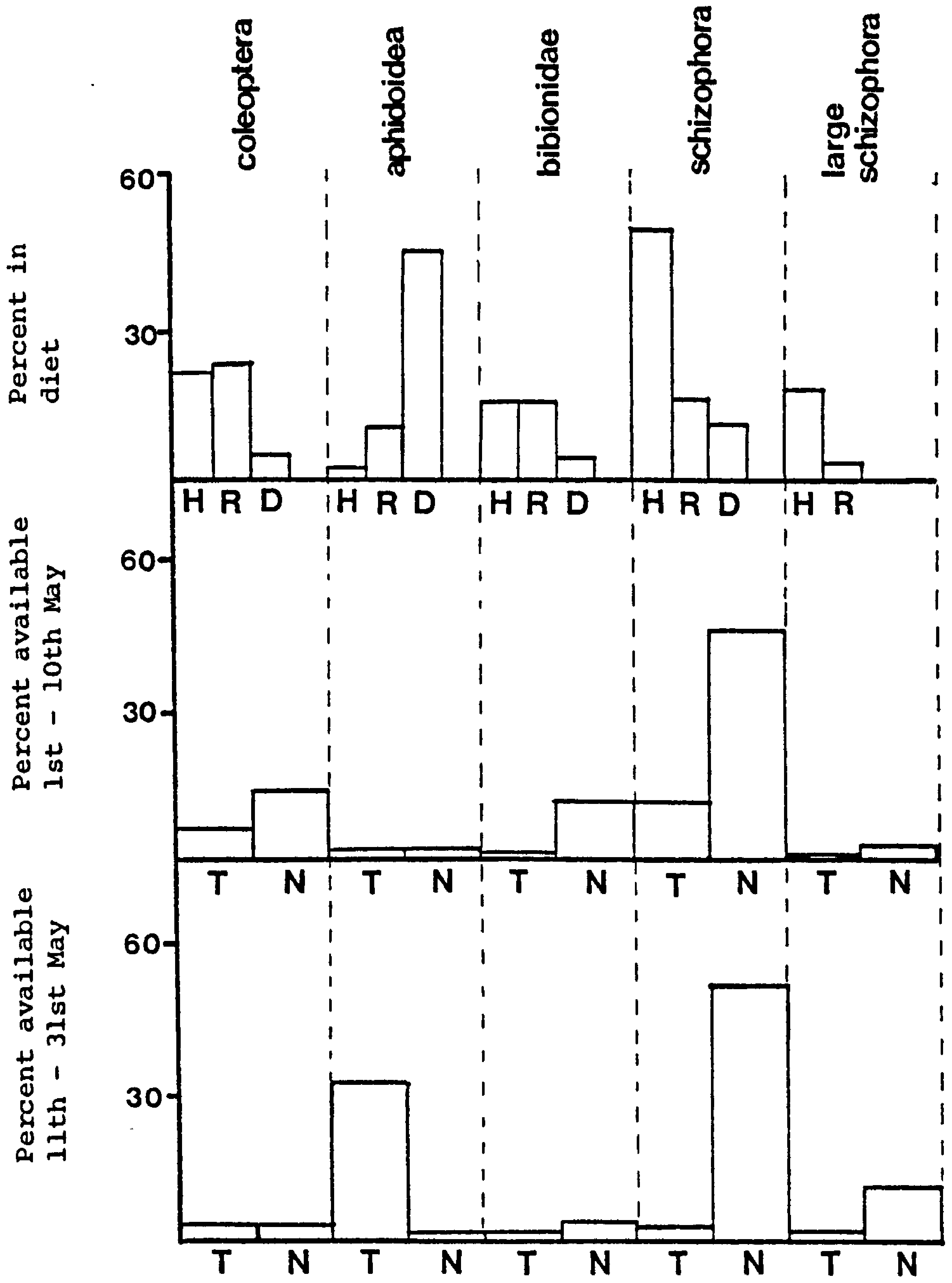
Although several factors thus affect the initiation of laying in birds, the food supply is of particular importance. Perrins (1970) suggested that food shortage would delay laying in Great Tits. The importance of the food supply in the timing of breeding has been demonstrated for the House Martin by Bryant (1972, 1975). The peak in the House Martin's reproductive output coincides with the period of greatest food abundance but in all three hirundines in Britain there is a period between first and second broods when a high food abundance is not being fully utilised. Bryant (1972) suggested that this, by chance, allowed fledglings to feed with minimal competition from adults. Early fledged birds are likely to have an enhanced survival rate (e.g. Perrins 1965) hence these young House Martins may be in the nest when food is occasionally scarce but may fledge at the time of high food availability. Bryant (1972, 1975) also suggested that daily aerial food abundance and stability, particularly the availability of aphids was important in initiating laying in House Martins. Thus the earliest laying pairs may be inhibited from breeding by a proximate factor such as daylength until the food supply becomes more stable towards the middle of May, so there is a low probability of food shortage during egg laying and incubation. Food abundance, quality and stability are also likely to be important to Swallows and Sand Martins at the start of laying.

The diets of egg laying hirundines differ in the size and type of prey taken (Tables 4.16 and 4.17). The Sand Martin feeds on small to medium sized Coleoptera, Bibionidae and Schizophora which are available at the beginning of May (Figure 5.1) so the Sand Martin can start to lay early. Large items become more abundant during May (section 2.5.1) so the Swallow may need to wait until later in May to start laying since it is more dependent on large items, especially Schizophora (Figure 5.1). The House Martin must wait until aphids or other comparable, small insects are available in the second half of May (Figure 5.1).

Besides the food quality and average level, the predictability of feeding conditions may also affect the timing of laying. This predictability may be best measured in terms of ambient temperatures (T°, see Appendix 4) which correlate well with the foraging rates (rate of assimilable energy gain) of the Sand Martin and Swallow (Figure 4.14). Although other variables such as the available prey size may correlate better with foraging rates (section 4.12) these variables are in turn correlated with temperature. Ambient temperature can thus be used as a common variable for both species.

Figure 5.1

The percentage occurrence of different insect types in the diet of egg laying Swallows (H) Sand Martins (R) and House Martins (D) in May and in suction trap (T) and net (N) samples early and late in May. Large Schizophora are ≥ 1.5 mg dry weight. House Martin data are from Bryant (1975).



Percent in diet
Percent available 1st - 10th May
Percent available 11th - 31st May
60
30
coleoptera
aphidoidea
bibionidae
schizophora
large schizophora
H R D
H R D
H R D
H R D
H R
T N
T N
T N
T N
T N

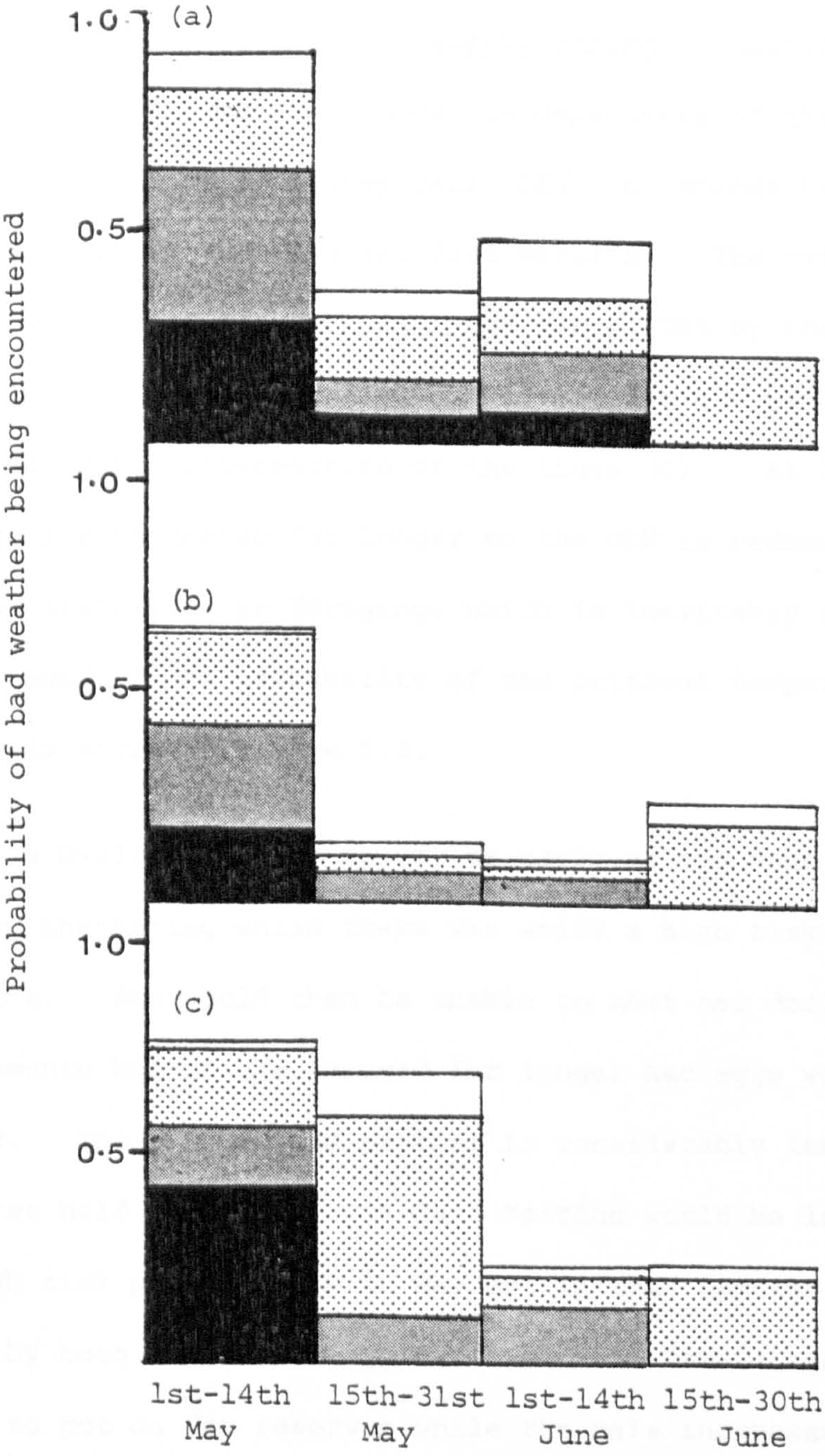
It also correlates with incubation intensity (see below) and daily records are available for predictive purposes. (It should be noted here that the foraging rate was measured only for adults feeding nestlings but since the diets are similar during the egg laying and nestling feeding stages, it can be assumed that the measured foraging rate also represents that of self feeding adults early in the season. Time spent travelling between the nest site and feeding site was excluded from the foraging rates calculated for self-feeding adults.)

During May the egg laying female has about 16 hours of day light at stirling in which to feed. If she were feeding all day the Swallow must have a foraging rate of at least 0.029 kcal min^{-1} and the Sand Martin must have a foraging rate of 0.034 kcal min^{-1} to meet her daily energy requirements. In practice the lower limit is likely to be higher to allow some time for the female to search for calcareous grit to form egg shells and for maintenance activities such as preening. The critical temperatures at which the foraging rate falls lower than these values are 8.6°C for the Swallow and 10.3°C for the Sand Martin, a little higher if it is also wet. The risk of the critical temperature being encountered during egg laying is shown in Figure 5.2. Maximum daily temperatures were used to investigate this risk, but since temperatures over most of the day are likely to be lower than the maximum, critical temperatures were assumed to be 1°C higher than those values given above. The risk of the Swallow meeting bad conditions is usually low in May whereas the risk for the Sand Martin is usually high. Hence, some factor additional to the predictability of the food supply during egg laying seems to be involved in determining the timing of laying.

Figure 5.2

Figure 5.2 shows the probability of bad weather (see text) being encountered by the Swallow during egg laying (black zone) and incubation (stippled zone) and by the Sand Martin during egg laying (grey zone) and incubation (unshaded zone) (a) in 1977, (b) in 1978 and (c) in 1979.

Probabilities are shown for four periods during 1st brood laying and incubation.


Probability of bad weather being encountered
1·0
0·5
(a)
1·0
0·5
(b)
1·0
0·5
(c)
1st-14th May
15th-31st May
1st-14th June
15th-30th June

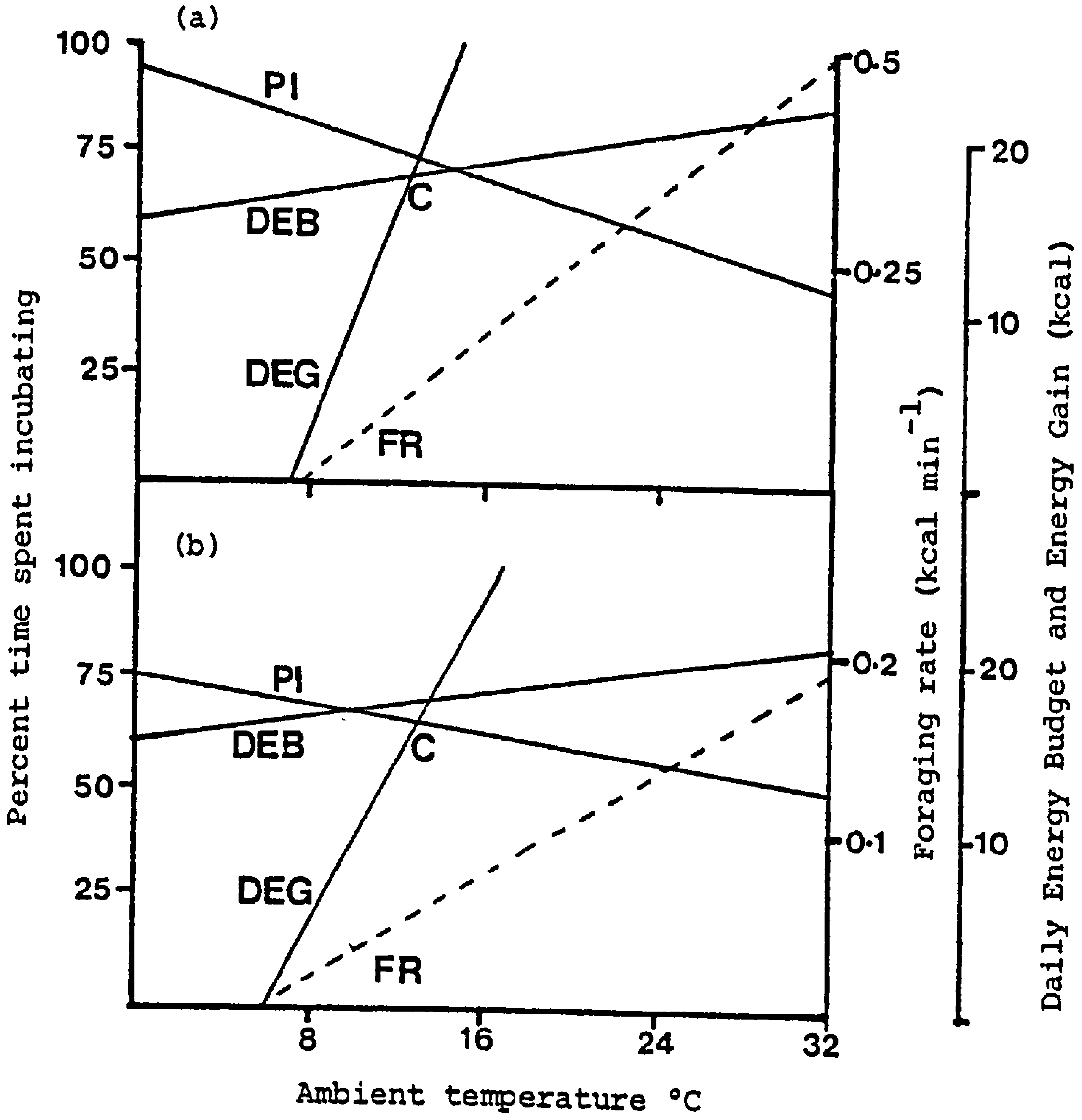
The stability of the food supply during incubation could also be important. Figure 5.3 shows the dependence of the daily energy budget (DEB) and daily energy gain (DEG) on ambient temperatures for incubating female Swallows and Sand Martins. The critical temperature at which the energy expenditure can be met by the energy intake (12.4°C for the Swallow and 13.2°C for the Sand Martin) is indicated by the intersection of the lines (C). At low temperatures the eggs are incubated for longer so the DEB is reduced. However, the time available for foraging, which is inevitably at a low rate, is shortened. The probability of the critical temperature + 1 being reached is shown in Figure 5.2.

If a Swallow started to lay as early as the Sand Martin she would be incubating while there was still a high risk of bad weather occurring. She would then be unable to meet her daily energy requirements but if she foraged for longer her eggs would risk being chilled. The risk of bad weather is considerably lessened after the first half of May. Some Sand Martins would be incubating during the high risk period early in May but in this species incubation is shared by both sexes. In good weather the female can stay away longer to put on fat reserves while the male increases the time he spends on the eggs (Figure 3.6). The male also increases his share of the incubation if the previous day's food supply was poor (Figure 3.7) allowing the female to replace any weight loss.

The importance of good feeding conditions during incubation for the Swallow is suggested by the pattern of laying dates in the present study. In 1977, seven out of nine pairs laid in May, in 1979 only one in nine pairs ($\chi^2 = 5.14$, $p < 0.05$). The risk for egg laying females in late May was low in both years but the risk

Figure 5.3

The dependence of the daily energy budget (DEB) and daily assimilable energy intake (DEG) of (a) Swallow females and (b) Sand Martin females on ambient temperatures during incubation. The incubation intensity (PI) decreases with increasing temperature. The foraging rate (FR) increases with increasing temperature. C indicates the temperature below which the female's daily energy intake could not match the required energy budget.


(a)
100
75
50
25
PI
DEB
C
DEG
FR
0·5
0·25
20
10
(b)
100
75
50
25
PI
DEB
C
DEG
FR
0·2
0·1
20
10
8
16
24
32
Percent time spent incubating
Foraging rate (kcal min^{-1})
Daily Energy Budget and Energy Gain (kcal)
Ambient temperature °C

for incubating birds in 1979 was 1.9 times that in 1977, (Figure 5.2).

The Sand Martin can thus start laying early because (1) it feeds on small to medium sized insects during egg laying which are available early in May and which require little energy to be expended in their capture; (2) it does not need to wait for a stable supply of small, swarming insects such as aphids; and (3) incubation is shared between the male and female so a pair could risk incubating in bad weather. The Swallow lays a week or two later since (1) it must wait for large items to become more abundant and stable and (2) only the female incubates so she cannot risk incubating in bad weather. The House Martin lays from mid-May onwards since it must wait until there is a stable supply of aphids or similar, abundant, small, swarming insects to avoid the consequences of laying under adverse conditions (Bryant 1975, 1979). Although both sexes incubate, the foraging rate of the House Martin is low compared to that of the Sand Martin, so late laying leads to a lowered risk for the House Martin. Feeding of the female by the male during incubation (as in the Great Tit, Royama 1966) would reduce the risk of bad conditions adversely affecting the female. Such feeding, however, does not occur in the Swallow or, incidentally the House Martin (Bryant 1979 and pers. comm.).

Selection is likely to be strong for females to lay as early as possible (Perrins 1970), within limits imposed by food abundance and quality. However, individual variation in the timing of laying is still to be expected. Birds of different ages, size or abilities may start at different levels of food abundance and stability. A young bird, for instance, may lay late in the season and thereby take few risks whereas an old bird with a low residual reproductive value (Pianka and Parker 1975) may lay early and risk encountering bad weather.

Although several factors clearly influence laying dates, this study has supported Bryant's (1975) hypothesis that birds delay laying until the food supply has reached a high level of abundance, (following Perrins (1970)), quality and stability and has shown in addition that for the Swallow a stable food supply is needed during the critical stage of first clutch incubation and is the principal factor limiting early laying in this species.

5.2.2 Productivity

The rate at which birds collect food might also be expected to limit the number of nestlings they can rear as well as affecting the date of laying. For example, there is a seasonal decline in clutch size in hirundines (Bryant 1975, table 3.4) paralleling the reduction in the time available for feeding the nestlings.

Large clutches of House Martins are the most productive of fledglings (Bryant 1975). This is also the case for the Swallow and Sand Martin (Mizuta 1963, Al-Rawy and Georg 1966, Snapp 1973) and is in conformity with the limited results obtained in this study (Appendix 6). However, large broods may be at a disadvantage if the parents are unable to meet their energetic and nutritional requirements (Lack 1947). Perrins (1965) put forward the view that since young in large broods of Great Tits suffer proportionally greater mortality than those in small broods selection acted against large clutch sizes. Great Tits from large broods may survive less well than those from small broods because they are lighter at the time of fledging. Brood size also affects nestling weights in hirundines: the effect is least in the Swallow and greatest in the House Martin (Snapp 1973, Bryant 1978b, this study - section 2.9.1). Hence, the parents may be unable to adequately feed larger than natural broods.

The time investment required to feed broods of different sizes is shown in Figure 5.4. In good feeding conditions both the Swallow and Sand Martin can adequately feed even a brood of six or seven. It was shown in section 4.12 that Swallows have high foraging efficiencies and they could theoretically collect more than enough food for the brood and themselves. Some extra food is used to lay down fat for future use when food is scarce, but the parents still have sufficient time to either rear a larger brood or rear a normal sized brood with a faster growth rate.

Faster nestling growth may not be possible because of limits to the rates of digestion and growth processes. Ricklefs (1979) suggested that overall body growth was determined by the growth of the most mature, hence slowest growing, component. There may be such an ultimate limit on growth rates but the growth pattern of hirundines is clearly influenced by the food supply. The growth of House Martins is correlated with aerial food abundance and the fledging period increases with brood size (Bryant 1973, 1975) suggesting that food is limiting growth. A flexible growth pattern characterised by fat storage during good conditions is better suited to an unpredictable food supply than a fast, sustained growth rate. The reason for hirundines not having larger broods or faster growing nestlings may alternatively be sought in the variable nature of the food supply.

Figure 5.4 shows that in poor feeding conditions both Swallows and Sand Martins would have difficulty in adequately feeding even a normal brood of four or five, especially if the day length were short. During this study the observed foraging rate (rate of assimilable energy intake) fell to or below the critical level for feeding a brood of five (0.05 kcal min^{-1} including travel time to and from the feeding site - Figure 5.4) on 31% of days (10 out of 32) for the Swallow and on 65% of days (22 out of 34) for the Sand Martin.

Brood size may thus be limited by the risk of bad weather depressing the foraging rate to such a low level that the demands of the brood cannot be met. This risk was twice as great during the study for the Sand Martin as for the Swallow. The number of hours of daylight available for feeding is an important factor. The day length in Stirling in August varies from about 16 hours to about 14.5 hours so the parents would not have time to rear a brood of five if conditions were poor (Figure 5.4). Broods of six therefore only occur early in the season and brood size decreases during the summer.

Nestling mortality is often associated with bad weather and food shortage either acting directly through starvation of a nestling or through desertion of the parents. Rheinwald (1971) recorded 48% mortality in House Martins in one week of bad weather in Germany. Mason (1953) noted a 65% mortality in Swallows in cold, wet weather. Bryant (1975) found that House Martin mortality within first broods was correlated with aerial insect abundance. Hence in bad conditions hirundines are evidently sometimes unable to meet the demands of normal brood sizes.

Figure 5.4

The time investment in broods of different sizes (age 9-21 days) (the time needed to feed one adult and half the brood).

H - Swallow

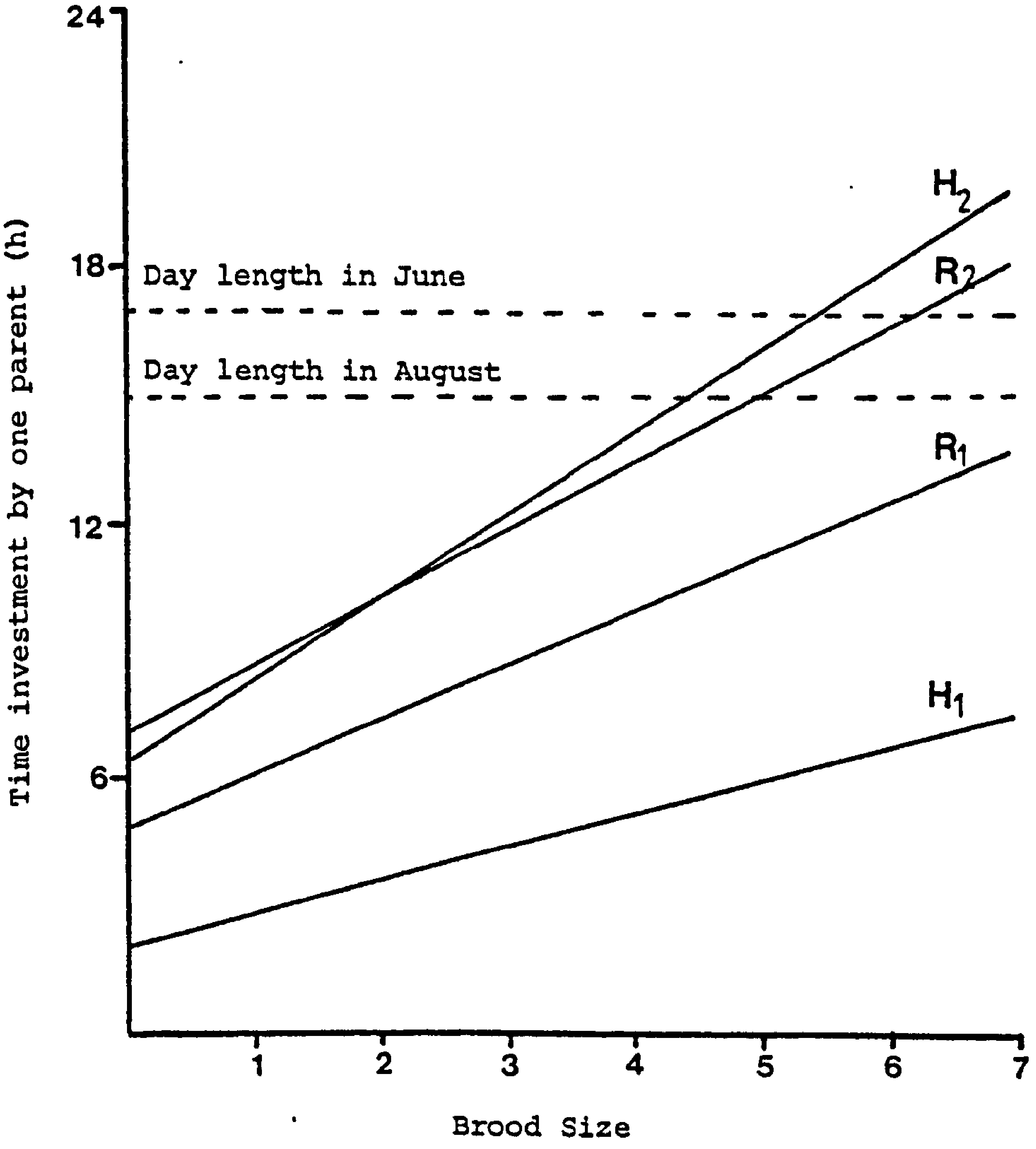
R - Sand Martin

1 - in good weather - foraging rate 0.14 kcal min^{-1} (Swallow), 0.07 kcal min^{-1} (Sand Martin)

2 - in bad weather - foraging rate = 0.05 kcal min^{-1} (Swallow), 0.05 kcal min^{-1} (Sand Martin)

These foraging rates include travel time and are means for good and bad feeding conditions. The dashed lines indicate average day lengths in June and August (1st brood and 2nd brood period).

Nestling energy requirements are calculated (for mean brood weights) from equations 1 and 2 on section 2. Adult requirements are from Table 3.27.


24
18
12
6
Time investment by one parent (h)
Day length in June
Day length in August
H_2
R_2
R_1
H_1
1
2
3
4
5
6
7
Brood Size

In general, however, nestling mortality in hirundines is low compared to most temperate passerines (Lack 1954, Ricklefs 1969, Bryant 1975). Bryant (1975) found that 5.8% of hatchling House Martins died before fledging. Adams (1957) shows that nestling mortality in Swallows was only 4.2% and Asbirk (1976) found that 12.1% of nestling Sand Martins died before fledging. Most of the nestling mortality in this study involved whole broods (9/13 deaths of Swallows and 14/22 deaths of Sand Martins) through predation, desertion (at times following investigator disturbance) or some other unknown cause. Mortality of young nestlings may also be due to poor egg quality, and hence hatchling quality, resulting from a food scarcity during egg laying (Bryant 1978b). Thus, mortality in the nest, due to the parents' inability to feed a brood, is not high, but long-term brood survival may still be affected by low nestling weights in large broods (see above) resulting from a reduced food intake.

The age, size and ability of the parents are also likely to play a role in determining the size of the brood (Bryant 1975, 1979). High quality pairs may be able to rear six nestlings under the same conditions as other pairs that only manage to rear four. Hence, it may be expected that each pair is usually able to adequately feed only its own brood size.

The reproductive effort, in terms of time and energy investment required to rear nestlings, whether influenced by the available day length and feeding conditions or determined by the 'quality' of the parents, is thus seen to be a major force in determining the upper level of brood size. Further analysis is required, however, to evaluate more precisely the constraints on adults of different quality.

5.3 Parental Investment

The present study has shown that male Sand Martins increase their feeding rate for large broods and for second broods to a greater extent than do the females. Hails (1977) and Hails and Bryant (1979) showed that House Martin males similarly increased their energy expenditure and feeding rates for large broods and for second broods; whereas the females' energy expenditure did not change and they increased their feeding rates to a lesser extent than the males.

Greater parental investment generally involves a cost in time and energy (although mobbing predators may involve a small time and energy cost but a high mortality risk). More time invested in reproduction reduces that available for activities concerned with self-maintenance. Reproductive costs are closely linked to the optimal allocation of time and to optimal foraging behaviour (Pianka 1976). The investment in a single brood must thus be balanced against the individual's need to maximise its lifetime contribution to the gene pool.

Trivers (1972) discussed the possible levels of investment by males and females with different reproductive strategies. One of his main points was that for the individual which has invested least in the offspring, desertion is a viable strategy provided its mate can rear those offspring. This has been criticised by Dawkins and Carlisle (1976) and Maynard Smith (1977) since future expectations of reproducing should be taken into account in deciding optimal strategies. In hirundines the level of investment by each sex changes during the breeding season, hence the likelihood of desertion also changes.

Burrowing and nestbuilding are shared evenly between the sexes. An early investment by the male, and the resulting long courtship period during burrowing or nest building may serve to assure the female that the male is not committed to another partner and thereby confirm the pair bond. The costs of egg laying, however, are borne by the female. The male protects his own interests by guarding his mate closely to prevent (a) other males mating promiscuously with her and (b) her desertion to another male (Beecher and Beecher 1979, this study).

Up to the time of incubation then, investment by the male is at a relatively low level. During incubation there is a marked difference between the Swallow and the Sand Martin since the male of the former does not incubate and the male of the latter does. In many species of bird incubation is solely or mainly by the female while the male may guard the nest site and feed the female. In the Hirundinidae the female does most or all of the incubation in the primitive genera which are solitary or nest in small groups rather than colonies and which make simple nests or use old burrows and holes (Mayr and Bond 1942) Table 5.2. Time investment in incubation by the male is high in relatively few species (Table 5.2). An investment in incubation by the male could evolve if the female were unable to incubate alone, especially if she were to desert through loss of condition. It is noteworthy that of the British aerial insectivores the sexes share incubation in those species (Swift and Martins) which have low foraging efficiencies (Koskimies 1950, Bryant and Westerterp 1978, this study, section 4.12).

The male increases his time investment once the nestlings have hatched and need feeding. However, he seems to have a more flexible

Table 5.2 Nesting Behaviour of the Hirundinidae

Species	Incubation by male	Incubation by female	Coloniality	Type of Nesting	Source
Tachycineta bicolor	+	+++	solitary or small groups	uses old hole	Kuerzi 1941
T. thallassina	0	++++	small groups	uses old hole	Bent 1942
Progne subis	0	++++	solitary or groups	uses old hole	Allen and Nice 1942
Stelgidopteryx ruficollis	+	+++	solitary or small groups	uses old burrow	Lunk 1962
Riparia riparia	++	++	small or large colonies	enclosed mud nest	Stoner 1936 this study
Hirundo atrocaerulea	0	++++	small groups	open mud nest	Snell 1963
H. rupestris	+	+++	small groups	open mud nest	Prenn 1937
H. rustica erythrogaster	+	+++	small groups	open mud nest	Kendeigh 1952
H. r. rustica	0	++++	small groups	open mud nest	this study
H. smithii	0	++++	solitary	open mud nest	Moreau 1939b
Petrochelidon pyrrhonota	++	++	large colonies	enclosed mud nest	Samuel 1971
Delichon urbica	++	++	small or large colonies	enclosed mud nest	Lind 1960
Psalidoprocne pristoptera	0	++++	solitary	open mud nest	Moreau 1940

Key: 0 no incubation
+ little incubation → ++++ all the incubation

Full details of nesting behaviour are unknown for most species of hirundines; these species are excluded from the table.

Artificial nest sites may cause otherwise solitary species (for example, *Progne subis*) to group together. However, these are not classed as colonies, (see Appendix 4).

pattern of investment than the female. The male increases his feeding rate for large broods and for second broods and decreases it for small ones whereas the female tends to feed at a more constant rate. Purchon (1948) also demonstrated the importance of the male Swallow's feeding rate in determining breeding success. Similarly, the amount of food delivered to the nest by male Common and Arctic Terns (Sterna hirundo, S. paradisea) correlates with total brood weights, weight of the last chick to hatch and fledging success of the last chick (Nisbet 1973).

The differences between the sexes may in part be due to past investment and in part to future reproductive potential. The female, having invested more time and energy early on, may have suffered a loss of condition. A further high investment, such as feeding a large brood or a second brood, may result in a high risk of mortality. The male, with a low initial investment, is less at risk when he devotes more time and energy to the nestlings.

However, sometimes the male invests less heavily in the nestlings than does the female (e.g. to small broods and in bad weather, section 3.7). Males, in these circumstances, are presumably more likely to desert than females, not because of a smaller cumulative investment, but because they may be more likely to obtain another mate or may, at least, fertilise another female. There is, furthermore, the possibility that the new female would provide a larger clutch than the deserted one. It would be possible for a male with a small brood to desert because its mate would be able to rear a brood of two alone for instance.

It has been shown (section 3.7) that the difference in investment between the sexes when feeding nestlings is greatest in the Sand

Martin. This may be due to the colonial nature of this species and the consequent increased opportunities for remating or mating promiscuously if a bird deserts. It may also be possible for a deserted female to attract a second partner because of the presence of lone, unmated males in the colony. If a lone male helps to rear her brood he can then mate with her and so rear his own nestlings. Otherwise he might have no opportunity to breed that season. There are not usually lone females in the colony so there are few possibilities of that nature for males. However, he can fertilise or steal females, thus spreading his genes promiscuously. Trivers (1972) argued that in monogamous birds the female should remain so but the male should behave promiscuously where possible.

Desertion and remating may occur at any stage of the breeding cycle. Indeed, the possibilities of attracting a mate would be higher during the early stages, for instance during burrowing when the pair bond is still weak. During incubation the male is again more likely to desert than the female since his commitment towards incubating the clutch is lower (section 3.5). This rarely occurs, however, presumably because his chances of remating with a high quality female are low.

A lowered investment and ultimately desertion may come about not as a means of avoiding parental responsibilities or gaining greater reproductive success but as a protection of the bird's self interest at the expense of the brood. Reproductive output over an individual's lifetime may even be maximised by the sacrifice of some or all offspring in a particular breeding attempt if, for example, there is a high risk of starvation or predation for the adult continuing to feed young.

The need for self protection can, through evolution, lead to a buffering of the brood against food shortage or, in the shorter term, to temporary neglect of the brood or to permanent desertion. House Martin eggs are able to withstand chilling for more than a day (D.M. Bryant, pers. comm.), nestlings have a fat store on which they can draw (Bryant and Gardiner 1979, this study - section 2.9), and brood reduction, to protect surviving nestlings, may occur progressively if food shortage persists (O'Connor 1977). The parents may thus maintain their own body condition with minimal harm to the offspring. These buffer effects are most marked in the House Martin and least in the Swallow reflecting the ability of the parents to forage efficiently (Bryant and Westerterp 1978, Turner and Bryant 1979). A long period of food shortage might, however, lead to further neglect of the brood with consequent weight losses. The nestling period might be prolonged or the nestlings might fledge at a lower than average weight. Desertion may occur in very bad conditions. Brood size may be important here since the parents could continue to feed two or three nestlings at an adequate rate but not a brood of twice that size.

Besides the prevailing feeding conditions, the level of an individual's investment must also be dependent on its experience and ability and its future reproductive potential (Pianka and Parker 1975). An old pair with a brood of five, for example, is more likely to be able to rear a brood of seven than a young pair with an initial brood of three. Old females may also be more willing and capable of investing in a current brood than a yearling. In support of this, Bryant (1979) showed no link between brood size and adult mortality but weight gains in females with experimentally reduced broods suggested a link with ability.

5.4.1 Hirundines as Optimal Foragers

It is usually assumed in optimal foraging studies that the predator is maximising its net rate of energy intake (Pyke, Pulliam and Charnov 1977). This seems to be a reasonable assumption for hirundines in the breeding season since much of their time is spent collecting food for nestling growth. Some studies, however, have suggested that other factors such as nutrients (Pulliam 1975, Belovsky in Pyke et al 1977) or predation risk (Milinski 1979) might be important. Predation risk for hirundines is discussed below; here nutrient demand will be considered.

The requirements of nestling and adult Swallows and Sand Martins have been described in sections 2.9 and 3.11. A knowledge of these requirements and of the rate of the parents' collection of food can be used to investigate whether the parents should maximise their net rate of energy intake or their net rate of nutrient intake during nestling rearing and egg laying.

During egg laying, protein, SAA and energy can usually be collected quickly (Figure 5.5). The limiting factor is calcium which is difficult to obtain in sufficient quantities even in good weather. There may be some selection for calcium-rich prey: Coleoptera and Bibionidae, which have above average calcium concentrations (Appendix 2B), are both taken in substantial numbers by Swallows and Sand Martins (Table 4.16). However, prey capture ~~selection~~ at this time may also be a reflection of what is most available. House Martins take mainly aphids early in the season even though the larger Bibionids are available and yet Bibionids are taken in the autumn (Bryant 1975). Aphids also have a fairly high calcium content but the diet would still have to be supplemented with

Figure 5.5

The time which would have to be taken by an egg laying female to collect sufficient energy and nutrients for herself and one egg. (a) Swallow (b) Sand Martin

DEB = Daily Energy Budget - (22.1 kcal for the Swallow
24.8 kcal for the Sand Martin)

C = Calcium

N = Nitrogen

S = Sulphur

Foraging rate: Swallow - 0.18 kcal $\min^{-1}$ in good weather
- 0.06 kcal $\min^{-1}$ in bad weather

Sand Martin
- 0.18 kcal $\min^{-1}$ in good weather
- 0.06 kcal $\min^{-1}$ in bad weather

The foraging rates exclude time spent travelling to and from the feeding site.

Figure 5.6

The time which would have to be taken by one adult to collect sufficient energy and nutrients for itself and half of a brood of 5 (age 9-21 days).

(a) Swallow (b) Sand Martin

A = Assimilation (calculated respiration + production)
DEB = Daily Energy Budget
C = Calcium
N = Nitrogen
S = Sulphur

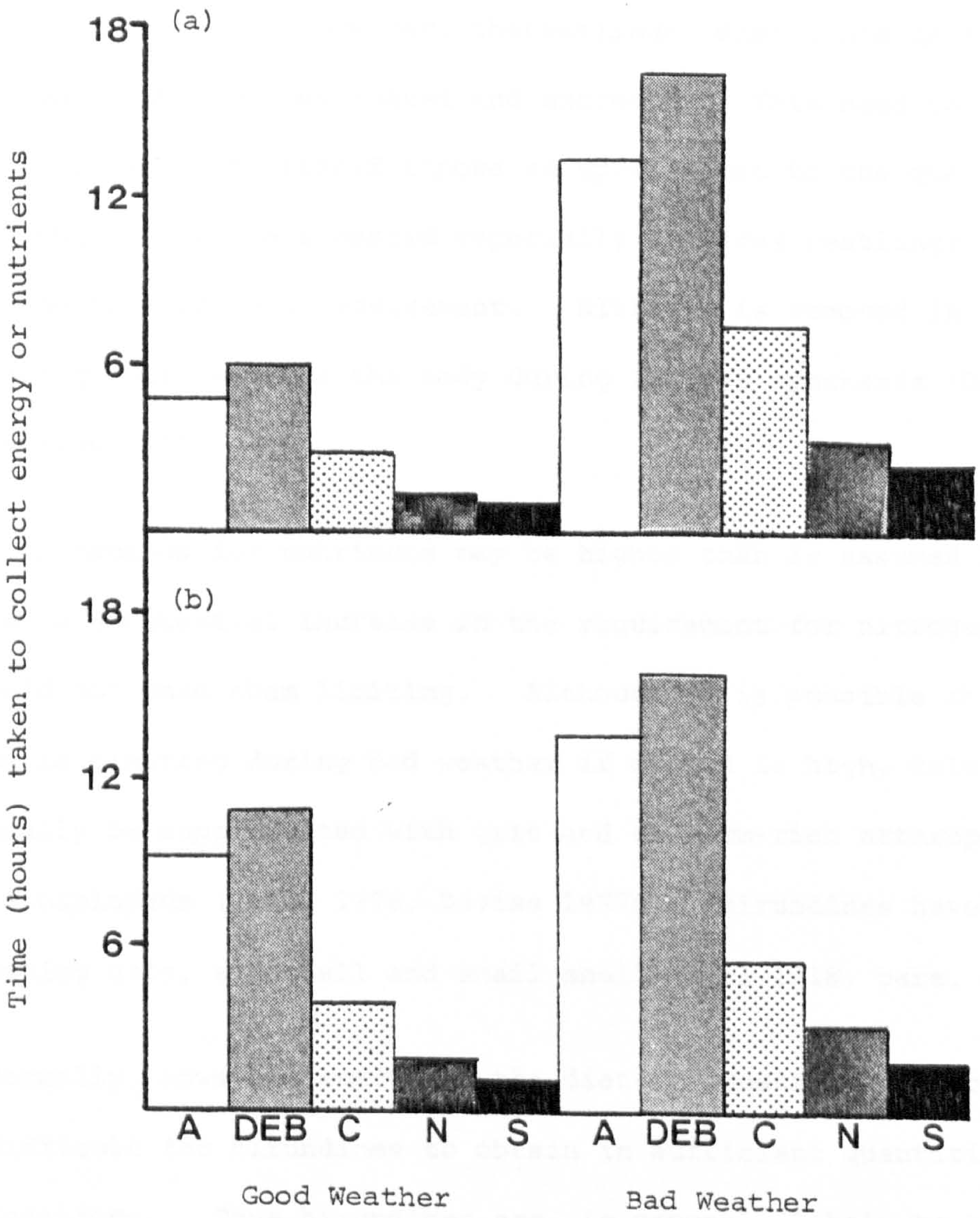
Adult DEB =

Swallow - 22.84 kcal in good weather
- 18.88 kcal in bad weather

Sand Martin - 25.50 kcal in good weather
- 20.47 kcal in bad weather

Nestling DEB calculated from equations given in Section 2.

Foraging rates as in Figure 5.5 for self feeding adults.


(a)
(b)
18
12
6
18
12
6
Time (hours) taken to collect energy or nutrients
A
DEB
C
N
S
A
DEB
C
N
S
Good Weather
Bad Weather

growth. The demand for protein would thus be increased under such conditions. Normally, however, thenestlings' diet contains excess protein which must be deaminated and excreted. This need to remove excess nitrogen might itself impose an upper limit to the quantity of protein which could be ingested especially in older nestlings where SAA is the main protein requirement. Nitrogen is removed in increased quantities from the body during feather synthesis (Dolnik and Gavrilov 1979).

Peak demands for nutrients may be higher than is assumed here. Even so, a substantial increase in the requirement for nitrogen and SAA would not make them limiting. Although it is possible that calcium is limiting during bad weather if demand is high, calcium can usually be supplemented with grit and calcium-rich arthropods such as Diplopods (Jones 1976, Davies 1977b); hirundines have been seen eating grit, egg shell and snail shells (Beal 1918, pers. obs.).

Normally, however, energy is the dietary constituent which is most difficult for hirundines to obtain in sufficient quantities in all conditions. Thus hirundines are, in general, likely to be maximising their rate of energy collection which will normally lead to other nutrient demands being met. Although more accurate knowledge of the peak demands for nutrients in hirundines is desirable, energy is clearly of major importance; this has only been assumed in most optimal foraging studies but in this study energy is demonstrated to be the currency whose intake rate is being maximised by hirundines.

5.4.2 Time Allocation

The time budget analysis in this study has revealed that parent hirundines spend much of their time feeding. However, it has also been clear that some time must be allocated to other activities some of which are compatible, some incompatible with foraging. Decisions must thus be made about the optimal allocation of time (Katz 1974).

The behaviour of the bird while foraging may be constrained by the requirements of predator detection and nest and mate guarding:

1. Predation Risk. When the parent is away foraging both it and the nestlings face the risk of predation (from raptors, cats, rats and weasels, Mead and Pepler 1975, this study). The structure and positioning of most hirundine nests make them fairly secure from predation. Therefore the parent may be most at risk when it is feeding far from the nest site or is feeding for longer than usual because of the high demands of a large brood. The risk may be less for a flocking bird, such as the Sand Martin, because of the high possibility of detecting a predator and the protection afforded by large numbers (section 5.5). The Swallow forages singly or as a pair so may face greater risks. Hence foraging behaviour may be influenced by the need to remain near the nest. The rate of energy intake may be low because the individual is watching for predators (Milinski 1979). A parent may also take a smaller than optimal food bolus because of the need to return quickly to the nest site (section 5.4.4).

2. Nest and Mate Guarding. During the later stages of nest building and during egg laying there are frequent chases and fights near and around the nest sites of the Swallow and Sand Martin (sections 3.3 and 3.4). Males of both species keep close to their females

especially when the latter are ready to copulate (Beecher and Beecher 1979, pers. obs.). These restrictions on movement may interfere with normal foraging behaviour.

It may seem reasonable that the best strategy would be to obtain the required daily energy in as short a time as possible and to remain by the nest for the rest of the day. However, there are two reasons why this may not be possible. Firstly, a digestive bottleneck (Kenward and Sibly 1977) may prevent the predator ingesting a large quantity of food. Secondly, watching for predators and for opportunities to steal other nest material or a mate and guarding one's own nest site and mate may lower energy intake rate and extend foraging time. In poor feeding conditions more time was spent foraging so less time was available for chasing and aggressive interactions (Table 3.2).

Foraging behaviour must be matched to the most demanding periods for the bird e.g. feeding nestlings or feeding in poor conditions. A male Swallow, for instance, before the nestling feeding stage, with a daily energy requirement of about 21 kcal is flying, apparently foraging, for nine hours giving a low energy intake rate of 0.04 kcal min^{-1} even in fairly good conditions. Extra time is needed for building up fat reserves for use overnight and in subsequent poor conditions but time is still available for increased alertness by the bird. Hence, when demands are low the bird may forage less actively.

Some activities, such as preening, nest building or brooding are not compatible with feeding, but are in themselves vital behaviours. It is thus frequently necessary to maximise energy gain over the short term in order to maximise fitness over the long term (MacArthur and Pianka 1966, Charnov 1973). Each activity must be given a priority which may change with time. The greatest priority is probably usually given to self feeding and thereby to self survival. In bad weather, hirundines increase the time allocated to this activity decreasing the time available for feeding the nestlings (Bryant and Westerterp 1979, this study - Section 3.7).

Recent analyses have been made of optimal switching behaviour (Sibly and McFarland 1976, McFarland 1977) but no field study has yet been completed.

5.4.3 The Foraging Strategy

The question of whether or not Swallows forage optimally can be examined in thelight of the results given in section 4.11: prey items are selected primarily by size; proportionately more large prey are included in the diet as their abundance increases and the proportion of small items taken depends on their relative abundance but not on their absolute abundance. The Swallow is of particular interest since it can provide evidence of the normal feeding behaviour of a predator in the wild. There have been few field studies on optimal foraging (Goss Custard 1977a, b, c, Davies 1977a, b, Waugh 1978) because of the difficulties of observation and of measuring the available prey and the prey eaten.

Many theoretical and laboratory studies, however, form a basis for comparison with field data. These studies (reviewed in Pyke, Pulliam and Charnov 1977 and Krebs in Krebs and Davies 1978) have been concerned with the decisions which a predator must take in order to maximise its net intake rate of energy (or of some other 'currency'). The predator must decide (a) which prey items to eat, (b) which patch to visit, (c) how long to stay in the patch and (d) which route to take in the patch. Several models have been developed which predict the animal's behaviour. Optimal diet models, for instance, have three general properties: (1) Food items are ranked according to their food value and associated handling time. The probability of an item being eaten depends only on the absolute abundance of higher ranking items. (2) The predator becomes more specialised as food becomes more abundant. (3) An item is completely included or completely excluded from the diet (MacArthur and Pianka 1966, Schoener 1971, Pulliam 1974, Werner and Hall 1974).

In some respects Swallows do conform to these theoretical ideas. Firstly, hirundines select prey items primarily by size (Bryant 1973, Figures 4.7, 4.8); large items providing more calories than small ones. However, the rank of some exceptionally large items at the limit of acceptability such as moths and bees may be lowered by a long handling time; hence, few of these items are generally taken. A variety of other predators have also been found to rank prey in this way, including shore crabs, <u>Carcinus maenas</u> (Elner and Hughes 1978) and Pied Wagtails (Davies 1977a). Secondly, the inclusion of an item in the Swallow diet indeed depended on the absolute abundance of large items not of the small ones (Figure 4.9) confirming Waugh's (1978) findings for Swallows. Again, this is the case for other predators such as the Great Tit (Krebs et al 1977) and Redshank (Goss Custard 1977c).

However, the diet of Swallows does deviate from these predictions of optimal foraging theory in that non-preferred small items are included when food is abundant, particularly when small items are relatively abundant. This effect of relative abundance is of particular importance since a basic tenet of optimal foraging theory has been that the inclusion of an item in the diet depends only on the absolute abundance of preferred prey. Estabrook and Dunham (1976), however, claimed that relative abundance of prey did have an effect on prey selection but in their model relative and absolute abundances were correlated.

The inclusion of non-preferred items in the diet may be due to one or more of several reasons:

1. Apparent size and recognition time. Common but low-ranking prey are taken by shore crabs because the crabs take a long time to reject unprofitable prey (Elner and Hughes 1978). Houston, Krebs and Erichsen (1980) have shown that if Great Tits spend a long time discriminating between large and small items they will take both sizes of prey. A Swallow might have difficulty discriminating between large and small insects if the large insect is seen at a distance and appears to be the same size as an insect close by (Bryant 1973). However, this is unlikely to be an important problem because the Swallow could probably judge how far away the item was by (a) the closing rate between it and the item and (b) from the accommodation rate of the eye. Small prey may also usually be distinguished from large prey by such characteristics as their slower flight, wingbeat pattern and swarming behaviour.

2. Encounter rate and switching. Small items would be taken if the encounter rate with large prey was low or if, at the beginning of a foraging trip, the predator did not know the capture rate of these items (Orians 1980). This is particularly likely if swarms of small insects are relatively common and so may be encountered

first. The predator may then concentrate on patches of the commonest prey type (Murdoch, Avery and Snyth 1975). However, in the case of the Swallow it is unlikely that no large flies are visible (or perhaps audible) when feeding conditions are good or that the Swallow does not recall from previous trips that large items are available (see below). Switching between prey types may also occur when different prey items occur in the same patch: the predator may become more efficient at dealing with an item that is frequently encountered (Lawton, Beddington and Bonser 1974) or may form a search image (Tinbergen 1960), for a particular type of cryptic prey (Dawkins 1971a, b). However, this type of switching implies a long-term learning or physiological response that is unlikely to occur over the few minutes of a Swallow's foraging trip during which a variety of prey items are usually taken.

3. Handling difficulties. If a predator has already loaded many large items it may be easier to capture additional small items than large ones (Orians 1980). Small prey would then be taken at the end of a foraging trip. However, Swallow boluses with either few or many items both include small insects so small items are unlikely to be taken only because of handling difficulties.

4. Orians (1980) suggested that since adult Redwinged Blackbirds, _Agelaius phoenicius_, and Yellow-headed Blackbirds, _Xanthocephalus xanthocephalus_, lose weight during nestling rearing a physiological feedback mechanism may indicate that feeding conditions are poor; hence low ranking prey should be taken. However, it seems unlikely that a predator would be constrained in this way when high ranking items are evidently abundant.

5. Sampling. Smith and Sweatman (1974), Krebs and Cowie (1976) and Krebs et al (1978) have shown that Great Tits, whilst spending most time in the most profitable patches, will also sample other patches. This is seen as insurance against possible changes in the environment (Oster and Heinrich 1976). Sampling might be particularly important to hirundines since prey distribution and abundance can change not only seasonally but also between days and hours (Lewis and Taylor 1965). When and to what extent sampling occurs cannot be tested easily but Swallows sometimes meander on leaving the nest and sometimes fly straight to a patch. Boluses usually contain more than one prey type indicating that more than one patch may have been visited, which might be due to sampling. Small items might then be taken during sampling periods.

However, considering single encounters with prey or patches gives a misleading view of foraging behaviour. It has been suggested that Great Tits have a sliding memory window of the last n patches visited (Cowie 1977, Krebs in Krebs and Davies 1978). If a Swallow has a comparable memory window it is reasonable to suppose that it can recall prey captured on the previous feeding trip usually just a few minutes earlier. Also, if a predator samples its environment it must retain a memory of which patches are profitable if sampling is to be advantageous. The Swallow can also take cues from the environment. On a warm, dry day there is a high probability of finding large prey not very far from the nest. Thus the Swallow is faced with the real choice of taking small prey if first encountered or travelling further with a high probability of finding more profitable prey. The direct encounter rate with prey will thus have less influence on the bird's behaviour.

None of these reasons satisfactorily accounts for the deviation of the Swallow's diet from the theoretical optimum; a further insight may thus be gained from a closer inspection of the Swallow's behaviour in the field. Figure 5.7 compares the energetic costs and gains to the bird when taking few or many small items during a single feeding trip. It can be seen that there is a compromise between maximising foraging efficiency and caloric intake per unit time. When a certain minimum amount of food must be caught for nestlings each day a small sacrifice in efficiency for the parent might be necessary in order to save time, maximise the quantity of food collected and reduce exposure to predators. Earlier in the season, when they have only themselves to feed, the parents can afford to take longer and maximise their foraging efficiency. Similarly, in poor feeding conditions it may be more important to maximise foraging efficiency than the quantity of food collected.

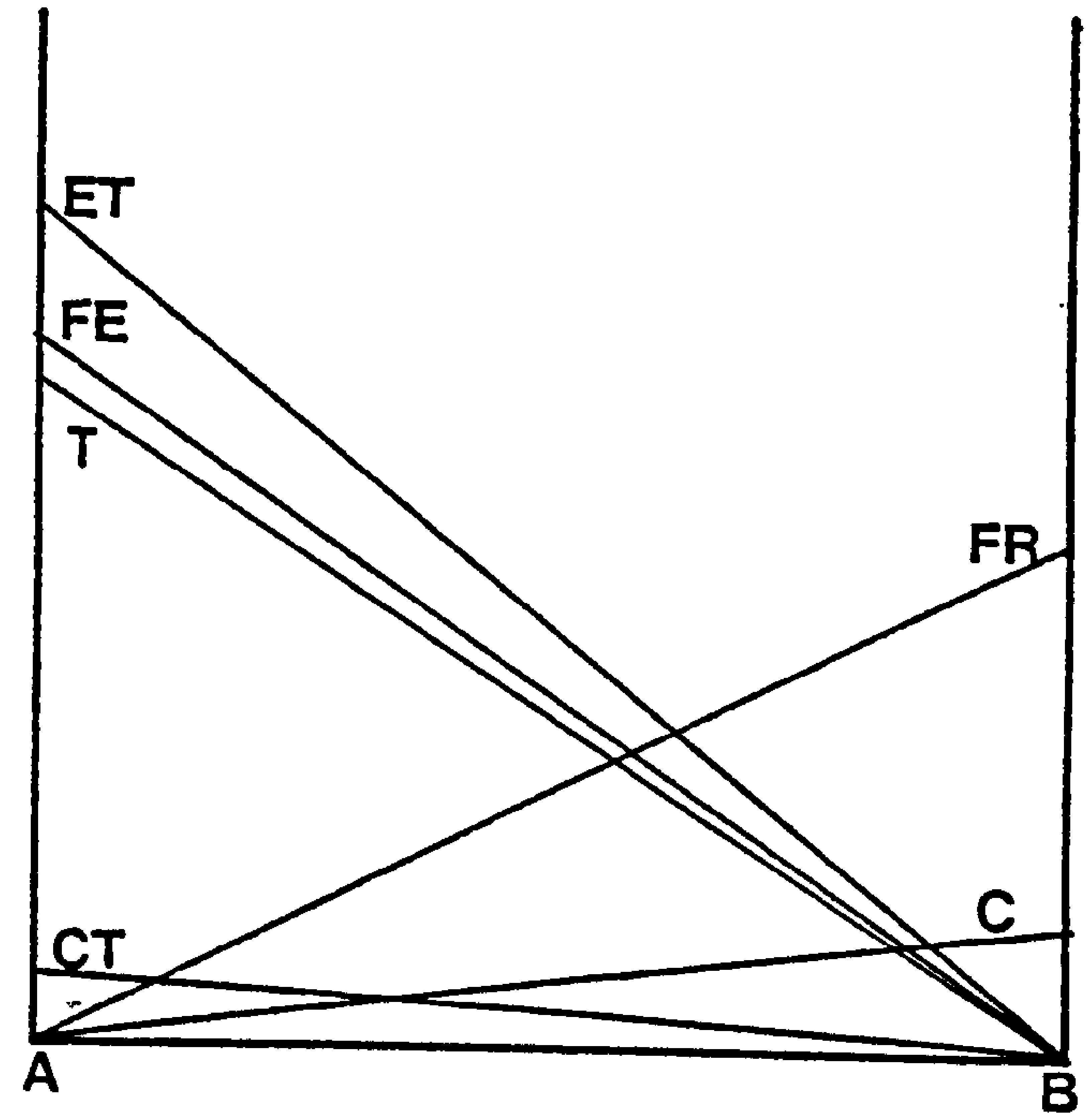
Hence small items are taken even in good conditions because they can be captured quickly and cheaply (in terms of energy) without reducing the foraging efficiency. Moreover, foraging efficiency is increased if capture rates are increased which may occur if small items are relatively abundant. Sampling of the environment and switching between prey types in different patches may well occur but the energetic cost and gains of selecting particular items and of visiting particular patches is of greater importance to the Swallow while it is foraging.

A major disadvantage of current optimal diet models is that they do not take into account heterogeneity in the environment and the predator's knowledge of the available prey and patch types. The present study, however, has shown that the type of prey in a

Figure 5.7

Advantages and disadvantages of including small items in the diet. A represents conditions when a bolus of 11 large and 40 small items is collected. B represents conditions when a bolus of 15 large and 3 small items is taken. The energy gain per trip (ET), the foraging efficiency (FE) the duration of the trip (T) and the flight costs per trip (C) all decrease as fewer small items are included. The foraging rate (FR) and flight costs per unit time (C) increase as fewer small items are included.

The relative rate of change for these parameters is indicated in the graph.



Many small
items

Few small
items

patch and the patch location can greatly influence a predator's foraging strategy to the extent that low ranking items may be taken and relative rather than absolute abundance of items becomes important as a basis for prey choice.

5.4.4 Hirundines as Central Place Foragers

The question of how much food should be gathered on a feeding trip is important for a predator, such as the Swallow, which must bring prey back to a focal point such as a nest. On the one hand, it is a waste of time and energy to take only a small amount of food per trip. On the other hand, once several prey items have been loaded the predator is likely to become less efficient at handling additional items so the net rate of energy gain during foraging will progressively decrease and it would not be profitable to feed for too long. The energy costs of carrying a load will also reduce the profitability of a large food bolus. Orians and Pearson (1979) predicted that the further the foraging site from the nest site the larger the load that should be brought back and that large loads should also be collected when the net rate of energy intake is high (for example, in patches where food is abundant).

It was shown in section 4.3 that there is a wide variation in the size of boluses collected by Swallows and Sand Martins and that bolus size depends on the distance travelled to the feeding site by Sand Martins but not by Swallows. There are very few data available on other central place foragers with which to make a comparison. House Martins also bring back larger boluses the further they travel (D.M. Bryant, pers. comm.). The number of prey delivered to nests per trip increases with distance travelled from the nest by auks and Brewer's Blackbirds (Cody 1973, Orians and Pearson 1979). The present study thus provides evidence on the one hand supporting Orians and Pearson's (1979) prediction for the Sand Martin but, on the other, contradictory data for the Swallow.

This problem can be explored further by using the "marginal value" model presented in Figure 5.8. It is assumed that:
(1) only one patch is visited. This is a critical assumption but is a simplification of the bird's behaviour since a hirundine may visit more than one patch per trip (Waugh 1978). (2) The predator searches simultaneously for prey of different types but selects only one item at a time. (3) The predator is itself at equal risk from predation while in the patch, travelling to and from the patch or at the focal point. This assumption may at times be invalid especially if the bird has a low risk of predation when feeding in a flock (section 5.5). (4) The prey are encountered randomly. Insect prey may often be clumped but if the patch is large the assumption will be nearly true. Despite these simplifications, useful predictions can still be made from the model about how the central place forager should select its prey.

In Figure 5.8 the curves show the net energy intake rate of the predator in each of three patches. The time taken to travel from the nest site, N, to the patch is the same in each case. The tangent from N to the curve indicates the optimal load size which should be collected in that patch (B_{1-3}) at that rate of energy intake. In patch H food abundance is high hence the energy intake rate is high and the optimal load size, as predicted by the marginal value model, is correspondingly large (B_1). In patch L,

Figure 5.8

Optimal load size as a function of energy costs and patch quality.

B_1 - B_3 optimal bolus sizes in terms of energy

T_1 - T_3 time spent in patch

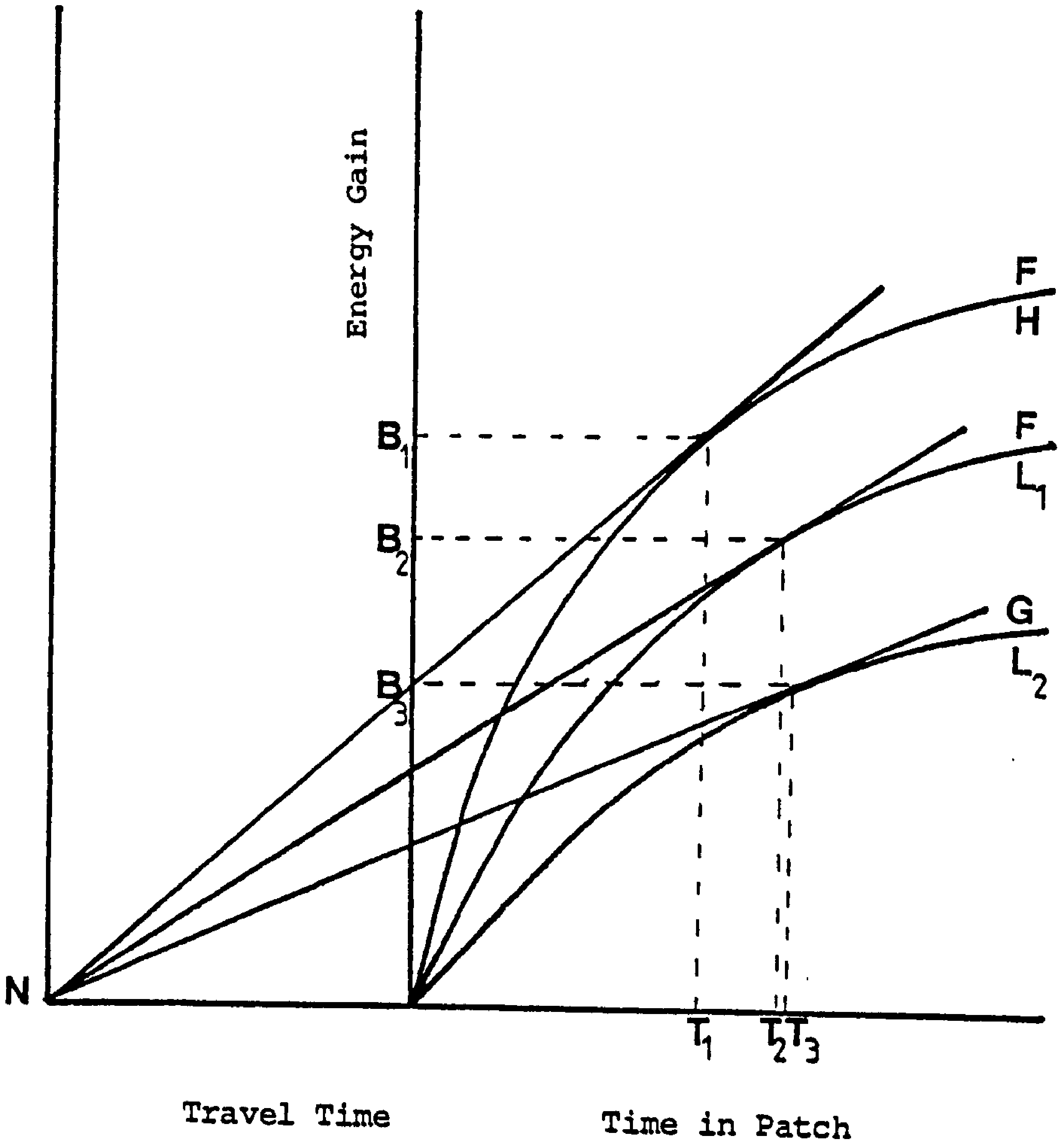
F - Fast search method

G - Slow search method

H - Patch where food abundance is high

L_1 and L_2 Patches were food abundance is low

The curves show the net rate of energy intake in each patch. The tangent from the nest site, N, to each curve indicates the optimal load size and time spent in the patch.


Energy Gain
F
H
B1
F
L1
B2
G
B3
L2
N
T1
T2
T3
Travel Time
Time in Patch

food abundance is lower hence the energy intake rate is lower and the predicted optimal load size is correspondingly smaller (B_2). In patch L_2 food abundance is the same as in L_1 but the predator uses a slow search method which results in a lower net energy intake rate: since the energy intake rate is lower the predicted optimal load size is still smaller (B_3). Thus the size of the load will depend both on food abundance in a patch and on the search method of the predator: a large load is predicted either if food abundance is high or a fast search method is used since in both cases the energy intake rate will be high. A small load is predicted if food abundance is low or if a slow search method is used since in both cases the energy intake rate will be low. It should be noted that these predictions are in addition to the effect of distance travelled on load size.

The field results, given in section 4.3, are in agreement with the predictions of the model: (1) when the Swallow is using energetically expensive, fast, flapping flight, it has a high energy intake rate (foraging rate), Table 4.20; (2) thus the bolus size of the Swallow increases with the bird's flight speed ($r = 0.51$, $n = 92$, $p < 0.001$) and with the use of energetically expensive, flapping flight (Table 4.3). The Swallow uses high-cost flight when pursuing large prey (section 4.13) which tend to be fast, mobile insects (e.g. Muscidae have a flight speed of $5.4 ms^{-1}$ compared to $2.3 ms^{-1}$ for Aphididae, Waugh 1978).

Some of the smallest Swallow boluses are collected far from the nest (Figure 4.2). There are two possible explanations for this. Firstly, the model predicts that a small bolus should be collected when the bird's energy intake rate is low (Figure 5.8).

Hence, when the Swallow is feeding in poor conditions at a distance from the nest, and consequently has a low foraging rate, it is expected that a small bolus would be collected. Secondly, it would take a long time to collect a large bolus in such conditions. If there is a high risk of predation either on the parent or the nestlings it may be best for the bird to make a short foraging trip at the expense of gathering a large load. Also, since the energy gained per total foraging time = [(energy/time)/trip] × (number of trips) the parent may do best by maximising the number of trips to swamp out the effects of a few bad trips (Orians and Pearson 1979).

In Swallows, both patch and prey quality and search costs rather than distance thus determines the bolus size since the Swallow rarely travels far from the nest compared to Sand and House Martins. When the foraging site is a long way from the nest site the effect of distance travelled becomes more important as in the Martins. Also, being a flock feeder, the Sand Martin may be better able to detect predators and be better protected from them (section 5.5) than the solitary Swallow hence it is less likely to shorten a foraging trip because of a predation risk.

The important points shown in this study for both the Swallow and Sand Martin are summarised in Figure 5.9. A large bolus is collected when total flight costs are high, a small one when total flight costs are low. The total energetic flight costs include the cost of travelling to and from the patch and the cost of searching for, pursing and capturing the prey.

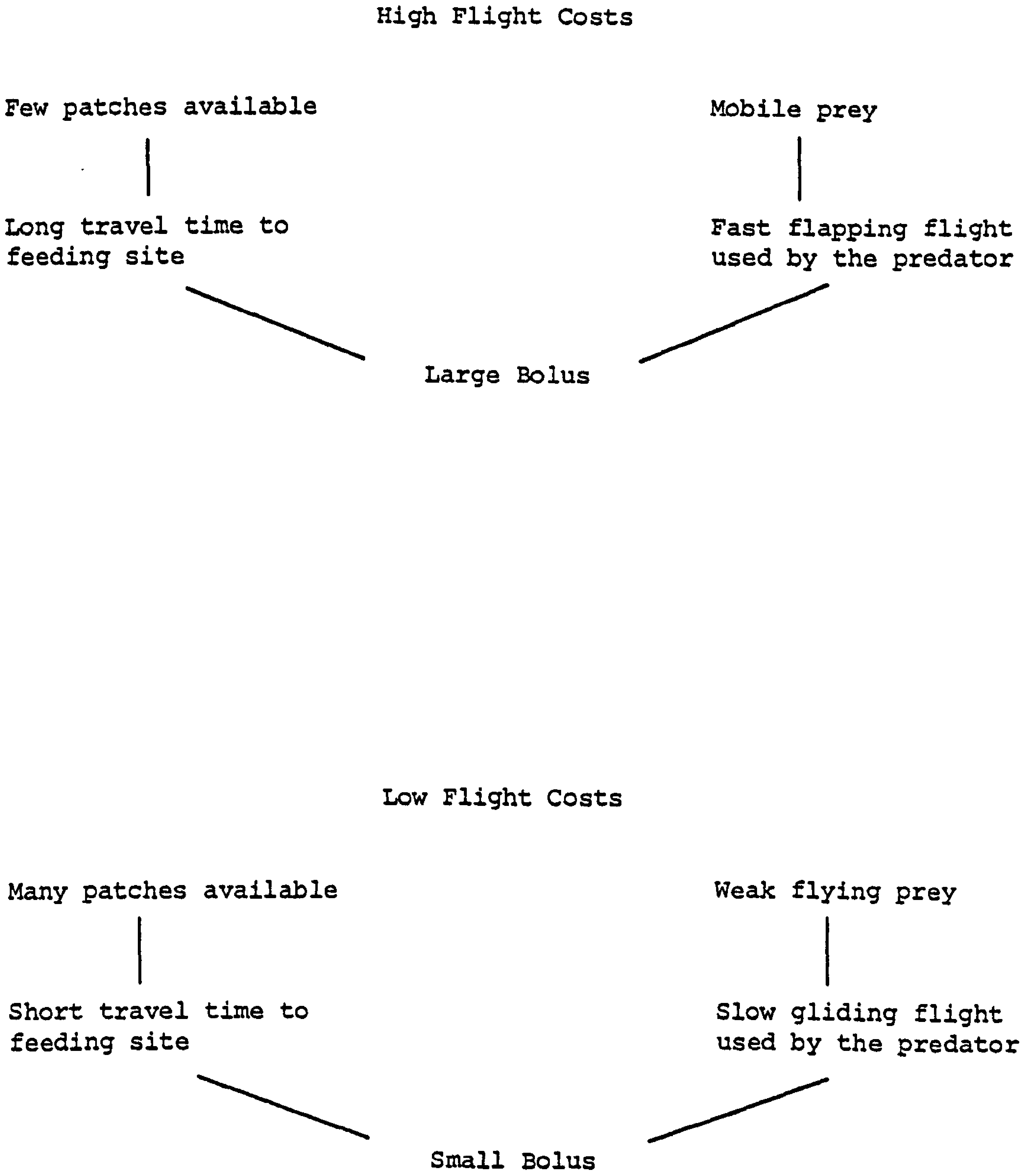


Figure 5.9

Factors affecting the size of the food bolus gathered by hirundines.

5.5 Breeding Systems in Aerial Insectivores

The degree of coloniality in a variety of birds such as the Ploceidae (Crook 1964) and marine birds (Lack 1968) may be influenced by the distribution of the food supply. A comparison of the British aerial insectivores also reveals a link between breeding systems and food supply: colonial species feed higher on small, more sparsely distributed prey than the Swallow since insect density diminishes with inceasing height above the ground (Johnson 1957). One advantage of coloniality to individuals may thus be in finding good feeding sites and in increasing the efficiency of feeding. This is discussed further below.

Other explanations for the adaptive value of coloniality have been put forward. Darling (1938) suggested that social stimulation and synchronised breeding in colonies would lead to a higher breeding success and Emlen (1971) considered that mutual stimulation of breeding was important within Bank Swallow colonies. However, Hoogland and Sherman (1976) concluded that Bank Swallows benefitted most from decreased predation in colonies. In section 4.10 it was shown that predators frequently occurred at the Sand Martin colony so protection from predation would be a useful function of coloniality. Protection may be afforded in several ways. The predator may be forced away from the nest site by mobbing. Group mobbing of predators by hirundines has been observed many times in Barn Swallows (Snapp 1973, Smith and Graves 197~~4~~5, Waugh 1978, this study), House Martins (Lind 1962), Rough-winged Swallows, Stelgidopteryx ruficollis, (Lunk 1962) and Sand Martins (Hoogland and Sherman 1976, Waugh 1978, this study). Sand Martins form a tight knit flock when a Sparrowhawk attacks (pers. obs.). The presence of others in such a flock may protect an individual from being selected by a predator (Hamilton 1971); flocks may also confuse a predator or prevent it from attempting to single out an individual (Tinbergen 1951, Neill and Cullen 1974). The risk of predation may also be reduced since there are more individuals to watch out for predators; each individual can then spend less time watching and more time feeding (Vine 1971, Thompson, Vertinsky and Krebs 1974, Siegfried and Underhill 1975).

Perhaps the most likely explanation of coloniality is that it provides some advantage to individuals in finding and collecting food, although this is not incompatible with other functions of colonies. Groups of animals might act as centres where information on a temporally or spatially varying food supply could be passed between individuals (Ward and Zahavi 1973). Emlen (1971) and Emlen and Demong (1974, 1975) argued that social facilitation of foraging was important to Bank Swallows. Social foraging has been recorded in several other colonial species such as the Great Blue Heron, *Ardea herodias*, (Krebs 1974), the Cliff Swallow, *Petrochelidon pyrrhonota*, (Emlen 1952) and Tricoloured Blackbirds, *Agelaius tricolor*, (Orians 1961). However, Bryant (1978b) showed that House Martins breeding during the peak period produced relatively light nestlings even though the foraging traffic, and hence information from the colony members, was at a maximum. This may have resulted from increased competition for food. Horn (1968) showed that colonial nesting is favoured for efficient feeding when the food source is highly clumped in time and space even without interactions between foraging birds.

Food collection may be enhanced by flock feeding. Cody

(1974) suggested that birds can exploit food more efficiently in a flock since they are able to avoid searching in places where others have recently fed. Co-ordinated hunting, causing confusion among the prey, may benefit flock feeders (Bertram in Krebs and Davies 1978). Alternatively, flocks may just build up in good feeding sites although they will also serve to attract individuals to the area (Krebs 1974).

The size of Sand Martin flocks increases with increasing distance of the foraging site from the colony (section 4.9) suggesting that these flocks are primarily groups of birds that have some together to exploit a food resource which has become, usually in bad weather conditions, very localised. Individuals may have been attracted to the spot by the presence of other birds or may have followed other birds out to feed. This will be most important early in the season and for juveniles since parents feeding nestlings many times a day and during the season are likely to learn both from experience and from sampling that certain sites were profitable in bad weather.

Feeding flocks of Sand Martins thus seem to be more related to the available food supply than to predation. Poor feeding conditions force the Sand Martins further from the nest site to a few patches. In good conditions more patches are available for feeding hence the birds are more dispersed.

There may also be disadvantages to living and feeding in groups. Predators may be attracted to an aggregation of individuals; competition may occur between individuals; time may be wasted in aggressive behaviour or in watching neighbours and individuals may disturb or remove prey before another can eat it (Goss Custard 1970, 1977a). These disadvantages may outweigh the advantages for solitary birds such as the Swallow (this is discussed further below).

Hirundines exhibit various degrees of coloniality from solitary hole-nesters such as the Tree Swallow and Rough-winged Swallow to the Sand Martin and Cliff Swallow breeding in large, dense colonies. Mayr and Bond (1942) considered that the evolution of hirundines has been characterised by a parallel increase in coloniality and in building and excavating nests, suggesting a link between coloniality and nest site availability. Snapp (1973) considered that groups of Barn Swallows occur passively where nest sites are available whereas Sand Martins clearly nest close to each other even when sites are available (Emlen 1971).

This difference between hirundines may be partly explained by their feeding behaviour. The most colonial species, the Sand Martin, House Martin and Cliff Swallow (Table 5.2) feed a long way, up to 4 km, from the nest site (Emlen 1952, D.M. Bryant pers. comm., this study) generally high up on small, patchily distributed prey (Samuel 1971, Bryant 1972, this study). These are also the only species in which a considerable part of the incubation is by the male (Table 5.2). These characteristics are associated with low foraging rates (Withers 1977, Bryant and Westerterp 1978, this study) and, thus, may be due to a dependence on other individuals either in locating a food source or in increasing foraging time and efficiency. This could come about through a decreased predation risk or, less likely perhaps, through social facilitation of feeding. These advantages will have most effect in poor feeding conditions when foraging efficiency is very low.

The Swallow, a more solitary nester, has a higher foraging rate and efficiency (section 4.12) than the colonial species and would not benefit from being in a colony where interspecific aggression would be high and feeding time thus lost. However, a cost is involved in solitary nesting since time will be lost in deterring predators resulting in fewer feeds to the nestlings (Waugh 1978). This cost is presumably low enough for solitary nesting to still be advantageous. Nest site availability determines how closely nests will be grouped in this species but even in comparatively large groups predator mobbing and feeding is usually carried out on an individual or a pair basis (pers. obs.). The Swallow feeds close to the ground on large, more evenly distributed items so is able to feed near to the nest site without needing conspecifics to attract it to a food source or to facilitate foraging. The high foraging efficiency may well make up for time lost in watching for or deterring predators and allows the female to incubate by herself.

The fourth British aerial feeder, the Swift, is similar to the Martins in that it tends to nest colonially and feeds high up on small insects at sites far from the nest (Lack and Owen 1955, Lack 1956, Waugh 1978). The male and female of this species also share incubation duties since they are inefficient feeders compared to the Swallow (Koskimies 1950, Lack 1956, Bryant and Westerterp 1978).

SUMMARY AND CONCLUSIONS

1. Insect abundance and quality increased during the spring providing a high-level food supply during June to August. The abundance of food then declined again. Net catches revealed changes in abundance and quality of the prey close to the ground. Weather had the most marked effect on the food supply but there were also changes due to time of day and the site. The net catches were correlated with suction trap catches. The prey were found to provide a balanced diet, rich in protein and with a high calorific value.

Nestling growth curves showed the weight recession typical of hirundines. This was principally due to a loss in the water content of the tissues. Fat was stored by the nestling, to a greater extent by the Sand Martin than by the Swallow. Assimilation efficiency was found to be 70%.

2. Time budgets were constructed for nest building/burrowing, egg laying, incubation, brooding and nestling feeding stages. The effects of a wide variety of variables such as weather and brood size are discussed. Flight costs were obtained for the Sand Martin and the Swallow by the D_2O^{18} technique. The Sand Martin was found to have relatively high energy costs. Energy budgets were calculated from the time budgets and flight costs. Seasonal changes in energy expenditure due to the adoption of expensive, flapping flight, or a change in distance travelled to the feeding site are discussed. The size of the bird also has an effect on energy expenditure. Wing length was found to increase with age.

Parental investment during incubation was investigated by temporary removal of 1 of a pair. Female Sand Martins maintain a higher rate of incubation than the male indicating a greater commitment to the brood and hence a greater likelihood of bearing costs. Male Swallows did not incubate. Brood sizes were artificially reduced and enlarged to examine the investment by the male and female in the brood. Males tended to increase their feeding rate to large broods and to second broods and decreased it to small broods and in bad weather. Females tended to feed at a more constant rate.

3. Factors affecting the size and composition of the food bolus brought to the brood and the feeding behaviour of the parents are discussed. The Swallow generally fed close to the nest, low over the ground and flew at high speeds. The Sand Martin fed further away and higher up than the Swallow, generally using slower speeds.

The Swallow selected large, mobile prey types especially Diptera. The Sand Martin specialised on small, swarming items, but large Ephemeroptera were also important. Small items were also taken by the Swallow, in greater proportions than was expected from optimal foraging theory; a greater proportion of small items was taken when they were relatively abundant. The foraging efficiency of the Swallow was maintained at a high level when small items were caught since pursuit costs were low and their capture rate was high. Capture rates of large items were low and pursuit costs were high which offset their high calorific value. Daily foraging efficiencies were similar for the hirundines in average conditions but the Swallow was capable of reaching very high efficiencies.

Feeding rates were increased for large broods and for second broods but the size of the food bolus decreased during the season so the same amount of food was delivered to first and to second broods.

4. The Sand Martin is the earliest British hirundine to begin laying. It is not as dependant on large prey items being abundant as is the Swallow. It can also risk incubating in bad weather since the male shares in the incubation duties. The female Swallow defers laying until the risk of encountering bad weather during incubation is low since she incubates alone.

Brood size may be limited by the risk of bad weather depressing the foraging rate to such a low level that insufficient time is available to feed the brood adequately. However, the effects of bad weather are offset to some extent by the presence of fat stores in the nestlings and adults.

Possible reasons for differences in parental investment are discussed. The female invests a lot of time and energy early on in the breeding season and may lower her chances of survival by continuing to invest at a high rate. The male, with a low initial investment, is less at risk when he devotes more time and energy to the nestlings. The male, however, is more likely to desert than the female since he has more opportunities for promiscuous matings especially in a large colony.

It is demonstrated that energy, rather than nutrients, is likely to be the 'currency' most sought after by the parents feeding nestlings. Energetics data are used to show that it is still profitable for a central place forager, such as the Swallow, to take a mixture of large and small prey items, whereas optimal foraging theory would predict exclusive specialisation on large items. Other possible explanations for the inclusion of small items in the diet are discussed.

Bolus size in the Sand Martin is determined mainly by the distance travelled to the feeding site. For the Swallow, patch and prey quality and the search methods employed are more important. This results in Swallows collecting large boluses close to the nest, whereas Sand Martins tend to collect large boluses further away from the nest.

The effects of coloniality are discussed. It is suggested that the most inefficient feeders are also the most colonial. Their foraging time is improved since less time need be spent detecting and deterring predators and feeding sites may be more easily located in bad weather.

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APPENDICES

APPENDIX 1 Composition of Sweepnet Samples (mean ± 1 s.d.)

1. Good Weather Conditions

Month	Time of Day	Mean Biomass mg dry weight	Mean Number of Items	Mean Number of Large Items[1]	Mean Prey Size (Biomass/Numbers)	n
May	04-0600	1.29 ± 1.10	4.30 ± 2.36	0	0.30	3
(egglaying period)	06-0800	2.32 ± 2.60	5.00 ± 2.45	0	0.46	4
	08-1000	25.46 ± 14.42	26.00 ± 16.88	2.00 ± 0.71	0.98	4
	10-1200	27.54 ± 14.27	20.33 ± 11.67	2.67 ± 0.47	1.35	3
	12-1400	39.83	44.5	5.00	0.90	2
	14-1600	14.34 ± 4.08	14.33 ± 6.34	2.33 ± 0.47	1.00	3
	16-1800	12.89	17.50	0.50	0.74	2
	18-2000	13.54 ± 4.95	10.00 ± 3.00	2.67 ± 0.94	1.35	3
	20-2200	3.47	3.50	0.50	0.99	2
June to Mid-July	04-0600	15.32	10.00	2.00	1.53	1
(1st brood period)	06-0800	29.35 ± 9.19	10.14 ± 2.29	4.29 ± 1.03	2.89	7
	08-1000	32.00 ± 21.93	11.67 ± 6.72	4.83 ± 3.02	2.74	6
	10-1200	38.59 ± 24.14	12.10 ± 6.74	5.70 ± 3.16	3.19	10
	12-1400	38.68 ± 15.39	13.43 ± 7.17	5.57 ± 2.50	2.88	7
	14-1600	28.39 ± 12.63	14.67 ± 7.93	4.33 ± 1.83	1.94	9
	16-1800	26.73 ± 11.68	16.00 ± 10.56	3.75 ± 1.48	1.67	4
	18-2000	8.89 ± 5.65	6.20 ± 2.48	0.60 ± 0.80	1.43	5
Mid July to August	04-0600	24.76 ± 29.89	5.67 ± 3.77	1.33 ± 1.25	4.37	3
(2nd brood period)	06-0800	27.56 ± 18.63	17.50 ± 2.29	2.17 ± 1.46	1.57	6
	08-1000	31.75 ± 17.92	10.00 ± 4.05	4.00 ± 1.26	3.18	5
	10-1200	28.52 ± 15.42	10.92 ± 4.86	5.15 ± 3.53	2.65	13
	12-1400	48.94 ± 22.03	19.50 ± 9.95	5.00 ± 4.78	2.51	7
	14-1600	42.03 ± 22.50	15.63 ± 6.23	3.00 ± 0.87	2.52	8
	16-1800	24.83 ± 23.62	8.45 ± 3.17	2.18 ± 1.11	2.94	11
	18-2000	14.84 ± 9.37	7.71 ± 2.55	2.00 ± 1.07	1.92	7

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[1] Large items are ≥ 1.5 mg dry weight

2./

APPENDIX 1 (continued)

2. Bad Weather Conditions

Month	Time of Day	Mean Biomass mg dry weight	Mean Number of Items	Mean Number of Large Items[1]	Mean Prey Size (Biomass/Numbers)	n
May (egglaying period)	04-0600	-	-	-	-	-
	06-0800	1.05 ± 1.82	1.16 ± 1.62	0.17 ± 0.37	0.91	12
	08-1000	4.19 ± 4.97	2.60 ± 2.65	0.67 ± 0.82	1.61	10
	10-1200	4.55 ± 4.69	3.71 ± 2.96	0.71 ± 0.88	1.23	7
	12-1400	2.09 ± 2.66	2.82 ± 2.90	0.18 ± 0.39	0.74	11
	14-1600	3.93 ± 2.15	6.20 ± 3.25	0.40 ± 0.49	0.63	5
	16-1800	-	-	-	-	-
	18-2000	2.05 ± 1.93	3.18 ± 3.41	0	0.64	9
	20-2200	0.42	2.5	0	0.17	2
June to Mid-July (1st brood period)	04-0600	1.97 ± 1.46	2.67 ± 2.05	0.33 ± 0.47	0.74	3
	06-0800	3.62 ± 2.75	4.00 ± 2.94	0.33 ± 0.47	0.91	3
	08-1000	1.29 ± 0.95	2.00 ± 1.58	0	0.65	4
	10-1200	2.91 ± 1.02	1.33 ± 0.47	0.33 ± 0.47	2.19	3
	12-1400	5.00 ± 5.15	4.75 ± 4.49	0.50 ± 0.50	1.05	4
	14-1600	3.56 ± 1.88	6.60 ± 3.50	0.20 ± 0.40	0.54	5
	16-1800	2.59	7.50	0.50	0.35	2
	18-2000	2.31 ± 1.31	2.75 ± 1.48	0.75 ± 0.83	0.84	4
Mid-July to August (2nd brood period)	04-0600	0.92 ± 0.42	3.00 ± 1.41	0	0.31	3
	06-0800	2.95 ± 2.50	6.00 ± 6.84	0	0.49	5
	08-1000	4.38 ± 2.97	9.80 ± 7.00	0.14 ± 0.35	0.45	7
	10-1200	5.08 ± 1.55	11.80 ± 4.40	0.25 ± 0.43	0.43	6
	12-1400	2.96 ± 2.89	7.80 ± 7.30	0.25 ± 0.43	0.38	4
	14-1600	2.91 ± 1.55	3.33	0.33 ± 0.47	0.87	3
	16-1800	2.46 ± 1.60	3.50 ± 2.29	0.25 ± 0.43	0.70	4
	18-2000	0	0	0	0	1

APPENDIX 2

Insect Size and Composition

2A. Insect Dry Weight/Winglength Formulae:

The relationship between dry weight (mg), y, and winglength (mm), x, is of the form $y = x^b/D$. Values of b and D for different taxa are given in the following table, together with the correlation coefficient, r, sample size n, and significance, p.

Taxon/Taxa	b	D	r	n	p
Ephemeroptera/Odonata/Trichoptera/ Neuroptera/Hemiptera/Psocoptera	2.32	47.86	0.94	58	<0.001
Lepidoptera	3.80	10^3	0.95	10	<0.001
Nematocera	2.24	44.67	0.95	90	<0.001
Culicidae	2.90	112.26	0.59	16	0.01
Scatopsidae	2.30	47.86	0.83	21	<0.001
Chironomidae	2.55	77.62	0.96	17	<0.001
Tipulidae	2.39	67.61	0.91	11	<0.001
Mycetophilidae	2.51	66.07	0.75	18	<0.001
Bibionidae	2.34	34.67	0.97	12	<0.001
Simulidae	2.93	44.67	0.80	11	<0.01
Brachycera/Aschiza/Schizophora	2.48	28.8	0.95	183	<0.001
Empididae	2.49	54.95	0.86	20	<0.001
Dolichopodidae	2.93	61.66	0.92	17	<0.001
Syrphidae	2.93	89.13	0.70	13	<0.01
Phoridae	2.44	20.42	0.93	16	<0.001
Lonchopteridae	2.79	74.13	0.89	9	<0.001
Acalypterae	2.40	30.20	0.95	82	<0.001
Borboridae	2.43	28.18	0.53	18	<0.02
Opomyzidae	2.97	52.48	0.68	11	<0.02
Sepsidae	1.26	7.59	0.81	9	<0.01
Calypterae	2.31	14.79	0.93	13	<0.001
Hymenoptera	2.98	81.28	0.95	92	<0.001
Cynipidae	3.24	120.23	0.92	16	<0.001
Ichneumonidae	2.81	61.66	0.86	19	<0.001
Braconidae	2.92	89.13	0.88	21	<0.001
Chalcidoidea	2.53	44.67	0.83	19	<0.001
Aculeata	4.29	1023.29	0.98	14	<0.001
Coleoptera	1.93	18.62	0.82	28	<0.001

Appendix 2 (continued)

2B. Composition of Insects[1]

Taxon	Percent. Water	Chitin content Percent. dry weight	Nitrogen content mg/g dry weight	Sulphur content[2] mg/g dry weight
Trichoptera	-	4.3		4.7
Dermaptera	76.41	-	-	-
Lepidoptera	74.17	10.6	-	17.3 (13.9-20.7)
Chironomidae	74.87	2.7, 5.1	102.0	5.1 (2.3- 6.6)
Mycetophilidae	-	5.2	-	2.5 (2.0- 3.0)
Simulidae	-	6.3	-	14.4 (13.5-15.2)
Bibionidae	-	-	-	13.2
Tipulidae	-	6.7	-	12.3 (2.8- 9.5)
Anisopodidae	-	4.6	124.9	13.3 (8.9-17.7)
Culicidae	-	6.8	-	6.4 (4.1- 8.7)
Scatopsidae	-	8.0	-	9.3 (3.3-16.2)
Brachycera	-	-	-	4.1 (1.1- 7.0)
Empididae	-	10.9	-	-
Dolichopodidae	-	7.5	-	-
Stratiomyidae	-	13.3	-	-
Phoridae	-	9.8	-	3.9 (1.9- 7.1)
Syrphidae	73.00	9.9	105.6	7.9 (7.5- 8.2)
Acalypterae	-	9.1	101.8	1.8 (1.5- 2.1)
Calypterae	70.61, 71.08	11.6	111.9	4.3 (4.2- 4.4)
Homoptera	72.43	6.9	-	1.1
Heteroptera	-	10.2	-	10.2 (4.4-16.0)
Aphididae	-	10.5	85.1	4.4 (0.6- 3.9)
Hymenoptera	-	10.2, 13.1	127.5	5.4 (4.2- 7.2)
Aculeata	79.07, 71.00	9.7	109.7	5.9
Coleoptera	70.96	18.3, 21.7	87.9	12.8 (8.8-22.6)
Mixed	73.02	-	-	-
	71.95			
	71.31			
	73.17			
	71.00			

APPENDIX 2 (continued)

Taxon	Ash content mg/g dry weight	Lipid content mg/g dry weight	Calcium content mg/g dry weight[3]	Calorific Value kcal/g
Trichoptera	-	176.5	2.2, 2.5	5.300
Lepidoptera	69.4	-	1.9 (1.7-2.1)	5.902
Chironomidae	51.6	-	2.8, 3.6 (1.5-4.0)	5.324
Mycetophilidae	-	92.4	5.5 (3.5-7.5)	5.400
Simulidae	-	45.9	2.7	-
Bibionidae	58.9	-	3.8	5.800
Tipulidae	48.7	-	1.3 (1.0-1.5)	5.783
Anisopodidae	-	-	5.8	-
Culicidae	54.4	69.3	3.3 (1.9-4.6)	-
Scatopsidae	-	138.7	3.7 (3.4-3.9)	-
Brachycera	-	42.7	4.0	5.300
Empididae	-	-	3.4	5.400
Dolichopodidae	-	-	-	-
Stratiomyidae	-	-	-	-
Phoridae	61.5	120.6	-	5.350
Lonchopteridae	-	136.2	3.9 (3.4-4.3)	-
Syrphidae	89.6	66.0	3.9	5.400
Acalypterae	61.1	55.1	-	-
Calypterae	-	43.1	2.2, 3.3 (1.1-3.8)	5.514
Homoptera	-	-	3.9	5.300
Heteroptera	-	-	4.9 (1.7-8.0)	-
Aphididae	66.6	132.8	3.5 (0.9-6.1)	5.500
Hymenoptera	47.9	-	2.85, 3.3 (2.0-4.6)	5.520
Aculeata	53.9	-	1.4 (0.5-2.3)	5.000
Coleoptera	47.1	142.6	3.5, 4.3 (2.3-6.1)	5.526

[1] Two values, or the ranges of values are given where more than one sample was analysed. Ranges are given in brackets.

[2] The quantity of sulphur-containing amino-acids (SAA) in insects was calculated assuming all the sulphur occurred in SAA (cysteine, cystine and methionine).

[3] The calcium values shown are for samples to which lanthanum chloride was added to counteract the phosphorus in animal tissues which depresses the sensitivity of the spectrometer for calcium. The concentrations of calcium obtained by adding lanthanum were compared to those of untreated samples and were found to be significantly higher ($p < 0.001$, Wilcoxon matched pairs test).

APPENDIX 3

Nestling and Egg Composition and Nestling Weights

Swallow

Lean dry weight (LDW) at hatching	0.4g	n = 1
LDW at 18-23 days	5.069 ± 0.529g	n = 3
Ash free LDW (ALDW) at 4 days	0.609g	n = 2
ALDW at 18-23 days	4.569 ± 0.563g	n = 3
LDW of plumage at 6 days	0.3750g	n = 1
LDW of plumage at 18 days	1.9927g	n = 1

Sand Martin

LDW at hatching	0.25g	n = 1
LDW at 18-22 days	3.8072 ± 0.1243g	n = 6
ALDW at 4 days	0.9007 ± 0.0963g	n = 4
ALDW at 13-21 days	3.3209 ± 0.2289g	n = 14
LDW of plumage at 7 days	0.3418g	n = 1
LDW of plumage at 18 days	1.6433g	n = 1

Egg Composition

Calcium content	20.92% of total dry weight	n = 11 (Turner unpub. data)
Sulphur content	0.56% "	n = 11 (Turner unpub. data)
Protein content	38% "	(Romanov & Romanov 1957)
Water content	81% of fresh weight	(Bryant 1978a)

The effect of brood size on nestling weights

Swallow - Nestling weight (g) = 23.80 - 0.67 Brood size n = 85

Sand Martin - Nestling weight (g) = 19.19 - 0.67 Brood size n = 76

APPENDIX 4

The dependent and independent variables used in the multiple regression analyses of time budgets, foraging behaviour and food bolus composition.

1. DEPENDENT VARIABLES

(a) Time budgets

Symbol	Variable
B - Building	This includes time spent gathering nesting material and working it into the nest and also the time spent flying between the site where materials were gathered and the nest site.
B - Burrowing	This includes periods when sand was kicked out of the burrow at short intervals indicating that a bird was burrowing, time spent gathering nesting material and flight time as above.
P - Perching	Total time spent on a perch or at the entrance to a burrow including time spent on preening and other maintenance activities, (excludes 'guarding' time - see below).
FT - Fighting	Time spent in intraspecific aggression either as the aggressor or the intruder including the time spent by male Sand Martins in chasing paired birds.
G - Guarding	Time spent by male Sand Martins perching and calling in the entrance to the burrow before incubation begins.
SG - Singing	Time spent singing by the male Swallow when perching or flying.
ST - Spare time	Time spent flying except foraging time, flights to and from feeding sites and also flights involved in nest-building or during intraspecific or inter-specific aggression.

APPENDIX 4 (continued)

(a) Time Budgets (continued)

Symbol	Variable
SF - Self Feeding NF - Nestling Feeding	The method of calculating the time spent by the parent in feeding itself and in feeding the brood is described in section 3.2.
F - Feeding	Total time spent feeding including travelling to and from the nest site, searching for and capturing prey.
FR - Feeding Rate	The number of feeding visits made to the brood per hour.
I - Incubating	Total time spent on the eggs.
BR - Brooding	Total time spent sitting on young nestlings.
A - Attentive Period	Mean time interval spent on eggs or young nestlings.
IP - Inattentive Period	Mean time interval spent away from eggs or young nestlings.

(b) Foraging Behaviour

Symbol	Variable
CT - Bolus Collection Time	Time taken for a parent, after leaving the nest, to collect a food bolus and return to the nest.
H - Feeding Height	Height above ground of the bird while feeding (1 = low, 3 = high)
D - Distance to Patch	Distance from the nest site to the site where the bird is feeding.
PT - Pursuit Time	Time interval between obvious swerves or changes in the flight path of the bird.
Sp - Speed	Timed or estimated speed in ms^{-1}.
GF - Gliding	Time spent gliding as a proportion of the total time spent flying during foraging (excluding flight to and from the nest site).

APPENDIX 4 (continued)

(b) Foraging Behaviour (continued)

Symbol	Variable
Tp - Time to Patch	Time taken to reach the feeding site from the nest site.
TR - Turning Rate	The direction of turning after prey capture. (1 = straight ahead, 4 = turn through 180°).
FS - Flock Size	The number of birds within a feeding flock.
FOR - Foraging Rate	The intake rate of assimilable energy (kcal min^{-1}) while the bird is feeding, including or excluding travel time to and from the feeding site. (Assimilation efficiency is taken to be 70%).
FE - Foraging Efficiency	The ratio of assimilable energy collected to the energy expended during its collection.

(c) Food Bolus Composition

Symbol	Variable
BS - Bolus Size	Mean dry weight (mg) of boluses collected over each observation period.
NBS - Number of Items	The mean number of prey items in a bolus.
TX - Number of Taxa	The mean number of prey taxa (families or orders) in a bolus.
SRB - Size Range	The mean range of weights of prey items in a bolus excluding the extreme 5% (by number) of items.
PST - Prey Size Taken	The mean dry weight of items in a bolus.
PLI - Proportion of Large Items	The mean proportion of items in a bolus that are ≥ 1.5 mg in dry weight.

APPENDIX 4 (continued)

2. INDEPENDENT VARIABLES

Symbol	Variable
Wt - Weight	Adult weight (g) - seasonal mean
Wl - Wing length	Adult wing length (mm) - maximum chord
Bill - Bill length	Adult bill length (mm)
Ta - Tarsus	Adult tarsus length (mm)
Tail - Tail	Adult outer tail feather length (mm)
DL - Laying Date	Date of laying of the individual's first egg of the year.
DMed - Laying Date	Date of laying in terms of the number of days before or after the median date of laying.
CS - Clutch Size	The number of eggs in the clutch
Col - 'Colony' Size	The number of pairs of Swallows on a farm or house or the number of pairs of Sand Martins nesting together in a colony.
P - Position	The position of a Sand Martin burrow in a colony (1 = central, 4 = peripheral)
TM_N - Temperature	Minimum daily temperature, °C.
TM_X - Temperature	Maximum daily temperature, °C.
Ta_n - Temperature	Mean daily temperature on day n, °C.
T_{n-1} - Temperature	Mean daily temperature on day $\frac{n + (n - 1)}{2}$, °C.
T_{n-2} - Temperature	Mean daily temperature on day $\frac{(n-1) + (n-2)}{2}$, °C.
T° - Temperature	Ambient shade temperature at the start of each observation period, °C.
W - Wind Strength	Subjective estimate of wind speed (1 = very strong, 4 = calm).
R - Rain Intensity	Subjective estimate of rainfall (1 = very heavy, 5 = dry).
C - Cloud Cover	Subjective estimate of the proportion of the sky covered by cloud (1 = heavy cloud, 4 = clear sky).

APPENDIX 4 (continued)

2. INDEPENDENT VARIABLES (continued)

Symbol	Variable
Rain - Rainfall	Rainfall (mm).
F_n - Food Abundance	$\log_{10}$ (volume + 1) of the suction trap catch on day n.
F_{n-1} - Food Abundance	$\log_{10}$ (volume + 1) of the suction trap catch on day $\frac{n + (n-1)}{2}$.
F_{n-2} - Food Abundance	$\log_{10}$ (volume + 1) of the suction trap catch on day $\frac{(n-1) + (n-2)}{2}$.
$F_{N°n \text{ to } n-2}$ - Food Abundance	$\log_{10}$ (number of items + 1) in the suction trap catch on day n to n-2 calculated as for $F_{n \text{ to } n-2}$.
PS1 - Available Prey Size	Prey size calculated as $Fn/F_{N°}$
PS2 - Available Prey Size	Mean dry weight of prey items in the suction trap (excluding culicids and chironomids).
PS3 - Available Prey Size	Mean dry weight of prey items in the suction trap (excluding culicids, chironomids and aphids)
FLIT - Available Prey Size	$\log_{10}$ (Number of items ≥ 0.32 mg dry weight in the suction trap).
PSN - Available Prey Size	Mean dry weight of prey items in the net sample (50 sweeps).
FLIN - Available Prey Size	$\log_{10}$ (Number of items ≥ 1.5 mg dry weight in the net sample).
NWT - Food Abundance	$\log_{10}$ (Total dry weight of the net sample).
NNO - Food Abundance	$\log_{10}$ (Number of items in the net sample).
TM - Time	Time (BST) at the start of the observation period.
TM$\pm$ - Time	Number of hours before or after 1300h BST.

APPENDIX 4 (continued)

2. INDEPENDENT VARIABLES (continued)

Symbol	Variable
Ph - Photoperiod	Number of hours between sunrise and sunset.
DY - Day	Day of the season. May 1st = 1.
Op - Observation Period	Length of the observation period.
St1 - Stage	Number of days after the start of building or burrowing.
St2 - Stage	Number of days before the start of incubation.
St3 - Stage	Number of days after the start of incubation (the day of laying of the penultimate egg).
NA - Nestling Age	Age in days of the brood (Day 1 is the day on which all the nestlings have hatched).
NN - Nestling Number	The number of nestlings in the brood.
BM - Brood Mass	Brood weight$^{0.67}$(g).
BM2 - Brood Mass	Brood weight (g).
BM3 - Brood Mass	The expected brood weight (the mean for nestlings of that age and number).
1/2B - 1st/2nd Brood	First or second brood.

APPENDIX 5

Energy Budgets

The daily energy budget (DEB) was derived in the following way:

DEB = (Weight of bird (g) × Hours spent in each activity × Metabolic Rate for that activity) summed for all activities in the time budget.

(a) Weight:

Mean values from this study were used, i.e. 19.0g for the Swallow and 13.7g for the Sand Martin. Few Swallows were caught early in the season hence this weight is appropriate for birds feeding nestlings. However, many egg laying Sand Martins were caught, hence the lower value of 12.6g was used for Martins rearing nestlings (see Table 3.25).

(b) Metabolic Rates:

The energetic requirements for each activity are given in this section. Rates were calculated to 4 decimal places.

1. Roosting The metabolic rate used is that at 15°C calculated from equations given in Kendeigh et al (1978):

The lower critical temperature of passerines in summer (T_{LC})

$= 40.73\ (\text{weight g})^{-0.1844}$

$= 25.1°C$ for a 13.7g Sand Martin

$= 23.7°C$ for a 19.0g Swallow

BMR for passerines in summer

= 0.8906 $(\text{weight})^{0.6884}$ kcal bird^{-1} day^{-1}

= 5.3976 kcal for the Sand Martin

= 6.7605 kcal for the Swallow

Metabolic rate at 0°C

= 3.457 $(\text{weight})^{0.5277}$ kcal bird^{-1} day^{-1}

= 13.7577 kcal for the Sand Martin

= 16.3492 kcal for the Swallow

∴ the metabolic rate at 15°C (the normal burrow temperature)

= 8.118 kcal day^{-1} for the Sand Martin

= 10.2600 kcal day^{-1} for the Swallow

2. Perching. The metabolic rate at 15°C × 1.5 is used (Utter and Lefebvre 1970).

3. Flight. For the Sand Martin the cost used was that obtained from the D_2O^{18} experiments (0.1288 kcal $g^{-1}h^{-1}$). For the Swallow the cost used was the mean of the D_2O^{18} results from this study and other values given in Hails (1979) (0.0732 kcal $g^{-1}h^{-1}$).

4. Chasing. The same costs were used as for flight.

5. Singing. Metabolic rate at 15°C × 1.5 × 1.1 (Utter and Lefebvre 1970).

6. Burrowing. Vleck (1979) investigated the energy cost of burrowing in the Pocket Gopher, *Thomomys bottae*, by direct measurement of oxygen consumption. The cost of excavating a tunnel for gophers and Martins is not directly comparable because of the differences in size and time investment but the cost in terms of multiples of BMR would perhaps be more similar. For the gopher

APPENDIX 5 (continued)

the cost ranged from 2.8 to 7.2 × BMR with a mean of 4.1 × BMR. These values are used here for the Sand Martin.

7. Nestbuilding. Mud collection is likely to be energetically expensive since the power required for flight at zero and at low speeds, especially at take off and landing, is greater than that for a medium speed (Pennycuik 1972). So the to-ing and fro-ing between mud and nest as well as the carrying of extra weight and the process of building itself will be at lease as expensive as normal flight. Hence normal flight costs are used for nestbuilding.

8. Sperm Production. The cost of sperm production was assumed to be negligible (King in Farner 1973).

9. Egg Production. Petersen (1955) deduced that, in the Sand Martin, an egg started to develop six days before being laid. Ova maturation takes four days, the egg remains in the oviduct for one day while the albumen and shell are deposited, and it is laid early on the sixth day. The same development time was assumed to pertain to the Swallow egg in this day. Bryant (1972) calculated that yolk deposition followed a sigmoid curve and was most rapid on the third day. The increment on any one day never exceeded the calorific value of a single egg for clutches of 2 to 5. The calorific value of the eggs of altricial passerines depends on their weight according to the equation:

$$\text{calorific value (kcal)} = 1.124 \times \text{weight}^{0.9438}$$

(Kendeigh et al 1978)

In the domestic fowl there is an efficiency of conversion of productive energy into energy deposited in the egg of 77% (Brody 1945). The same was assumed to pertain to hirundines.

10. Incubation. There has been considerable discussion on the expected energy expenditure of an incubating bird. Energy must be used to maintain the eggs at a high and constant temperature. Extra energy may be required for this but some or all of this energy may come from normal heat loss via the brood patch which is greatly vascularised. The lower the ambient temperature, however, the more heat will be required so the energy cost then increased (El Wailly 1966). Kendeigh (1963) formulated a widely used equation for the calculation of the energy required for incubation:

$$M = n.w.c.b.(t_e - t_a).i.(1 - s.pc.) \ . \ 10^{-3} \text{ kcal bird}^{-1} \text{ day}^{-1}$$

n = number of eggs in the clutch;

w = weight of egg (g);

c = specific heat capacity of eggs = 0.8g cal g^{-1} $°C^{-1}$;

b = rate of cooling of eggs;

t_e = mean egg temperature;

t_a = mean nest air temperature;

i = interval in hours (24);

s = proportion of egg surface covered by brood patch - usually taken as 0.25;

pc = proportion of i that the bird is on the eggs;

10^{-3} = conversion of gcal into kcal.

For the Swallow $n = 5$, $w = 1.97$, $b = 3.10°C \ h^{-1} \ °C^{-1}$,

$t_e = 35.7°C$, $t_a = 30.1°C$, $pc = 0.834$ (this study).

For the Sand Martin - as above but $w = 1.42$,

$t_e - t_a = 10°C$, $pc = 0.985$ (this study).

APPENDIX 5 (continued)

Energy is also required to reheat the eggs after an inattentive period:

$M = n.w.i. (T_{mx} - T_{mn}). n_{att}.10^{-3}$ kcal day^{-1} (Kendeigh et al 1978)

T_{mx}, T_{mn} = maximum and minimum egg temperatures;

n_{att} = number of attentive periods.

For the Swallow T_{mx} = 35.7°C, T_{mn} = 27.8°C, n_{att} = 50 (this study).

For the Sand Martin - it was assumed that Sand Martin clutches would not require reheating since the eggs are rarely left unattended.

Insulation and/or an enclosed nest reduces heat loss from both the clutch and the sitting bird. Hummingbirds in a nest with half their body exposed save 40%, and with a quarter exposed 60%, of the heat loss of fully exposed birds at 0 - 4.6°C (Calder 1973). Nest air temperatures would also be hept high in an insulated nest. The metabolic rate of an incubating Swallow was therefore calculated at 20°C during the day.

Some of the heat necessary for incubation may be provided by the embryo. Precocial birds such as Calidris spp. can provide 35-40% of the heat required when nearing hatching time (Norton 1973). Altricial species, however, could only provide a few percent of the necessary heat since they are poikilothermic.

11. Brooding. The heat required and the heat produced by young nestlings depends on the number and age of the young and the brood mass. Several nestlings can huddle together to reduce the collective surface area exposed. The heat production of a brood of Great Tits, Parus major, was found by Mertens (1969) to be related

to the (brood mass)$^{0.67}$ due to this huddling effect at 12°C. The heat production also varies with age. O'Connor (1975) obtained different equations relating metabolic rates to brood weights of 6-7 day old and 11-12 day old Blue Tits, P. caeruleus, at 15°C. Metabolic rate is reduced to some extent by the insulative properties of the nest (O'Connor 1975). Mertens (1969) found that Great Tit nestlings in a wooden nest box need

$$0.0719\ W_b^{0.613}\ (T_b - T_a)\ \text{kcal day}^{-1}$$

W_b = weight (g) of the brood

T_b = mean chick temperature

T_a = ambient temperature

This equation was used for calculations in this study with T_b = 34°C and T_a = 25.5°C (this study).

SPEED OF FLIGHT:

The theoretical minimum power speed (V_{mp}) is

$$\frac{0.76W^{V2}}{\rho^{1/2}\ A^{1/4}\ Sd^{1/4}} \qquad \text{(Pennycuik 1972)}$$

W = weight (Newtons); ρ = air density (1.22 kg m^{-3} at 0m a.s.l.)

A = equivalent flat plate area = $(6.2 \times 10^{-4})\ W^{2/3}$ sq.m.

Sd = disc area - $\pi b^2/4$ where b = wingspan (wingspan was measured in this study and is 0.273m for Sand Martins and 0.327m for Swallows).

V_{mp} is the speed at which a bird can travel as long as possible on as little fuel as possible.

V_{mp} = 4.61 for Sand Martins, 4.67 for Swallows.

$V_{mr} = 1.8\ V_{mp}$.

Measurements of Speed

For the Swallow the mean flight speed was 10.4 ms^{-1}. For the subjective estimate of speed (Section 4.2) the mean speed was taken to be 8.4 to 12.4 ms^{-1}, slow speed as < 8.4 ms^{-1} with an average of 6.9 ms^{-1}, and fast speed as > 12.4 ms^{-1} with an average of 13.9 ms^{-1}.

For the Sand Martin the mean speed was taken to be 6.2 to 10.2 ms^{-1}, slow speed as < 6.2 ms^{-1} with an average of 4.7 ms^{-1} and fast speed as > 10.2 ms^{-1} with an average of 11.7 ms^{-1}.

APPENDIX 6

Productivity of hirundines

1. Swallow

Clutch size	Number fledging per nest[a] 1	2	3	
6	5.25	4.76	5.5	(n = 2)
5	4.00	4.45	4.6	(n = 33)
4	3.36	3.88	3.7	(n = 13)
3	1.40	3.00	2.5	(n = 2)

[a] 1. Al-Rawy and George 1966
2. Mizuta 1963
3. This study

2. Sand Martin

Clutch size	Number fledging per nest (this study)	
6	6	(n = 1)
5	4.3	(n = 21)
4	3.5	(n = 3)
3	2.7	(n = 3)

3. House Martin

Clutch Size	Number fledging per nest (Bryant 1972) 1st brood	2nd brood
6	6.00*	-
5	3.64	5.00*
4	3.22	3.37
3	2.47	2.52
2	1.80	1.86

* artificially enlarged

Growth of nestling Sand Martins

by A. K. Turner and D. M. Bryant

Nestling Sand Martins are heaviest at 12 days old (on average), but then lose weight. Rapid early growth of the tarsi enables nestlings to move along the burrow towards incoming parents. The nestling period averages 22.3 days, and the young are dependent on their parents for a further 4–5 days after fledging.

ECENT STUDIES OF THE BREEDING BIOLOGY of the House Martin *Delichon urbica*
ryant 1975) and the Swallow *Hirundo rustica* (McGinn and Clark 1978) have
th included observations of nestling growth. However, there has not been a
tailed study of the development of Sand Martins *Riparia riparia* (the only other
rundine to breed in Britain), although the conspecific Bank Swallow has been
vestigated in North America (Petersen 1955). The present paper describes the
owth of nestling Sand Martins and draws comparisons with growth data for
ouse Martins and Swallows.

STUDY AREA AND METHODS

he study was carried out during the summers of 1977 and 1978 at a sand quarry
ar Dunblane in Perthshire (56°12′N, 3°56′W), where over 200 pairs of Sand
artins were nesting. The site lay amongst mixed agricultural land at around
0 m asl.

A pit dug at the back of each Sand Martin burrow allowed nestlings to be
moved for observation. Each nestling was individually marked with a water-
oof dye and weighed regularly with a 50 g Pesola spring balance to the nearest
1 g; wing length (maximum chord) and length of the 9th primary were also
easured. The day on which all the nestlings in a brood had hatched (day 1) was
own precisely for four broods, while the ages of other broods on the first day
weighing were calculated from fitted lines.

Sand was still being quarried from one part of the colony; after destruction of
eir nest sites several young were taken for carcass analysis. These birds were
eze-dried and their lipid extracted with a soxhlet (80% ether: 20% chloroform).
dditional measurements of tarsus, bill and tail length and gape width were made
these nestlings and on some others in the field.

RESULTS

he Sand Martin growth curve (Figure 1) shows the typical hirundine pattern of
pid growth to a peak followed by a period of weight recession (Edson 1930,
icklefs 1968). The mean peak weight is 16.2 g on the 12th nestling day, although
t all the nestlings within a brood would be at the peak weight simultaneously.
one brood, for example, this was spread over the 12th to the 15th nestling days.
he peak weight is lower and occurs at an earlier age than in the Bank Swallow
etersen 1955) which reaches 18–19 g at 15–17 days (Table I).

The nestling period of the Sand Martin is 22.3 days and the fledging weight is
out the same as an adult's. The scale of the weight loss is about 18% of the peak

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TABLE I. BASIC GROWTH DATA (MEAN±1 STANDARD DEVIATION) FOR SAND MARTIN, BANK SWALLOW, SWALLOW AND HOUSE MARTIN

	Sand Martin	*Bank Swallow*	*Swallow*	*House Martin*
Nestling period (days)	22.3±2.1 (30)	20–23	21.7±1.8 (33)	27.2±2.1 (51)
Peak weight (g)	16.2±1.7 (16)	18.5	23.2±1.9 (33)	24.9±2.6 (68)
Age of peak weight (days), from growth curve	12	15–17	14	16
Hatching weight (g), chicks<24 hours old	1.5±0.2 (8)	1.5	1.9±0.3 (11)	1.8±0.4 (52)
Fledging weight (g)	13.3±1.1 (23)	15	19.6±1.4 (15)	18.3±1.5 (54)
Fledging winglength (mm)	96.6	—	102	89.4
Adult weight (g)	13.7±1.3 (301)	14.3 (121)	19.0±1.8 (52)	19.6±1.5 (392)
Adult winglength (mm)	107.2±3.2 (108)	—	128.1±3.6 (24)	111.5±3.4 (188)
Weight loss as % of peak weight	17.9	19	15.4	26.8
% of adult wing achieved as nestling	90.1	—	79.6	80.2
Adult tarsus length (mm)	11.1±1.1 (25)	—	12.2±0.9 (24)	11.9±0.2
% of tarsus growth completed at 7 days	77	—	70	87
Source	This study and Turner in prep.	Petersen (1955)	This study and Turner in prep.	Bryant (1978*a*,*b*) and in press; O'Connor (1977)

NOTE. Figures in brackets are sample sizes. Fledging winglength calculated from nestling period and growth curve information.

weight; similar figures are given by Petersen (1955) for the Bank Swallow. Continuous watching at three nests showed that young were dependent on their parents for food for 4.7 ± 1.2 days after the last youngster fledged.

The growth of the wing and tail is slow for the first 6–8 days and then increases rapidly with age (Figure 2). The nestlings fledge with a wing length of 90% that of the adults. The primaries emerge on days 6–7 and the feather tips sprout on days 9–10, the length of the primaries increasing linearly with age. There were close correlations between both age and wing length and between age and 9th primary length; the appropriate regression equations were used for ageing nestlings when the hatching day was not known (see Appendix). Nestlings less than 7 days old were aged from the age/weight curve alone.

The tarsus grows rapidly for the first 6–8 days, by which time it has reached 77% of the adult length; growth then slows down considerably. Early growth (see Figure 3) facilitates an upright posture during begging, and allows the nestlings to move along the burrow towards their parents to be fed. The bill also grows most rapidly during the first 7–8 days, with gape width reaching a maximum at about the middle of the nestling period, and then decreasing slightly.

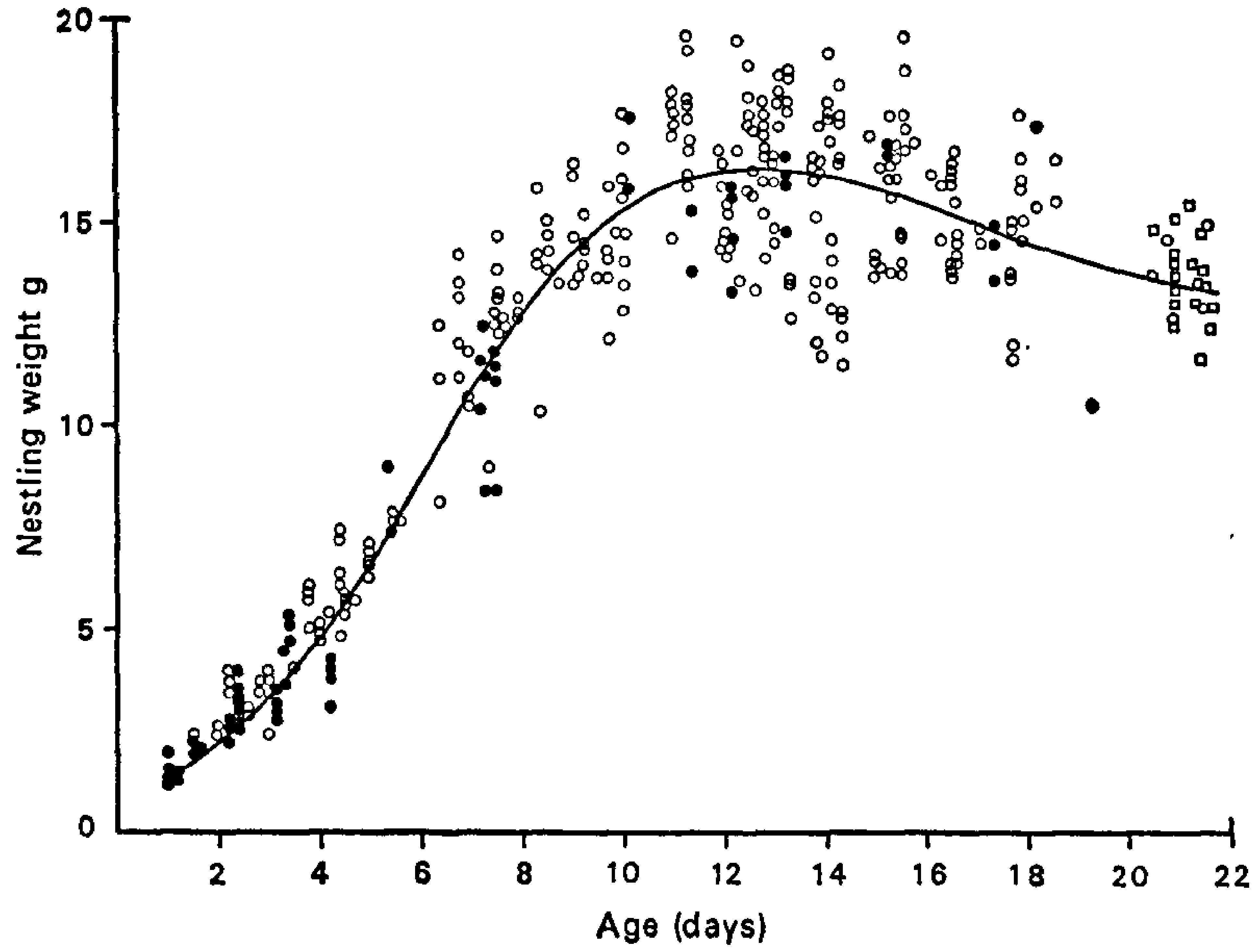

Figure 1. Growth curve for nestling Sand Martins (fitted by eye). Closed symbols = individual nestlings aged at hatching; open symbols = nestlings aged after day 1 using equations given in Appendix 1.

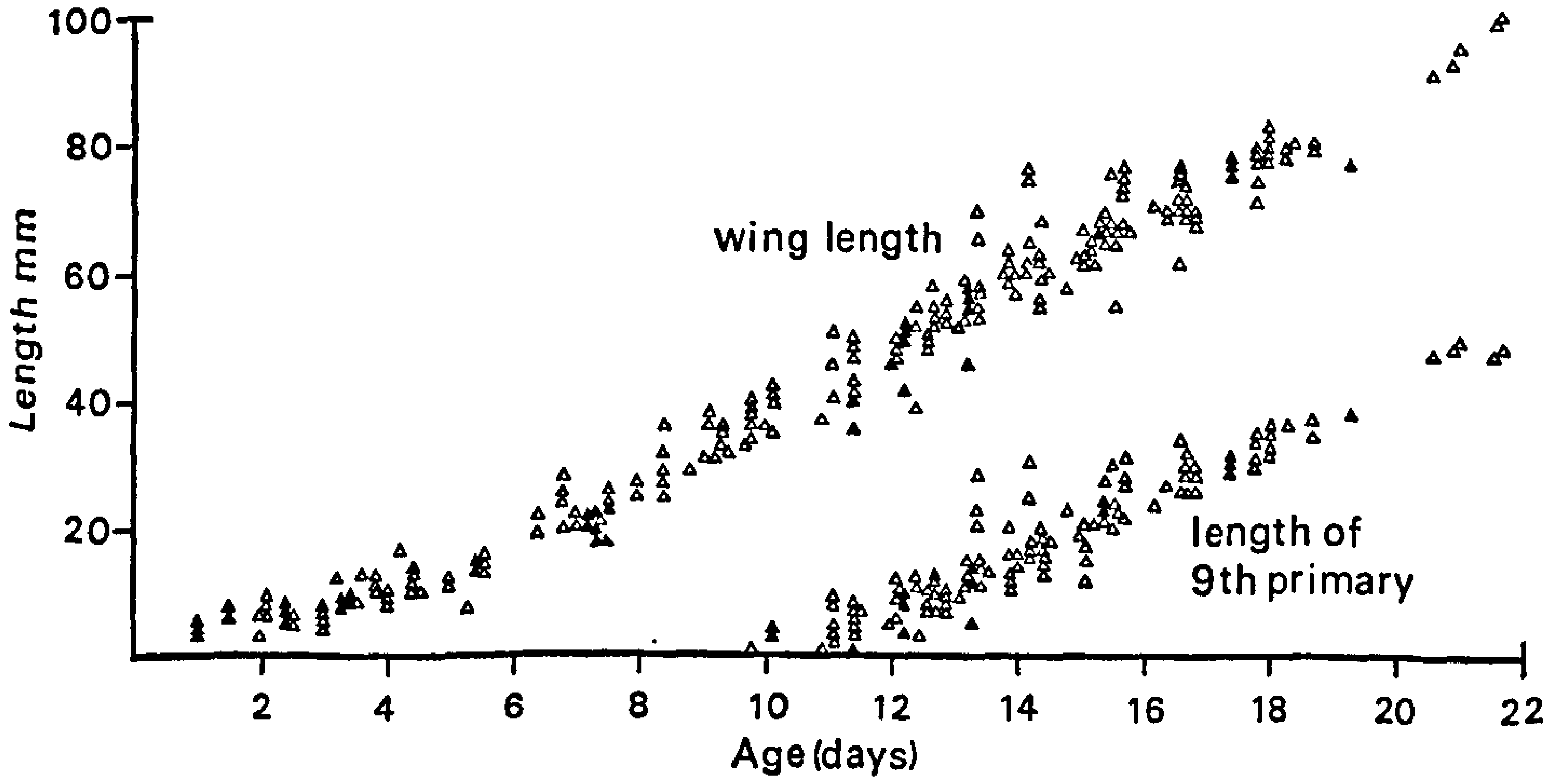

Figure 2. Growth of wing-length and 9th primary in nestling Sand Martins. Open and closed symbols as in Figure 1; regression equations are given in Appendix 1.

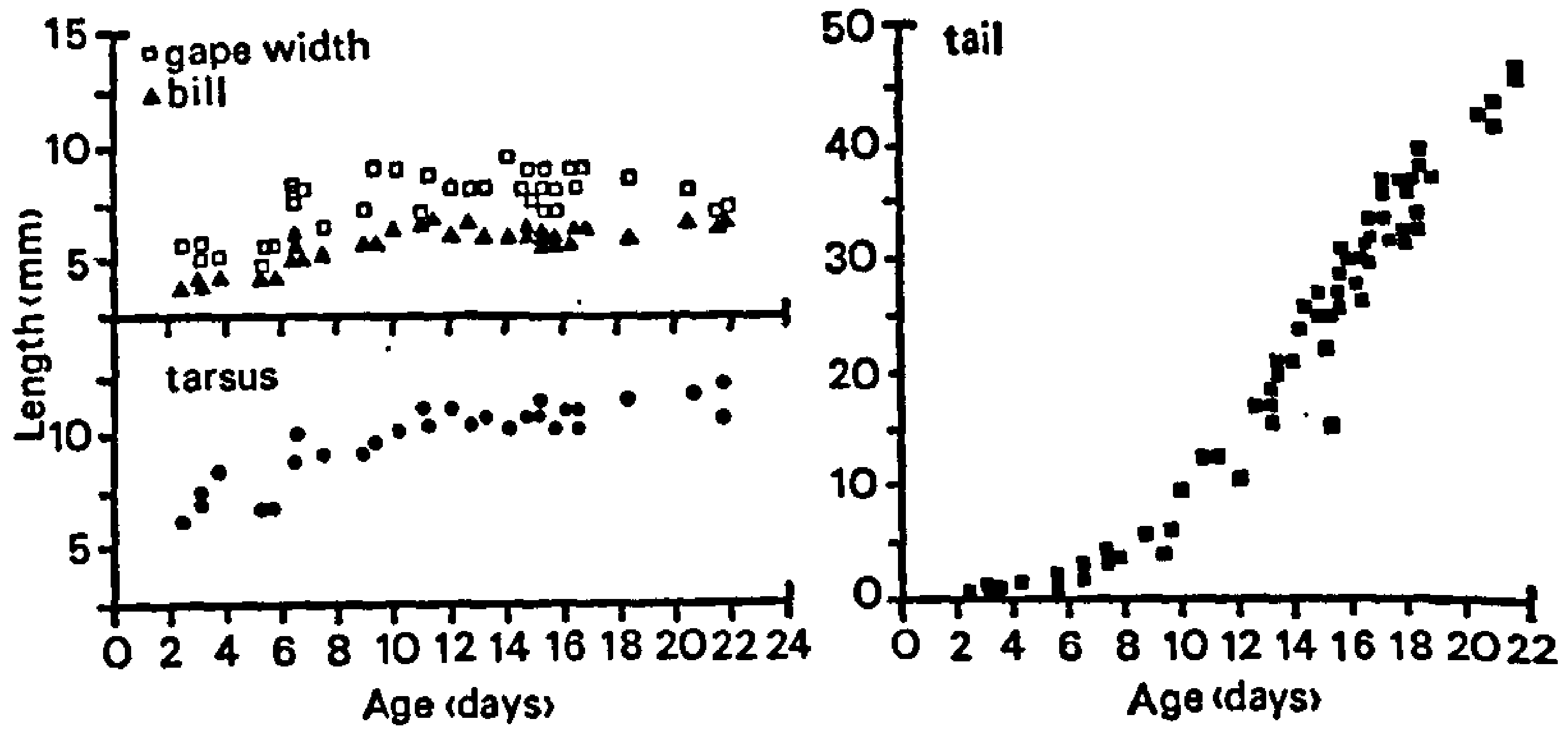

Figure 3. Gape width, bill length, tarsus length and tail length in relation to age for nestling Sand Martins.

During the period of rapid growth Sand Martins begin to put on fat (Figure 4). Once the peak weight has been reached a high, although variable, proportion of the weight of the nestling is fat.

DISCUSSION

The main features of the growth of the Sand Martin are compared in Table I with those of the Bank Swallow, Swallow and House Martin. The nestling periods of the Sand Martin and Swallow are similar, despite differences in body size, whereas the House Martin has an extended time in the nest and subsequently fledges at a lower weight (relative to the adult) than the other species. The nestling period of hirundines is longer than for many other passerines of similar weight and at fledging the young remain around the nest for several days. Sand Martins and House Martins are fed at the nest entrance for up to a week after their first flight, though Swallows, having more vulnerable and open nest sites, are fed away from the nest itself.

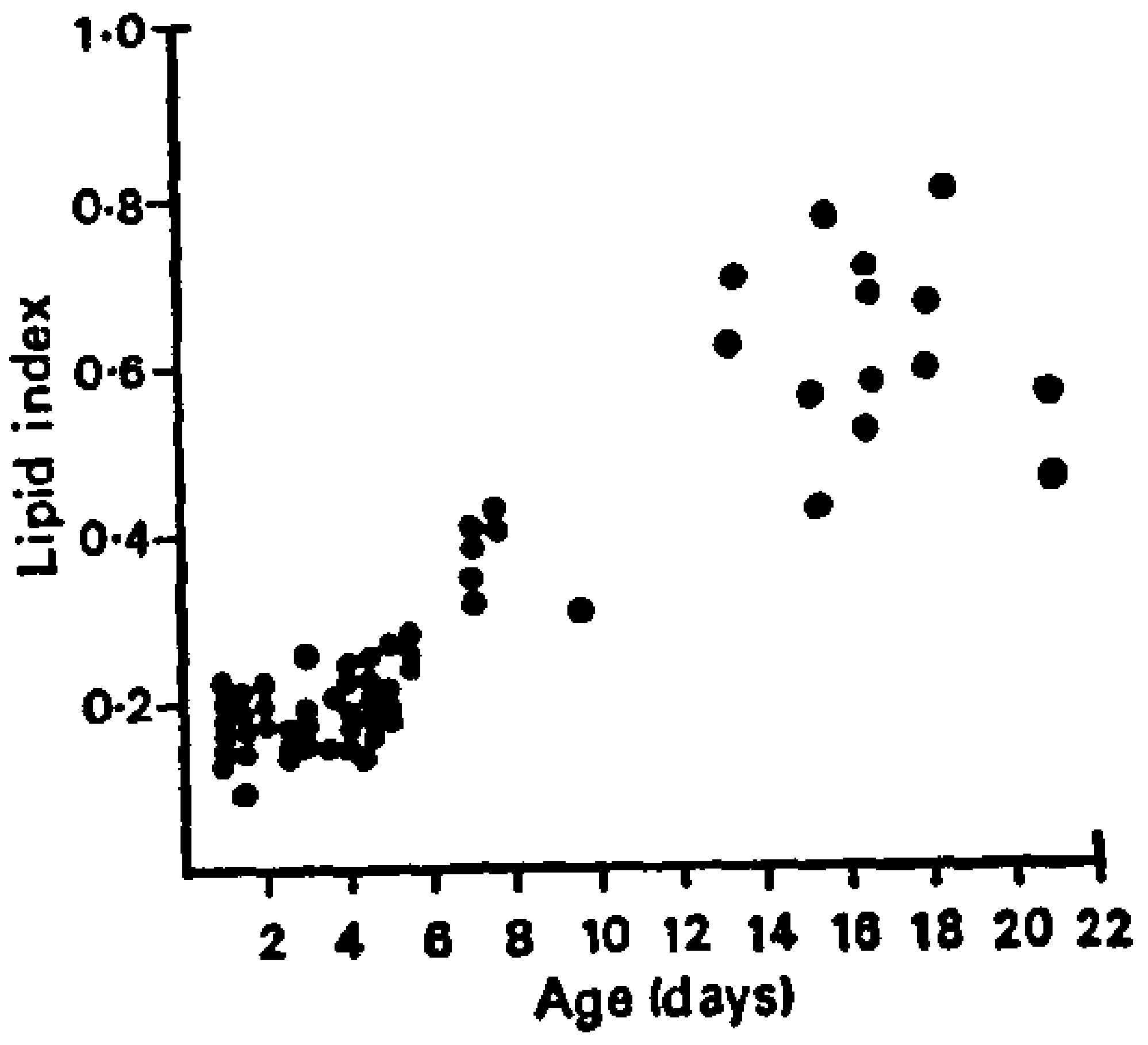

Figure 4. Lipid index in relation to age in nestling Sand Martins (Lipid index=lipid weight/lean dry weight of carcass).

Associated with the differences in nestling period is the extent of the weight ecession, which is greatest for the House Martin and least for the Swallow. The House Martin also reaches the peak weight later than the Swallow and Sand Martin but at a similar age to the Bank Swallow. Within a brood the nestlings may attain peak weight over several days, so that the maximum demand for food is spread over a relatively long period. Any potentially limiting effect of food supply on brood size is thus lessened (Bryant 1978*a*). The weight hierarchy could also allow brood reduction to occur during periods of sustained food shortage Lack 1968); but this is infrequent in hirundines in Britain, and it is likely that the most conspicuous weight hierarchies are due to a scarcity of food during the laying period affecting the quality of the eggs (Bryant 1978*a*).

The growth of wings, feathers, tail, bill and tarsus in the Sand Martin are similar to those in the Swallow and House Martin. The tarsus grows more rapidly at first in the two martins than in the Swallow, reflecting the formers' need to move towards the nest entrance rather than simply beg for food.

Certain differences in growth in these hirundines reflect their susceptibilities to an unpredictable food supply. The abundance of insects can change markedly over the nestling period; times of food shortage can depress the growth rate of nestling House Martins and may lead to an extended nestling period (Bryant 1975). A scarcity of food could also account for the relatively long time taken by the Bank Swallow to reach peak weight in Petersen's (1955) study. In general, however, the Sand Martin and Swallow forage more efficiently than the House Martin (in terms of net energy gain per unit foraging time), and are affected to a lesser extent by bad weather and consequent food shortage (Bryant and Westerterp 1979; Turner, in prep.).

Associated with these different foraging efficiencies is the relative amount of fat put on by well-fed nestlings: the greater the potential effect of a food shortage, the larger the fat store. The fat deposit is important to help the nestling survive under extreme conditions and to avoid the formation of fretbars in the feathers when food is scarce (O'Connor 1977). Such buffering against food shortage has been described for the Swift *Apus apus* (Lack 1954) and for the Bullfinch *Pyrrhula pyrrhula* (Newton 1968). The Lipid Index (the ratio of fat in the nestling to its fat-free dry weight) for birds at or over peak weight ranges from 0.3–0.6 in the Swallow, 0.4–0.8 in the Sand Martin, 0.5–0.9 in the House Martin, to well over 1 in the Swift (Koskimies 1952) which is a less efficient aerial feeder than the hirundines. Clearly, the size of the fat store is linked to the probability of each species experiencing difficulty in feeding the young. A fat store will also be useful to fledglings, especially in bad weather and before they become proficient at catching insects (O'Connor 1977, Bryant in press).

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SUMMARY

Several aspects of Sand Martin development were investigated at Dunblane (Perthshire) in 1977 and 1978. Measurements were made of weight, wing length, length of 9th primary, tail, tarsus, bill and gape width. The lipid content of some nestlings was als measured. The Sand Martin nestling reaches a peak weight of 16.2 g on the 12th da but then loses weight, fledging at about 13 g. The nestling period is 22.3 days. The lipi index (ratio of fat content to fat free dry weight) is 0.4–0.8 for nestlings at or over pea weight. Comparisons are drawn between the Sand Martin and the Swallow, Hous Martin and Bank Swallow. Regressions of wing length and 9th primary length on ag were calculated and used for ageing nestlings of unknown hatching date.

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APPENDIX 1.

Regression equations used for calculation of age of nestling Sand Martins.

Equation 1. Regression for winglength (mm) on age (days) for day 7 onwards:
$y = 5.43x - 18.91$, $r = 0.98$: $P < 0.001$.

Equation 2. Regression for length of 9th primary (mm, excluding sheath) on age fo day 11 onwards:
$y = 4.72x - 51.18$, $r = 0.98$: $P < 0.001$.

Equation 3. Regression for weight (g) on age for day 2–7:
$y = 1.58x - 1.11$, $r = 0.93$: $P < 0.001$.

Nestlings were aged using an average from equations 1 and 2, except for those under days old when equation 3 was used. The age of the brood was taken as that of th youngest nestling.