233

PREDATION STRATEGIES IN AERIAL FEEDING BIRDS

A thesis submitted to the
University of Stirling
for the degree of
Doctor of Philosophy
by
D. R. WAUGH, B.Sc.

Department of Biology
University of Stirling,
Scotland.

December, 1978

ABSTRACT

The predation strategies of four species of aerial feeding bird, the Swallow, *Hirundo rustica*, Sand Martin, *Riparia riparia*, House Martin, *Delichon urbica* and Swift, *Apus apus*, are examined during their breeding season in Britain.

The abundance of aerial insects upon which they feed increases in April and reaches a plateau in May which is maintained until September. Aerial insect density is higher nearer the ground, the spring rise in abundance occurs earlier, a greater proportion of larger insects are available and insect numbers fluctuate less than at higher levels. The arrival times of the different predator species into the breeding area are staggered and this is linked to their preferred prey and feeding station, and to the distribution of aerial insects.

Throughout the breeding season the four species of bird are ecologically isolated with respect to feeding station in the air-space and various characters of the insect prey, primarily size and mobility. It is suggested that to coexist they segregate along a combination of axes of the feeding niche, although segregation in air-space may be the most effective. Morphological adaptation to feeding niche is shown for tail shape, wing-length and bill shape, which respectively influence manoeuvrability, mode of flight and prey handling ability of the predators.

Both Sand Martin and Swallow show increases in their prey size and mobility niche breadths in favourable feeding conditions whilst all four species simultaneously show decreases in air-space niche breadths. It is postulated that both within and between species there is a tendency to switch between patch specialisation and prey specialisation. Current theories of optimal patch and prey choice are discussed in relation to this hypothesis.

Under very adverse conditions prey size overlaps are small and, when they increase, air-space overlaps simultaneously decrease. This suggests competition between aerial feeding birds in adverse conditions.

Swallows deliver more meals per unit time to larger broods, with an increase in the feeding rate of the male most evident. Males also increase their feeding rate to second broods, but these receive the same amount of food as first broods indicating a seasonal decline in meal size. There is a seasonal decline in size of prey items even though a higher density of available large (> 5 mm body length) insects occurs during second brood feeding. It is shown that the largest insects are in patches too far from second brood nests to be profitable. For first and second broods an optimal foraging strategy is to choose patches with the largest mean insect size, if the patches are within a given distance from the nest. Selection of an optimal size for fast-flying taxa is influenced by time and energy costs of pursuit.

It is suggested that rearing larger than normal broods is constrained by the requirement of equal parental investment and the extra reproductive cost likely to be incurred by the male bird.

Based on a very small sample of nests it is tentatively suggested that in colonial nesting Sand Martins there is an advantage in nesting early, with more birds feeding communally to aid location of food concentrations. Because individuals with centrally placed burrows

are more able to minimise time spent deterring predators, and because early centre nesters suffer less time loss through competition at the nest-site, these same individuals have more time for locating other feeding birds and food concentrations. Thus the early season, centre colony nesters may collect more food per unit time and raise more off-spring.

Comparison of aerial feeding bird communities in three zoogeographical regions indicates that selection for characters contributing to mode of flight and manoeuvrability are more important than selection for bill character.

In Africa the Palearctic species maintain essentially the same feeding stations as in their breeding season although the air-space niche breadths show contraction and overlap is reduced except between Swift and House Martin. The indigenous species have different feeding stations and small air-space niche breadths, and where overlap is high the species involved apparently do not breed during the "winter" of the Palearctic species, possibly because of food shortage.

The prey size niche breadth of the Swallow, H. rustica is very similar between Britain and Africa. With many more species utilizing this niche axis, compensation is likely along another axis, probably air-space.

ACKNOWLEDGEMENTS

My foremost thanks go to my supervisor, Dr D. M. Bryant, for much stimulating discussion throughout the duration of this project. He has allowed me to lean heavily on some of his ideas, whilst clarification of my own ideas has been constantly encouraged by his candid appraisal of my work. I thank him for being so patient.

My colleague, Dr C. J. Hails, provided much encouragement through help with field-work and discussion of various relevant topics, for which I am most appreciative.

The study would not have been possible without the generous cooperation of many farmers and landowners within the area. I extend my thanks to them all, in particular Messrs. Fleming of Barbush Quarries, Dunblane.

I have much appreciated the extended use of facilities within the Biology Department, University of Stirling, allowed me by Professor H. Meidner. Within the same institution I also thank Dr P. Bannister and Dr S. Matthews for advice on statistical matters.

Dr J. Whiteley, S.U.R.R.C., East Kilbride gave considerable help with the automatic nest recorder, Rothamsted Experimental Station loaned insect sampling equipment, Mr. I. C. J. Galbraith, British Museum (Natural History) and Mr. I. H. J. Lyster, Royal Scottish Museum allowed me unfettered access to their respective bird collections. I thank them all.

(cont.)

Mr. C. W. Benson and Mr. R. J. Dowsett generously provided much unpublished data on African species for which I am extremely grateful.

Many thanks are due to the various people who participated in ringing and measuring Sand Martins, in particular Mr. A. B. Mitchell, and to Ms. A. Turner, for allowing me perusal of some of her insect data.

I gratefully acknowledge the financial support of N.E.R.C., and thank Mrs. M. Abrahamson for a superb typing job completed in record time.

CONTENTS

CONTENTS (cont.)

CHAPTER I

INTRODUCTION

I. INTRODUCTION

The foraging behaviour of predators (using the term predator in the broadest sense) has increasingly become the focus of attention for theoreticians, ecologists and ethologists during the past two decades. There has been a gradual change in approach to the study of predation (reviewed by Krebs 1973), beginning with the experiments of Holling (1959a, b, 1965, 1966) from which he derived the "functional response" curve. Tinbergen (1960) introduced the concept of a predator developing a "searching image" for particular types of prey, and Gibb (1958, 1962a) proposed "hunting by expectation", whereby a predator learns to expect a certain density of prey. Discussions of these ideas (e.g. Dawkins 1971 , Simons and Alcock 1971) include that of Royama (1970) who proposed an alternative model; "niche" (= patch) hunting and profitability of prey types.

However, most of the recent foraging theory and tests have been derived from the assumption that animals are efficient in their foraging activities, and therefore should either maximise net gain of a particular "currency", usually regarded as energy, or minimise the time required to collect a fixed amount of the currency; these are collectively known as optimal foraging theory. Beginning with MacArthur and Pianka (1966) and Emlen (1966, 1968), there have been a number of models proposed (e.g. Schoener 1969, 1971a, Rapport 1971, Charnov 1973, Pulliam 1974, Werner and Hall 1974), which reach essentially similar conclusions indicating that animals may be expected to forage optimally. Most evidence in support of this hypothesis comes from studies on birds (e.g. Krebs et al 1974, Gill and Wolf 1975, Davies 1977a, 1977b, Goss-Custard 1977, Krebs et al 1977), but also mammals (Emlen and Emlen 1975, Anthony and Kunz 1977), fish (Werner and Hall

1974, Werner 1977), and insects (Charnov 1976, Hubbard and Cook 1978): useful reviews may be found in Charnov (1973), Krebs (1973), Krebs and Cowie (1976), and Pyke, Pulliam and Charnov (1977).

Underlying these specific aspects of predation has been the more general concept of exploitation of the food supply and its ultimate importance in the regulation of animal populations. Major discussion of changes in animal numbers (Andrewartha and Birch 1954, Lack 1954, 1966, Wynne-Edwards 1962) coincided with a re-appraisal of the niche by Hutchinson (1957), which provided a useful insight into the role of other species, both competitors and predators, in determining the extent to which all potentially available resources, and in particular food resources, may be utilized by an organism. Hutchinson's treatment of the niche provided much of the impetus for the modern formulation of niche theory (e.g. MacArthur 1968, Roughgarden 1972) and experiment, and concurrent ideas of resource overlap, competition between species, and the structure of communities (e.g. MacArthur and Levins 1964, 1967, MacArthur and Wilson 1967, MacArthur 1971, 1972, Cody 1974).

There is widespread acceptance that where species occupy the same habitat, differential selection of food resources gains prominence as the means by which they will achieve co-existence, any evolutionary outcome of these differences being termed ecological isolation (Moreau 1948). The importance of reducing overlap in food requirements to permit the co-existence of different species emphasises the relevance of detailed studies, as outlined above, of predator diet, foraging behaviour and related morphology, since only these will ultimately predict the extent of food resource use (e.g. Werner 1977). Furthermore, when the extent of food resource use is determined for a species, it is instructive to know not just that there is an overlap in food requirements with another species, but how much common resource use can be tolerated for co-existence. Thus, defining the limits to similarity of species has been the subject of recent theoretical study (MacArthur and Levins 1967, MacArthur 1972, May and MacArthur 1972). A parallel approach to quantifying the limits to utilization of similar foods, and hence to co-existence, has been to measure the differences in morphology, mainly in body size and of feeding apparatus, between sympatric species (Hutchinson 1959, Klopfer and MacArthur 1961, Schoener 1965, Van Valen 1965, Hespenheide 1973, Willson, Karr and Roth 1975, Wilson 1975). This has led to a number of studies where, for each member of a particular species guild, predator body size and/or size of feeding apparatus or other morphological dimensions have been related to the size or range of sizes of prey taken (e.g. Kear 1962, Hespenheide 1971, Ashmole 1968, Holmes and Pitelka 1968, Ricklefs and Cox 1977). In addition, morphological differences between sympatric and allopatric populations of species, referred to as character displacement (Brown and Wilson 1956, Grant 1972), have reinforced the notion that differences in morphology may be useful for predicting limits to food resource use.

This thesis investigates the foraging behaviours of four aerial-feeding bird species, the Swallow, Hirundo rustica, Sand Martin, Riparia riparia, House Martin, Delichon urbica and the Swift, Apus apus. The intention has been to relate differences in their respective diets, that result from differences in foraging behaviours and morphology, to the question of how they co-exist in a single habitat, the air-space. The basis of this approach results from previous contrary interpretations of segregation in aerial-feeding birds. Thus, Lack (1971), in his extensive review of ecological isolation in birds, suggested that hirundines in Europe were segregated by nest-site choice, but he gave no indication as to how the swift species might segregate. Hoever, Hespenheide (1971) found prey size differences correlated with body size differences in North American hirundines, with the implication that they may segregate in prey size. Additionally, Bryant (1972) found the four aerial-feeding species in Britain to be taking different mean sizes of prey, and to be feeding at different mean heights from the ground. The latter study in particular provides a sound base upon which to test the relative importance of segregation by differential utilization of the aerial insect food supply. Analysis of the foraging behaviours that result in possible differences in diet has been with particular reference to optimal foraging theory, niche theory and community structure.

In a situation where time and energy demands on an animal are high, natural selection should favour those individuals which make optimal choices between various activities. Recent analyses of whether or not animals have optimal behaviour sequences have been made by Sibly and McFarland (1976) and McFarland (1976, 1977). Since the present study has been principally conducted during the breeding seasons of the birds, and hence at a time of high demand, the relative importance of foraging as just one of a number of essential activities has also been examined.

Finally, since the study species are all long distance migrants that winter extensively in the tropics, a comparison has been made of the foraging strategies in the wintering and breeding stages of the annual cycle. This is with particular reference to increased species diversity in the tropics (Klopfer and MacArthur 1961, Pianka 1966), and how foraging strategies may change from the temperate to tropical situation where co-existence is achieved within a much enlarged [illegible] [illegible] [illegible] [illegible]ld.

CHAPTER 2

LONG TERM STRATEGY : INTERACTIONS BETWEEN SPECIES

2. LONG TERM STRATEGY : INTERACTIONS BETWEEN SPECIES

Natural selection can be expected to affect behavioural and morphological adaptations in animals. An individual animal however, is unlikely to be optimally adapted to its niche at all times, given both genetic variation and competition between individuals and the patchiness and variability of the environment. Nevertheless, subject to the above constraints, average adaptation within a population should be close to that which results in maximum fitness. The following section examines behavioural and morphological adaptations associated with foraging in four species of aerial-feeding bird. Timing of the breeding seasons is investigated in relation to the food supply, and the between-phenotype component of variation in foraging niche size (Roughgarden 1972) during the breeding seasons is examined, together with the effects of this variation on overlap in food and foraging space between the species.

2.1 Description of the study area

This study was centred on the University of Stirling (O.S. 1:63,360, reference NS 808965). Within a four mile radius there is considerable topographical variation with an altitude range from sea level to at least the 400m contour in the Ochil Hills. The collection of field data was restricted to the lower-lying, predominantly mixed agricultural land. Scattered urban localities and the presence of open water ensured sufficient representation of all four study species for observations of feeding behaviour, and enabled coverage of all likely foraging habitats. The most frequent nesting sites for Swallows were the fairly evenly spaced farms, whilst most Sand Martin breeding colonies were confined to the vicinity of water-courses with nests in natural river banks, or sand quarries (Figure 2.1.1).

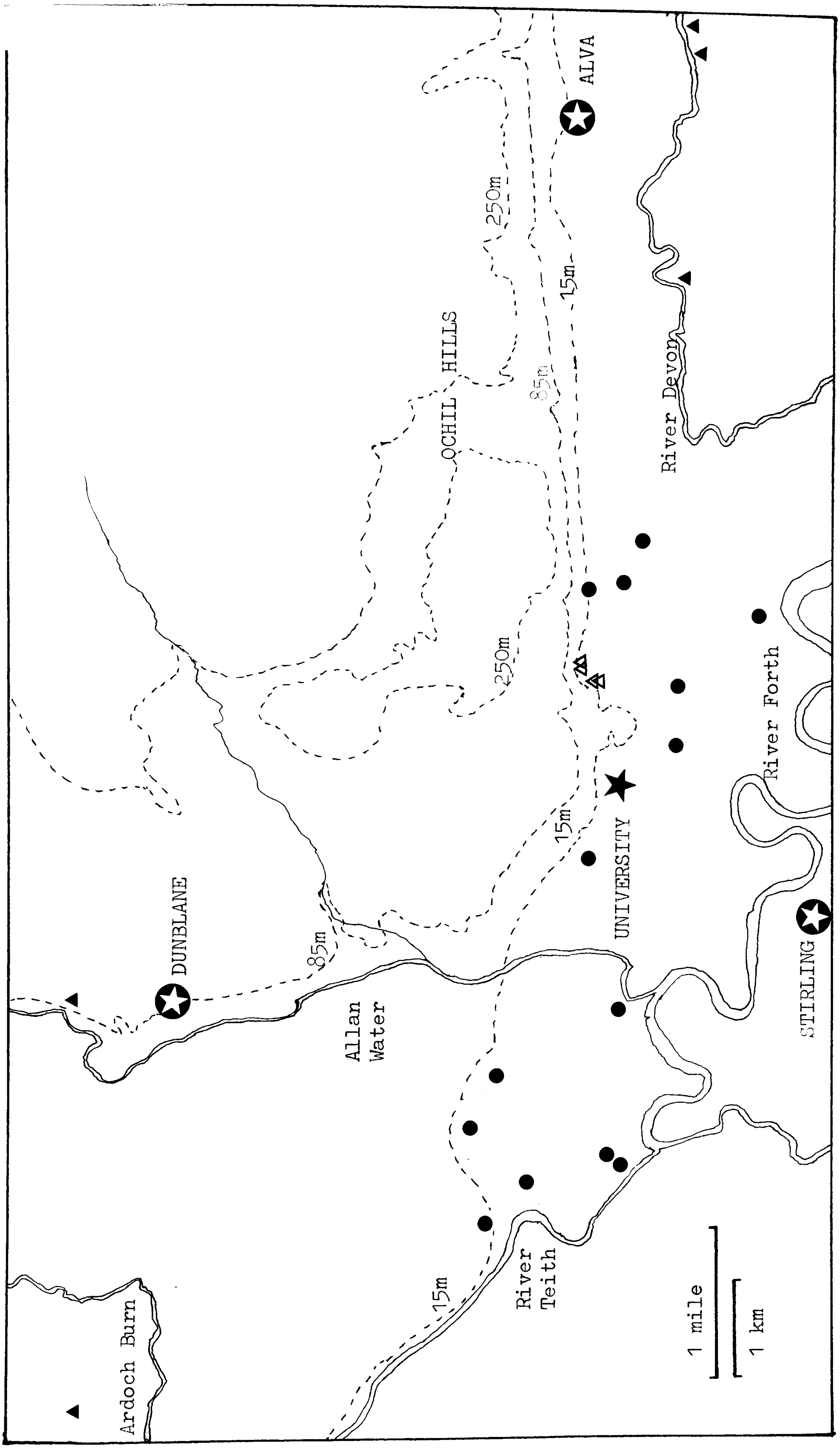


Figure 2.1.1. The study area. ▲ = Sand Martin colonies, ● = Swallow nest-sites, △ = site of insect suction traps. Broken lines indicate contours.

METHODS

2.2 Aerial insects: description and measurement of the food supply

The food supply was monitored with suction traps (Johnson 1950a, b, Taylor 1962, Taylor and Palmer 1972, Bryant 1973), at 12.2m, 1.8m and ground level, these being sited within the study area (Figure 2.1.1). The 12.2m aerofoil trap and the other Vent-axia (23cm diameter) traps all drew air vertically downwards (to avoid directional effects), through 1 mm mesh gauze, and all trapped insects were collected in plastic bottles at the base of the conical filter. The inlet of the ground level trap was set flush with the ground, the conical gauze filter being suspended into a pit and exhaust air escaping either side of the trap. Incidence of ground crawling insects falling into the trap was minimised by clearing surrounding vegetation and providing a wooden lip around the inlet periphery. Any water that may have entered the traps was drained out through the gauze bottom on each collecting bottle.

The availability of particular insect taxa to aerial-feeding birds depends largely on their periodicity, duration of flight and aerial density, although some high densities measured by the traps may not be significant for aerial-feeding birds if above a theoretical upper limit to the catching rate. Because the 12.2m trap sampled air at a constant rate throughout the day, was non-selective with respect to insect size, and was neutral in attraction, the resulting insect samples were considered to be a good reflection of the availability of each taxon as food for aerial-feeding birds. Additionally, no overt daily peaks in feeding activity have been reported for House Martins (von Gunten 1961) or Swallows (Purchon 1947), although some fluctuation in Swallow feeding rates is apparent in the present study. The 12.2m trap was designed to sample from a randomly dispersed aerial insect population and therefore high enough to exclude local insect populations, the effects of which increase nearer the ground. Another advantage of this trap is that the centrifugal fan ensures constancy of air intake in almost all wind speeds (Taylor and Palmer 1972). In using the lower suction traps the local insect populations effect was minimised by installing them in as open an area as possible. Two traps at 1.8m were sampling for the duration of the 1975 season to provide a check on possible local insect population variation. The inflow of air at the inlet to the 12.2m trap was 2.86×10^3 m^3 h^{-1}, whilst inflow into the smaller traps was 5.81 times less than this (Taylor 1955) and therefore resulting samples were standardised, together with allowance for increased wind effects on smaller traps. The insect samples collected using the lower suction traps were probably more relevant to this comparative study than samples collected with alternative trapping systems. It was not feasible to install a large number of suction traps widely spaced over the study area.

Each trap was emptied daily at 10.00 hours B.S.T. and the daily catch at each of the three trap levels was then counted before storing them either in methanol/glycerol (10:1) solution, or freezing them prior to freeze-drying for dry weight determination. Seven days was selected as a suitable interval for monitoring seasonal changes in aerial insect availability, and each seventh day a 24 hour sample was sorted into readily identifiable taxa using a low-power binocular microscope. The 24 hour samples were usually large and 20 percent sub-samples were counted and sorted in the case of the largest catches. To parallel the method used in faeces analysis (Section 2.4) the insect types were identified by wing-patterns alone, and the frequency occurrences in the total sample were calculated. Because very small

Thysanoptera can sometimes be very numerous they were excluded by Bryant (1973) in his study of House Martins, but they were never numerous in the present study and therefore were included in all calculations. Exclusion of other taxa not normally contributing to the diets of aerial-feeding birds, e.g. large Hymenoptera, was not considered necessary since they form an insignificant proportion of the total. Again, the taxa indicated by Lewis and Taylor (1965) as having 50 percent of their flight periods after dusk and before dawn form only one percent of the total and were necessarily included because of the known crepusular feeding habits of the Swift.

Individuals of each taxon were measured in wing and body length to the nearest millimetre, each size grouping being expressed as a percentage of the total summed taxa, thereby presenting a frequency distribution of available prey sizes at each trap level and hence of overall availability.

Mobility of available prey : measurement of insect flight-speed

For each prey item caught the energy gained by the predator will have been diminished by the energy cost involved in pursuit and handling of the item. It may be expected that faster flying insect types will be less easily caught and therefore increase the energy cost of capture. Lewis and Taylor (1967) have loosely correlated increasing flight speed with increase in size in insects. However, the considerable variation in flight speed between different insect types indicates that energy cost of pursuit and handling may not be simply a direct function of prey size increase. Therefore, if a number of predators were to take insect prey of the same size but selected different types, it is possible that the net energy gains would vary in relation to flight speed of the prey.

The precise energy cost to the predator of taking each prey item cannot realistically be measured, but relative costs of different prey types can be approximated by their flight speeds. No direct measurements of insect flight speed were possible and therefore to be consistent with measurements of the predator flight speeds, calculations were based on Pennycuick's (1969, 1972) equations for flight speed. Maximum range speed (Vmr) was used:

$$V_{mr} = 1.8 \frac{0.76W^{0.5}}{p^{0.5} \; A^{0.25} \; S_d^{\;0.25}} \quad \text{m/s}$$

where, W = weight in newtons

S_d = disc area

A = equivalent flat plate area

p = air density.

Individual insects of differing sizes from a representative sample of insect types were measured and weighed (wet weight) and relationships of insect size to flight speed were derived from substitution into the above equation. Mobility is considered synonymous with calculated flight speed in the present study.

2.3 Aerial feeding birds: description of the predators

The general appearance and habits of the Common Swift and the three hirundines breeding in Britain are described fully elsewhere, e.g. Witherby et al (1938-41). Detailed biometrical data of the morphological features most important for aerial-feeding are lacking however, and therefore the measurements specified below were taken.

Size of each species

The two adopted measures of size were live weight (g) (measured with a Pesola spring balance) and wing length (mm) using a stopped rule and measuring from the carpal joint to the tip of the longest primary. For Swallows and Sand Martins these data were collected from breeding adults by mist-net catching in the evening throughout the breeding season. Data for the Swift breeding weights were taken from Lack and Lack (1951) and wing measures were from museum specimens. House Martin weights were from Bryant (1975b) and wing-lengths from C.J. Hails (pers. comm).

Measurements related to flight performance

Although swallows and martins will sometimes peck food from vegetation, the diets of the four predators under consideration are largely comprised of winged insects caught in the air. Therefore, it is probable that adaptations to ecological niche will be most evident in those morphological features associated with flight performance. Differing flight speeds were considered possible important adaptations to particular feeding stations, particularly with regard to the encounter rates of prey items and changing quality of the aerial insect fauna. Calculation of flight speeds was again based on Pennycuik (1969, 1972), using maximum range speed (V_{mr}). These derived flight speeds were for comparative purposes and do not represent exact flying speeds for adult birds feeding themselves and nestlings. The use of wing-span to calculate flight speed necessitated the correction of wing length field data by adding the carpal to carpal distance derived from a sample of museum specimens.

In flight the tail assumes an importance with regard to the manoeuvrability (i.e. braking, turning) of the bird. Observations of aerial-feeding birds indicates that the tail has a major role in efficient pursuit of prey items and the relevance of the forked shape common to all four species was investigated. An index of manoeuvrability was devised to illustrate the turning capabilities of the predators in two situations,

(a) $$\frac{\text{Length of inner tail feathers (mm)}}{\text{Body weight (g)}}$$

a theoretical situation where all four species have square-tails,

(b) $$\frac{\text{Length of outer tail feathers (mm)}}{\text{Body weight (g)}}$$

the real situation with forked-tails.

Tail feathers of hirundines breeding in the study area and museum specimens, particularly Swifts, were measured to the nearest 0.5 mm.

Measurements of bill size

To illustrate possible further morphological differences data were collected on bill dimensions including culmen length, and width and depth at the nares (all measurements to the nearest 0.1 mm). Schoener (1965) introduced the term character difference as defining the measured difference in size of trophic appendages among sympatric congeneric species, and the measurements in this study adhere to this definition rather than the character displacement of Brown and Wilson (1956).

Examination and monitoring of nest contents

Throughout the breeding seasons of 1974 and 1975 regular checks of nest contents were made on Swallow and Sand Martin nests to provide basic information on egg-laying dates, clutch sizes, hatching dates, brood sizes and nestling growth rates. Weighing was performed between 09.00 and 10.00 hours B.S.T., using a 50g range Pesola spring balance.

2.4 Techniques of dietary analysis

The need for a continuous diurnal sample of both the aerial insects available and the diets of the birds was fulfilled for the latter by collection and analysis of faeces.

Validation of the faeces sampling method

Analysis of faeces was considered to be the only method of continuously sampling the diet without disturbing the birds. Hartley (1948) discussed possible errors in this technique, but it was satisfactorily employed to sample the diet of House Martins by Bryant (1973). 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.

A diet of known insect composition was fed to a single nestling Swallow (starting age 11 days) over a period of 60 hours, with the gut first being cleared using an artificial food. Faecal sacs were collected as produced and times of feeding and faeces production noted. Each faecal sac was separated out and the constituent items identified using a low-power binocular microscope. As in the studies of Bryant (1973) and Davies (1976a, b, 1977a), the insect wings were the most readily identifiable and easily quantified parts of the undigested cuticular remains. All proportional estimations of insect types in the diet were therefore based on the number of wings.

To further test the acceptability of faeces sampling, comparisons were made between the food collected from nestling Swallows and Sand Martins (using neck-collars, see Chapter 3) in field experiments and the faeces produced at the same time.

Seasonal monitoring of the diet

Throughout the months of April to September inclusive, a 24 hour production of faeces was collected every seventh day to compare directly with the aerial insect samples. The sampling interval was considered short enough to expose major changes in prey selection through the season.

Faeces were collected from Swallows and Sand Martins between 09.00 and 10.00 hours B.S.T. The proportion of adult to nestling faeces varied with season, i.e. more adult faeces at the beginning of the season, and they were collected and analysed separately. For both species, collection from many nests over a wide area eliminated possible bias in certain prey types due either to individual preference or local aggregations of prey.

Sand Martins nest in closely packed colonies in banks and therefore faeces were collected from areas of ground below the burrows which had been scraped clean 24 hours before-hand. The adults transport nestling faecal sacs from the burrows and drop them before setting out on the next foraging trip. Adult faeces were easily distinguishable from those of nestlings of all ages by the slim shape. Swallow nestling faeces were collected by placing boards beneath the nests (and cleared 24 hours before) since faecal sacs are voided from the rim of the nest. The male Swallow often roosts on a perch near the nest and it was possible to collect faeces from below these. Faeces collected from a variety of sites were mixed in a methanol/ glycerol solution and a constant sub-sample (10 percent by volume) analysed by identifying insect wings. It was possible to identify most wings to family level, but a small proportion had to be allocated to order. All individual wings of each taxon were directly measured or, in the case of fragments, estimated to the nearest millimetre. The percentage occurrence of each taxonomic group was then calculated for each sample day together with the size frequency distribution of all taxa combined. These samples could then be compared with the 24 hour suction trap samples, and both to meteorological data from a meteorological station situated near the suction traps. Swift faeces were difficult to collect and were therefore not sampled on a regular basis. However, collections made irregularly throughout the season were expected to represent the typical diet. Data on the diet of House Martins were from Bryant (1973 and unpublished).

Diet determination in conditions of low food availability

It may be expected that the abundance of aerial insects will be low during bad weather conditions. At these times aerial-feeding birds, faced with a reduction in the food supply throughout the entire air-space, should manifest changes in foraging behaviour. One of these changes could be increased generalisation by the inclusion into the diet of normally less preferred prey items (Emlen 1966, MacArthur and Pianka 1966, Schoener 1971a, Pulliam 1974, Werner and Hall 1974, Charnov, 1976). This possibility was tested in two ways. For Sand Martins and Swallows a comparison was made between the diets determined for good days and bad days (from the collection of faeces throughout the season). A "bad" day will usually involve a combination of low air temperature, strong wind and extended periods of rain. A "good" day will usually have a high air temperature and long periods of sunshine. High aerial insect abundances can still occur with strong winds and short showers providing the other two conditions prevail. The second, more direct, test was to mist-net adult hirundines whilst they were feeding low on bad days and collect faeces and live weights. The diets from this latter method were then compared with the known diets in all conditions.

2.5 Partitioning of the air-space: measurement of feeding stations

Given that no two species at any one time can utilize exactly the same resources within the same habitat, it is of interest to determine the effect of changes in the food supply throughout the air-space on the feeding stations adopted by the different aerial-feeding species. If the aerial insect fauna available at all heights was uniform in composition then equal numbers of each species may be expected to feed at any given height, and consequently segregate largely on food type (since they can all be found feeding at the same time of day). If preferred food types of each predator species occurred in higher densities at certain heights then the feeding birds should show a corresponding vertical, within-habitat segregation. Of course, complete segregation by air-space could also indicate that each species exploits all insect types within its own area, but the differences in morphology weigh against this possibility.

The air-space as a "patchy" environment

To determine feeding stations the air-space as a habitat was sectioned into a number of "patches" (Figure 2.5.1). These patches were inclusive of all areas available to aerial-feeding birds from close to low vegetation to open air high above any obstacles. Observations of feeding birds were carried out at a number of sites, each encompassing all patches within viewing range. The heights of the birds were estimated from fixed reference points of known height at each site and compared with estimates of an independent observer to eliminate bias. For each ten minute observation period numbers of each species were assigned to particular patches according to height, and distance from objects (usually vegetation) forming potential shelter-belts, i.e. likely to cause local aggregations of prey. For each species, the proportion of birds feeding in one patch

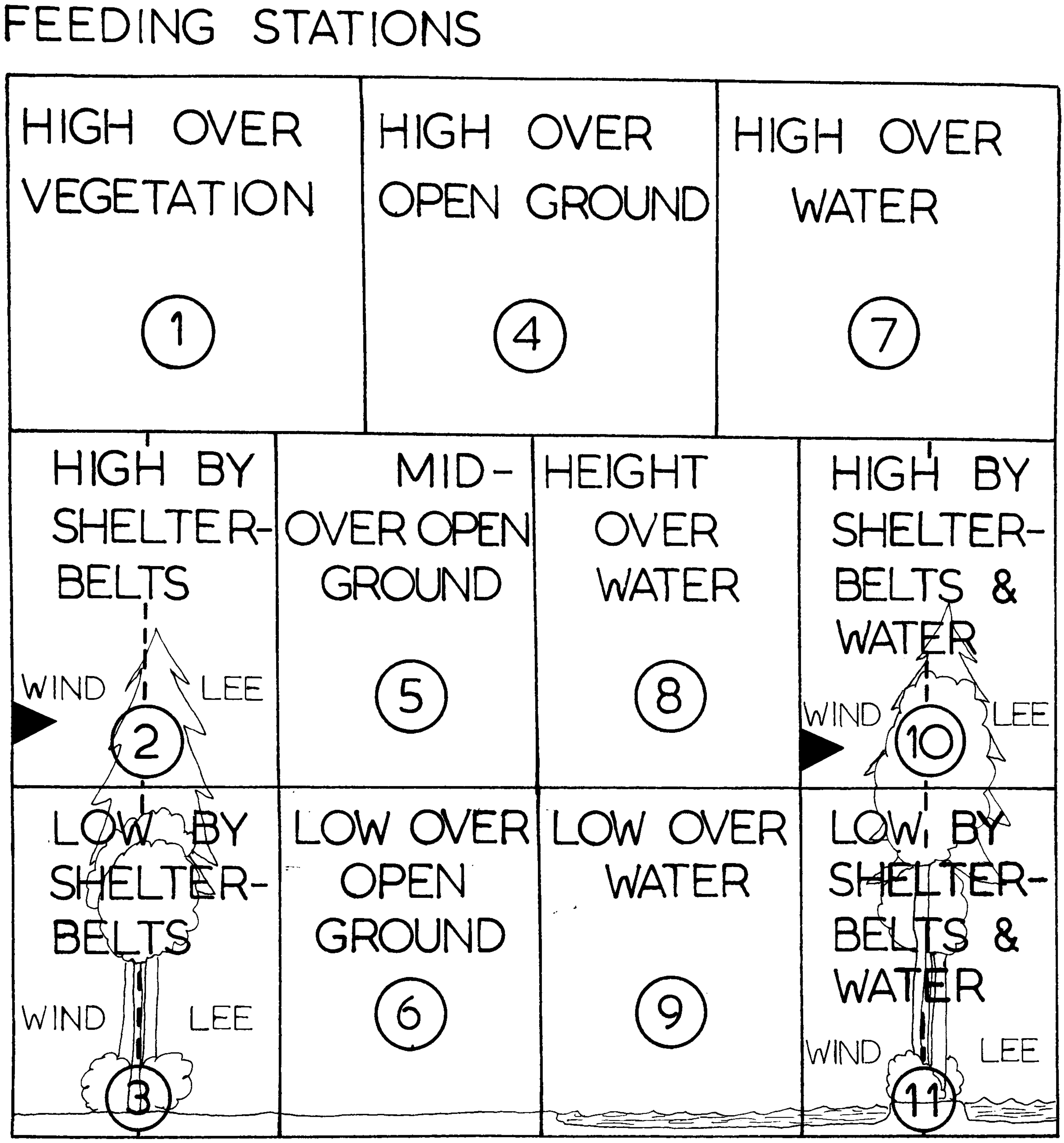


Figure 2.5.1. Diagrammatic representation of the air-space partitioned into constituent patches.

for one observation period was expressed as a percentage of total feeding birds in all patches. The vertical limits of the patches themselves were determined from the ranges of heights noted for all observations, and with no defined upper limit to the higher level were inevitably unequal in size.

Observations were carried out from time of arrival of the birds until time of departure, with a set number of observation days for each month and extra observations on bad days. Certain of the routine observations were timed to coincide with days when faecal samples would be collected. On a daily basis observations were at four stages: (a) early morning (pre-08.00), (b) mid-morning (10.00-11.30), (c) afternoon (15.00-1630), (d) evening (post-19.30, all hours B.S.T.). In addition to noting the standard daily meteorological measurements, subjective categories were assigned to the weather variables at each observation period in an attempt to expose diurnal variation. Weather variables included were wind speed, air temperature, amount of sunshine, rainfall and cloud cover, and the categories were from one (low) to five (high).

The association of flight mode with feeding station

If preferred prey types for each species occur with greater regularity in certain patches, it may be expected that the most economical mode of flight (given the morphological characters of the species) would be adopted for capturing those prey. Hence, the aerial-feeder preying on the smallest, least mobile prey could reduce energy expenditure per unit of hunting time by gliding proportionately more than an aerial-feeder that needs active (flapping) flight to pursue large, mobile prey. To test this hypothesis the ratio of gliding flight to active flight was measured for each species feeding within the different patches. During observations of individual birds, separate signals for gliding and active flight were recorded onto a cassette tape and the two components were later timed (s) by stop-watch.

Since patch utilization will not be independent of weather effects, the gliding/active flight ratios for some species on some days will have been determined in unfavourable feeding conditions.

2.5.3 The measurement of niche breadth and overlap

In any study of potentially competing species two pertinent measurements, which quantify in a repeatable manner how much and what part of a resource each species is using, are niche breadth and overlap indexes respectively.

Niche breadth was expressed as the standard deviation of the species utilization curve of the particular resource continuum in question (provided this curve exhibited a normal distribution). This measure of niche breadth, as discussed by May and MacArthur (1972) and MacArthur (1972), is particularly useful for predicting accurate limits to the number of species able to co-exist in an environment of known variability. If the utilization curves were essentially non-gaussian then niche breadth was determined using Simpson's index (B),

$$B = \frac{1}{\sum_{i}^{n} p_i^{\,2}}$$

where p_i is the proportion of observations falling in the i:th of n categories. B varies from 1 to n (Levins 1968). With this second method total niche size could be calculated by summating the individual breadth measurements. Total niche size can be the product or the sum of the individual niche breadths depending on whether the separate dimensions are independent or dependent respectively (May 1975, Pianka 1975), although they can be somewhat intermediate (Pianka, 1975). Ulfstrand (1977) demonstrated a close correlation between the two for a Pariform guild, and a similar situation holds for this study. The notation of ΣB was used to represent total niche size.

The overlap measurement was that of Morisita as discussed by Horn (1966),

$$C^{\wedge}_{\chi} = \frac{2 \sum_{i=1}^{s} x_i \, y_i}{\sum_{i=1}^{s} x^2_i + \sum_{i=1}^{s} y^2_i}$$

where class i has a proportion of the total observations for n classes for species x and species y respectively. This index is identical to α_{ij}, the index used by MacArthur and Levins (1967), where values of K, the carrying capacity of a habitat for the species, are equal for both species. In this study the carrying capacities of the environment were assumed to be the same although it is unlikely that in the real world they would be precisely equal. Lack of relevant data in this instance precluded the possibility of introducing realistic estimates of K for the different species.

Similarly, weighting factors (Schoener 1974, May 1975) were not introduced into the equation, thereby also avoiding the problem associated with logarithmic scaling of a resource axis in relation to body size of the predator (Wilson 1975, Armstrong 1977). For an investigation into the possible influences of environmental factors on niche breadth and overlap in a number of dimensions, only data for Swallow and Sand Martin were extensive enough. Data for the House

Martin diet used in these niche breadth and overlap analyses were from Bryant (1973). To standardise all data, some regrouping of taxonomic categories determined for the other species in this study was necessary.

RESULTS

2.6 Validation of the faeces sampling method
The laboratory experiment

The results of the experimental feeding of a nestling Swallow show that the proportions of different prey types ingested and the proportions recovered in the faeces are in very close agreement (Figure 2.6.1). This essentially means that no significant differential digestion exists between types with soft bodies and flexible wings and heavily chitinised prey. The mean proportion of all prey types recovered in the faeces was 34.2% which is comparable with the 31.9% found by Davies (1976b) in a similar experiment with a captive Pied Wagtail. However, in feeding trials with nestling Spotted Flycatchers, Muscicapa striata, Davies (1977a) recovered 92.5% of the wings of prey eaten and therefore the amounts of fragmentation and conspicuousness of remains may vary with predator species.

The proportion of remains recovered varied for different prey sizes (Table 2.6.1) but these differences were not significant ($\chi^2 = 2.850$, 6 df, $p > 0.8$), even between those size categories with lowest and highest recoveries (16-20 mm and 9-10 mm, $\chi^2 = 0.367$, 1 df, $p > 0.5$).

The time taken from ingestion for over 90% of the identifiable prey remains to appear in the faeces ranged between five and seven hours, although the first item appeared as soon as two hours after ingestion (Table 2.6.2). Because the nestling was not induced to

TABLE 2.6.1

Feeding experiment with nestling Swallow: comparison of the prey ingested with the remains in the faeces

Prey taxa	Wing length (mm)	Prey eaten: No. (fore)wings	No. wings recovered in faeces	Percent recovered
Chironomidae, Psychodidae	2-3	900	298	33.1
Chironomidae, Mycetophilidae, Anisopodidae Lonchopteridae, Acalypterate, Ichneumonidae	4-6	526	173	32.9
Chironomidae, Mycetophilidae, Muscidae Cordilurinae, Formicidae	7-8	130	46	35.4
Syrphidae, Muscidae, Cordilurinae	9-10	386	148	38.3
Neuroptera, Syrphidae, Muscidae	11-12	226	77	34.1
Syrphidae, Muscidae, Vespula	13-15	42	14	33.3
Tipulidae	16-20	8	2	25.0
TOTALS		2218	758	

TABLE 2.6.2

Feeding experiment with nestling Swallow: time after ingestion that prey remains appear in the faeces

Cumulative % wings recovered		Time (hours) after ingestion							
		2	3	4	5	6	7	8	9
Psychodidae	2-3mm				43.4		99.9	-	-
Chironomidae	2-3			18.9			92.6	-	99.9
	4-6		30.0	80.0	90.0	99.9	-	-	-
Mycetophilidae	4-6	11.1	38.9	50.0	94.4	99.9	-	-	-
Muscidae	11-12		8.3	16.6	91.6	99.9	-	-	-

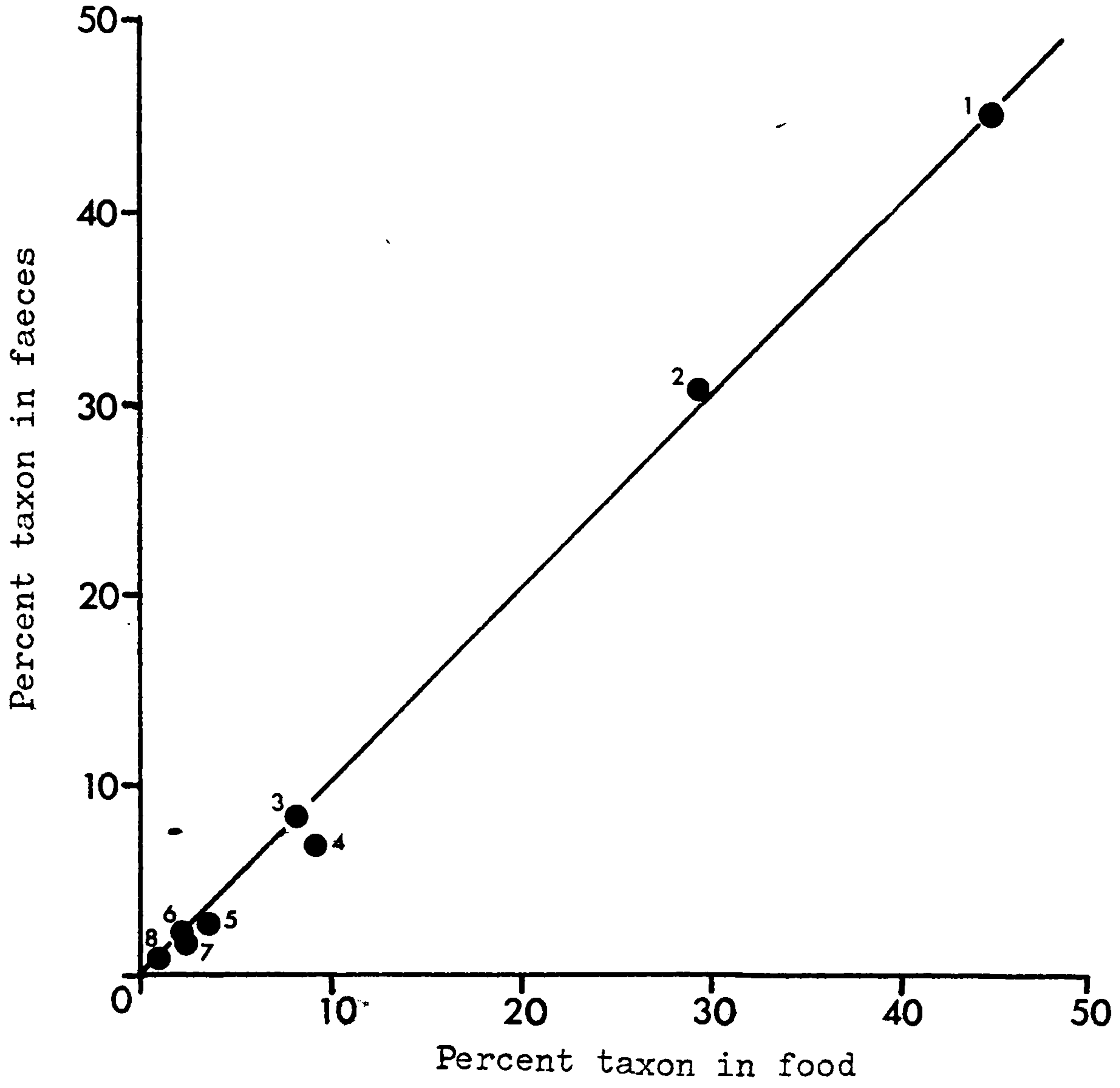


Figure 2.6.1. Experimental feeding of nestling Swallow. Relationship between the proportions of prey types ingested and those recovered from the faeces. Key: 1, Chironomidae. 2, Muscidae. 3, Mycetophilidae. 4, Psychodidae. 5, Ichneumonidae, Lonchopteridae, Anisopodidae. 6, Acalypterates. 7, Syrphidae, Cordilurinae. 8, Tipulidae, Neuroptera, Vespula. $y = 1.034x - 0.240$, $r = 0.999$, $P<0.001$.

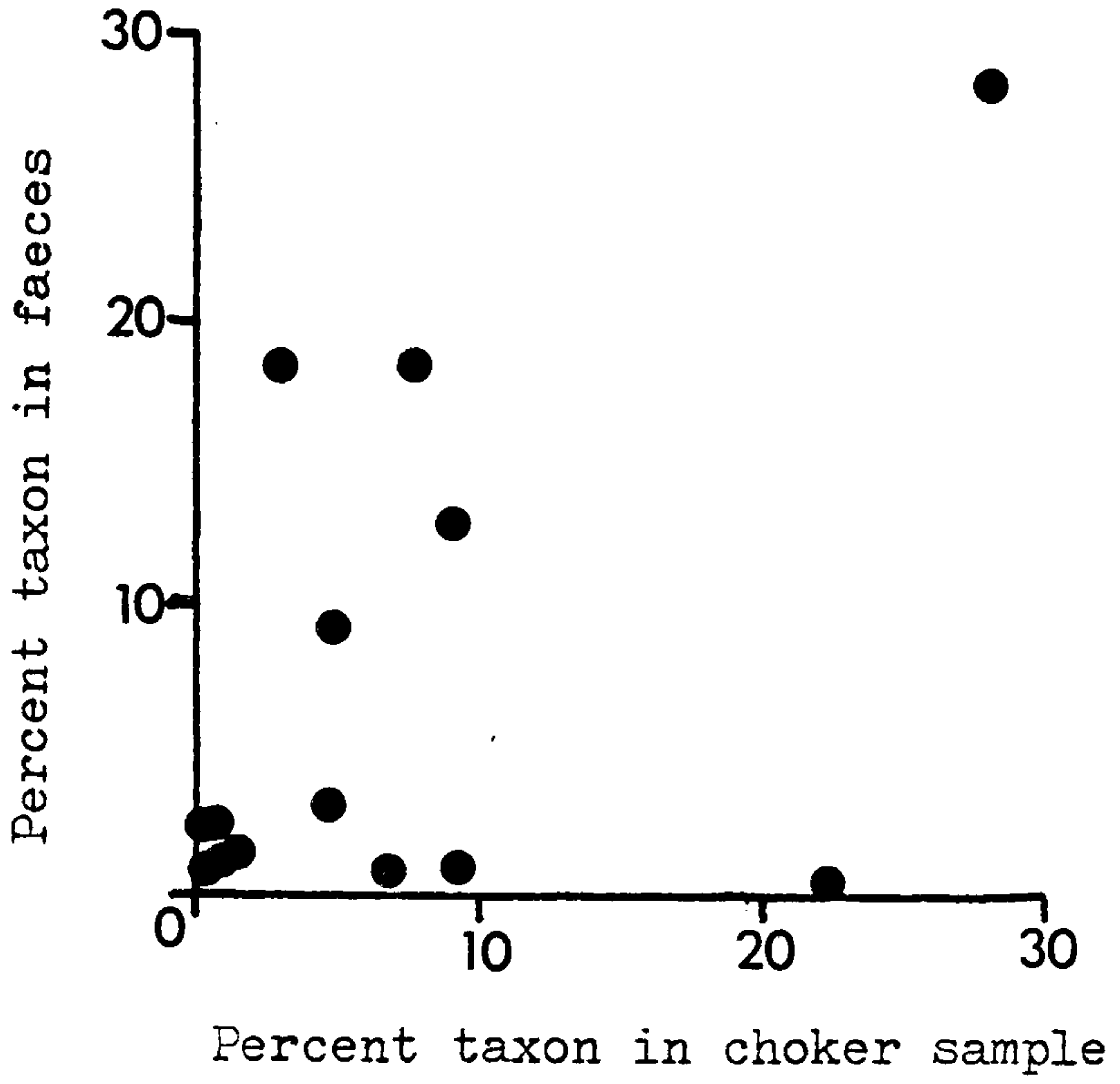


Figure 2.6.2. Comparison between two methods of measuring food brought to nestling Swallows. Relationship between the percent prey found in choker samples and the remains found in faeces. Total of twenty-seven taxa; points represent groupings of similar types.

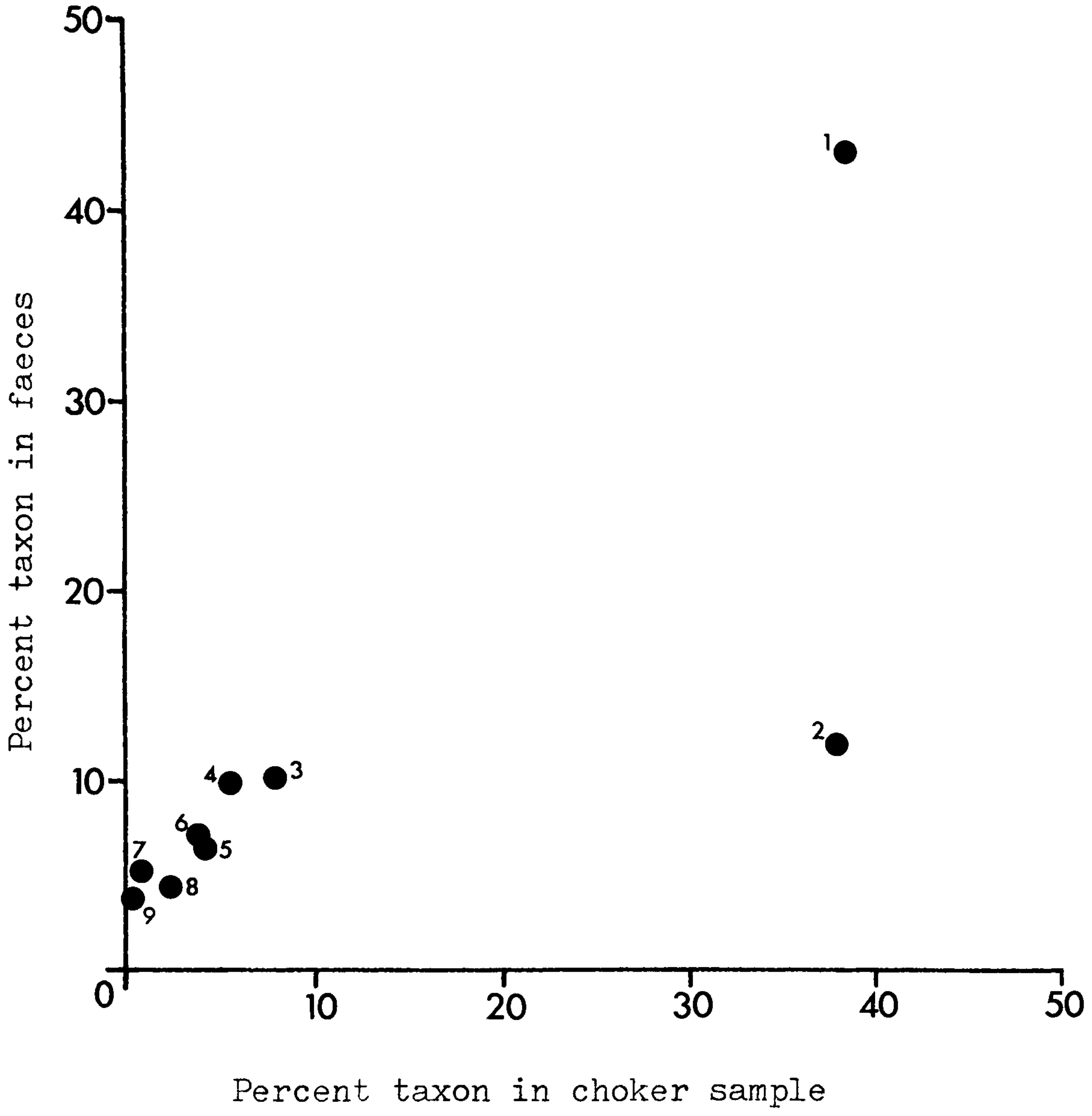


Figure 2.6.3. Comparison between two methods of measuring food brought back to nestling Sand Martins. Relationship between the percent prey found in choker samples and the remains found in faeces. Key: 1, Aphididae. 2, Ephemeroptera. 3, Chironomidae. 4, Acalypterates. 5, Nematocera. 6, Hemiptera. 7, Coleoptera. 8, Brachycera. 9, Parasitica.

produce faecal sacs, the 5-7 hour digestive period may be regarded as a maximum since this probably reflects the time interval for natural faeces production. Similarly, no significance can be attached to differential rates of appearance of the different size categories in this instance. Davies (1976b) recovered over 90% of identifiable prey remains in Pied Wagtail faeces after only two hours and found no difference in the rate of passage of larger and smaller prey through the gut. From the present experiment it appears to be safe to collect faeces from field sites before 10.00 hours B.S.T. when conducting correlative studies involving environmental conditions during the previous 24 hour period.

Field trials with Swallows

A comparison was made between the proportions of different prey types collected in choker samples (see Section 3 for method) between 09.00 and 17.00 on 8th and 9th August 1975, and the proportions of prey types identified in faeces derived from the food brought to the nest in the other daylight hours. The proportions of the 27 insect taxa involved were significantly correlated ($r = 0.644$, $p < 0.001$, Figure 2.6.2). Considering the different times of day for collection with each method and the probable variation in flight periodicities of the different prey types, this relationship amply supports the laboratory findings.

Field trials with Sand Martins

A comparison was made between the proportions of different prey types identified in the food brought to two nests and those identified in the faeces collected from beneath the entire colony on 6th July 1976.

It was found that most prey types were represented in similar proportions in both food and faeces samples (Figure 2.6.3, $r = 0.782$,

$p < 0.01$). The correlation of the proportions was improved if Ephemeroptera were excluded ($r = 0.997$, $p < 0.001$). These results again broadly support the laboratory results but suggest that taxa with large fragile wings (such as Ephemeroptera) may be under-estimated by faeces sampling.

2.7 The food supply and the arrival of the birds into the breeding area

The populations of aerial-feeding birds breeding in the Palearctic region are migratory, all wintering at lower latitudes and with the highest proportion in Africa (Moreau 1972). The exceptions are Crag Martins, *Hirundo rupestris*, and the Near and Middle East races of *H. rustica* i.e. *transivita* and *savignii*. Migration is a product of natural selection (Lack 1968), and is maintained by aerial-feeding birds in the present-day as a strategy to enhance their reproductive value (Grinnell's theory as in MacArthur 1972). An individual bird can find more food, and hence increase its chances of surviving to breed the next year, if it vacates the Palearctic breeding area in winter. An individual will also find more food, and therefore be able to raise more off-spring, by returning to the Palearctic in the summer rather than remaining in Africa.

The scarcity of aerial insects in the winter months within the breeding areas is well illustrated by samples taken at 12.2m (Figure 2.7.1). Relative to the average insect abundance of the summer the densities in the months preceding April are apparently too low to support even non-breeding populations of aerial-feeding birds. At the tail-end of the summer the densities of aerial insects decline more gradually than the spring rise in April, but the birds have completed their breeding cycle and begin southward migration before

Figure 2.7.1. The seasonal pattern of aerial insect abundance (12.2m) in 1971 and 1972 in the study area (data from Bryant unpubl.).

insect abundance becomes too low. Arrival at the breeding areas of the bulk of the populations coincides with the rise in aerial insect abundance that occurs throughout April and levels off to a plateau in May (Figures 2.7.1, 2.7.2).

Although a few individuals of each species may arrive on early dates in spring, they are not representative of the populations as a whole, the bulk of which may arrive up to a month later. These major influxes of all four species are slightly staggered (Table 2.7.1) and, although there is some variation between years, Sand Martins always arrive first followed by Swallows and finally the combined arrival of House Martins and Swifts. The influx of the last species is a less protracted arrival than those shown by the hirundines, and even House Martins show more of a build-up in numbers. Sand Martins and Swallows show the most gradual recruitment of individuals up to full breeding strength. If arrival at the breeding area is delayed until the spring rise in aerial insect densities is realised, then the sequential arrival of the different species may also be attributable to the food supply. The basic seasonal pattern of the aerial insect populations is maintained throughout the air-column (Figure 2.7.2a, b, c) but important differences linked to height emerge:

TABLE 2.7.1

Arrival dates of the birds at the study area in three successive years

	1974		1975		1976	
	First sighting	First major influx	First sighting	First major influx	First sighting	First major influx
Sand Martin	4 April	26 April	14 April	23 April	30 March	23 April
Swallow	27 April	10 May	16 April	3 May	21 April	4 May
House Martin	7 May	13 May	23 April	14 May	4 May	15 May
Swift	9 May	13 May	2 May	14 May	8 May	15 May

Figure 2.7.2. Daily insect suction trap catches in 1975 and 1976 (triangles). Monthly means ± S.D. are indicated. The markers show major arrival times of the predators.

3
2
1
0
APR
MAY
JUN
JUL
AUG
SEP
b. 1·8 m.
5
4
3
2
1
0
A
M
J
J
A
S
AERIAL INSECT ABUNDANCE (LOG N + 1)
c. Ground Level.
5
4
3
2
1
0
A
M
J
J
A
S
Sand Martin
Swallow
artin

(a) the spring rise in insect abundance occurs earlier nearer the ground,

(b) insect abundance increases nearer to the ground,

(c) the day to day fluctuation of insect abundance is less nearer the ground, indicating a lower sensitivity to changing weather conditions.

Therefore, if Sand Martins and Swallows arrive first (Figure 2.7.2) it may be expected that they both would feed predominantly at a low level (at least at the start of the breeding season) where food is more abundant and predictable. Conversely, the later arrival of House Martins and Swifts indicates their greater utilization of the less predictable aerial insect supply at higher levels early in the season.

The arrival of birds into the breeding areas occurs as a gradual northward progression and, as shown for Swallows (H.N. Southern in Hosking and Newbury 1946), is at first well correlated with the 8.9°C (48°F) isotherm. However, from mid-April onwards Swallows are arriving in northern breeding areas (at least in Europe) at much lower temperatures. Since the arrival in the study area has been shown to be a function of increasing aerial insect abundance, it is possible that birds arriving in more northerly areas exploit a cold-adapted aerial insect fauna. There are at present no data to confirm this.

The insect abundance profiles were expressed in logarithmic form, the theoretical basis for this being outlined in Southwood (1966). Bryant (1972, 1973, 1975a) has shown that various aspects of House Martin breeding biology are related more to the logarithm of insect abundance than the linear form.

2.8 Ecological isolation in aerial-feeding birds

The evolution in birds of differential utilization of resources is known as ecological isolation (Moreau 1948) and as a principle has become widely accepted, Lack (1971) giving many examples. Ecological isolation or segregation in birds may be effected in three main ways:

(a) spatially, where species may be separated by habitat or geographic range,

(b) temporally, where the same resource may be exploited by different species during different times of day or season,

(c) where species occupy the same habitat and segregate by selecting different foods.

It is in the latter case that co-existence is achieved by the evolution of differences in resource use, these differences being termed co-existence mechanisms (Hardin 1960, Cody 1968).

The four predator species in the present study are not separated geographically within Britain and likewise throughout most of their Palearctic ranges (Voous 1960). They can all be found feeding in the same habitat, the air-space, at the same time. Hence, it would be expected that some or all species would have evolved behaviours to avoid competitive exclusion.

Lack (1971) suggested that there may be differences in the insect food taken by European breeding swifts, and that segregation of hirundines was by habitat as a result of separation in nesting sites. Bryant (1972) has shown that the four aerial-feeders in Britain form a displacement pattern along the prey size continuum, and that they also separate in mean height of feeding above the ground. The present study furthers his approach.

2.8.1 Predator size and prey size

Many studies of competition between species utilizing a common food resource have focused attention on the positive relationship between the size of predator and the average size of its preferred prey. Distinction has been made between the actual body size, usually measured as weight or a consistent linear measurement, and size of trophic appendages, that of the feeding apparatus being of over-riding importance. For birds, the evidence to date has equally supported the relationships of bill size and body size to prey size.

Prey size

Comparisons of the sizes of prey taken by the different species were made, together with comparisons between prey sizes and sizes of insects available (Figure 2.8.1a, b). These distributions refer to the months of May to September inclusive (Swift faeces collected in June, July and August only). For comparative purposes the size categories of prey in faecal remains and insects in suction trap samples were expressed as 'wing span × body length' (mm^2) on a logarithmic scale (Taylor 1962). This unit of area has been demonstrated to be a satisfactory indicator of size (Lewis and Taylor 1967), making allowance for physical attributes of the insect type which could contribute to flight speed. Since prey sizes of the birds were necessarily derived from single wings, some estimate of body length relative to wing length was required. A wide variety of insect types selected from the suction trap samples (example taxa listed in Appendix I) were assigned to five categories,

(a) very short body relative to wing length

(b) short body relative to wing length

(c) long body relative to wing length

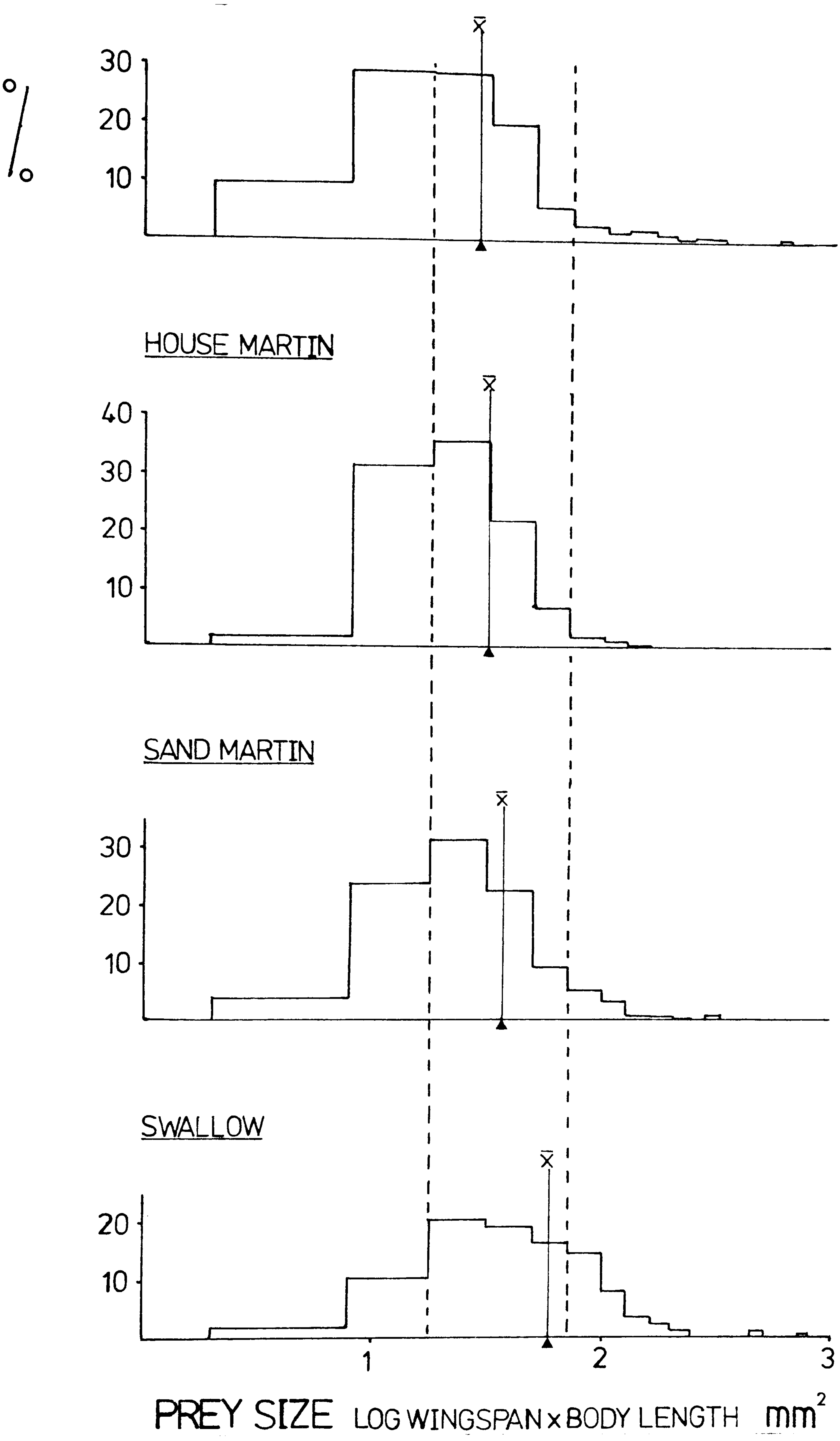


Figure 2.8.1.a. Frequency distributions of sizes of prey taken by the predator species as determined from faeces analysis. indicated.

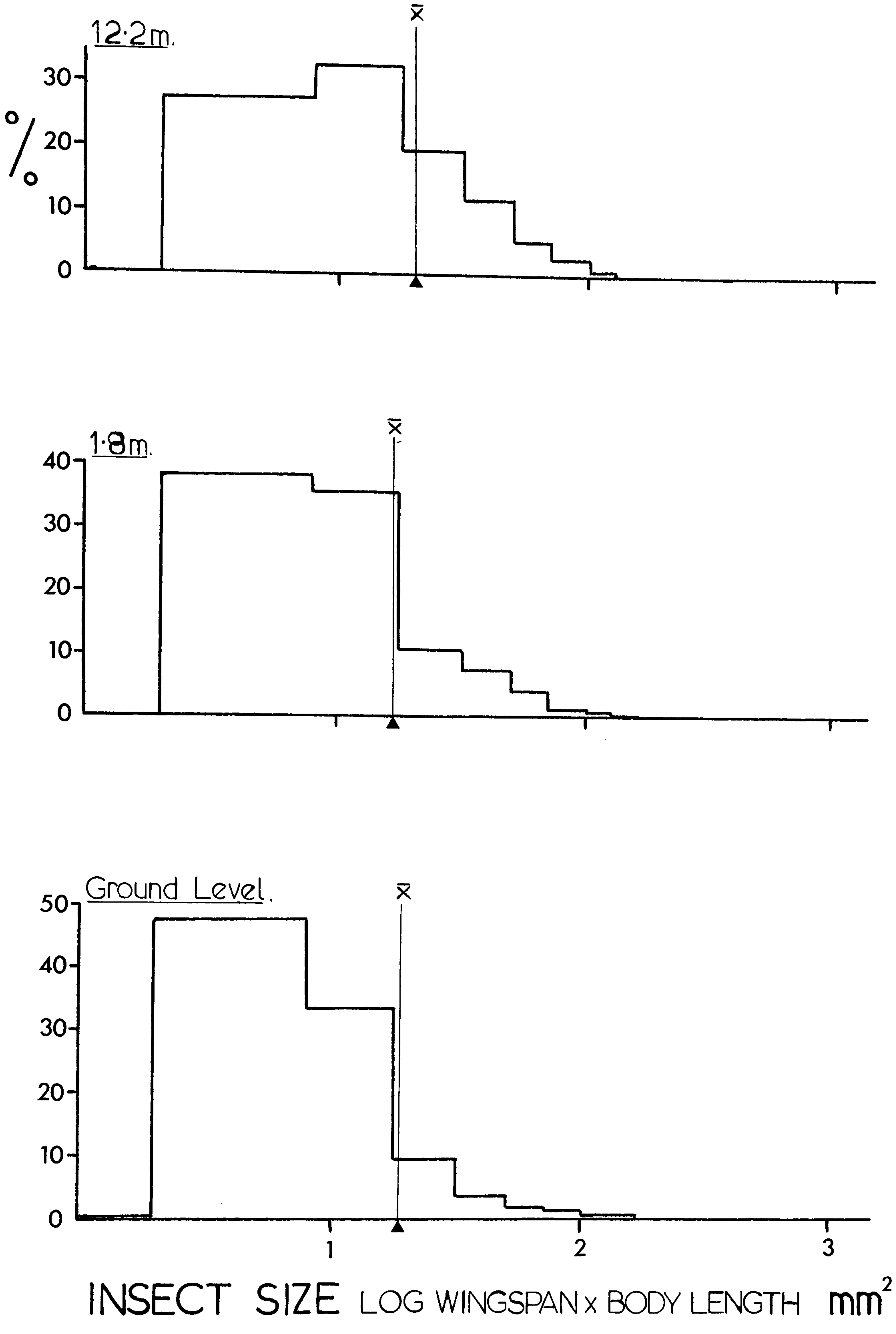


Figure 2.8.1.b. Frequency distributions of sizes of aerial insects available at the three suction trap sampling heights. Mean sizes are indicated.

(d) very long body relative to wing length

(e) body equal to wing length.

A log/log regression was calculated for each category together with the slope for all categories combined (Figure 2.8.2). The only significant difference was of the two long-bodied (c, d) categories compared to the two short-bodied (a, b, $Pd < 0.01$ to < 0.001). The overall slope (f) was not significantly different from the equal body length/wing length slope (e, $Pd > 0.1$), and a subsequent test of the difference between 'wing-span × body length' and 'wing-span × wing-length' proved non significant ($Pt > 0.1$). Cursory examination of the variety of taxa taken by each predator species indicated no extreme selection of either short or long bodied prey types. It was decided therefore to use size categories based on an equal body/wing length ratio in this general study of the diets.

Hespenheide (1971) has shown that the prey size distributions of certain insectivorous (including Hirundinidae in the Nearctic), and non-insectivorous birds are log-normal, or nearly so. Log transformation (Base 10) of the size classes in the present study likewise brought the prey frequency distributions to near normality (Bliss 1967). The effect of transformation of single wing lengths was almost identical (see Appendix I). The size distributions of the aerial insects all displayed a highly positive skew (Figure 2.8.1.b), and transformation was not expected to normalise them. Each predator had a preferred mean prey size (Table 2.8.1) and, although considerable overlap in the diets was evident (reference the utilization curves in Figure 2.8.1a), these differences represent a partial contribution towards co-existence during the breeding season. It will be noted that niche breadth (represented by standard deviation) increases with increase in mean prey size for hirundines, but the Swift is anomolous in this respect with a niche breadth nearly as large as the Swallow.

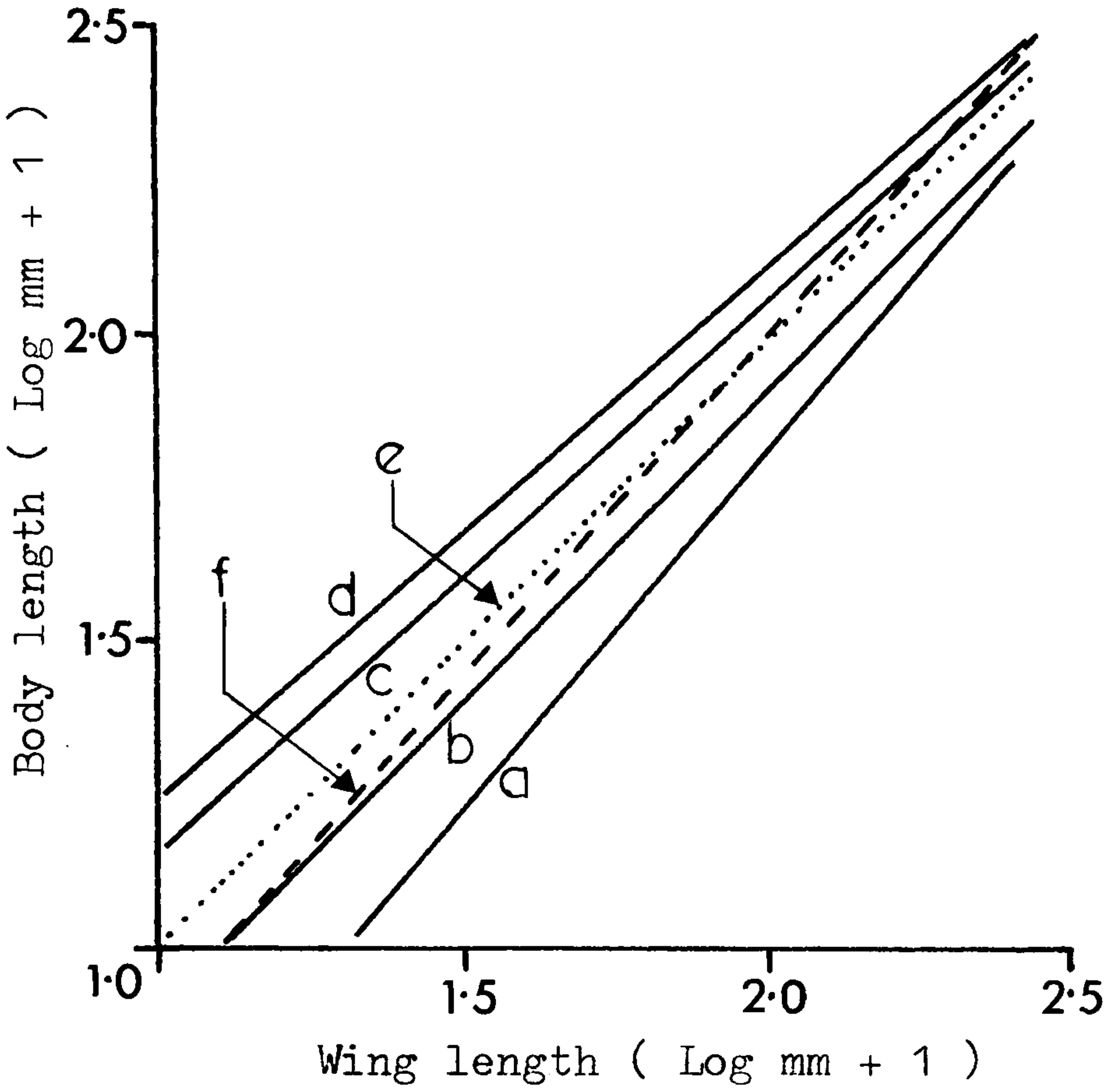


Figure 2.8.2. The relationship of body length to wing length for a wide variety of taxonomic groups (appendix I).

Line a. $y = 1.1898x - 0.5547$, $r = 0.875$, very short bodi

b. $y = 1.0254x - 0.1339$, $r = 0.975$, short bodies

c. $y = 0.9078x + 0.2471$, $r = 0.986$, long bodies

d. $y = 0.8845x + 0.3584$, $r = 0.985$, very long bodie

e. Equal body length/wing length

f. $y = 1.0937x - 0.1844$, $r = o. 879$, all body lengt combined.

TABLE 2.8.1

A comparison of the mean prey sizes taken by aerial-feeding birds and the mean insect sizes available

Species	Prey size Mean Log_{10} mm^2 ± SD	Suction trap height (m)	Insect size Mean Log_{10} mm^2 ± SD
Swift	1.4660 ± 0.3320	12.2	1.3040 ± 0.3270
House Martin	1.5003 ± 0.2265	1.8	1.2350 ± 0.3410
Sand Martin	1.5677 ± 0.3073	Ground level	1.2640 ± 0.3650
Swallow	1.7640 ± 0.3345		

The mean size of available insects appears to decrease nearer the ground (Table 2.8.1). Because aerial insect abundance increases as an inverse function of height, the proportionate increase of the more abundant smaller sizes obscures the fact that larger items at lower levels are more abundant than those same sizes higher in the air-space. The decrease in standard deviation with increase in sampling height (Table 2.8.1, Figure 2.8.1b) gives some indication of the fewer large items found at higher levels.

The mean size of prey taken by each predator species is greater than the mean insect sizes available to them (Table 2.8.1), and this accords with results from other insectivorous bird studies (e.g. Hespenheide 1971, his figures 3 and 7). The differences of the prey distributions from the aerial insect distributions are highly significant for each predator against each sample height (χ^2 test, $p < 0.001$ in all cases). However, the possibility that all four species forage equally over the entire air-space would probably require greater segregation by prey size than observed here. The alternative possibility, that the separate species adopt different foraging heights, is supported by the gradient of mean aerial insect size and parallel differences of mean prey size between the predators.

Factors influencing size selection of prey

Variation may be observed in both the mean size of prey taken by aerial-feeding birds, and the range of sizes, i.e. the niche breadth along the prey size continuum. The factors causing variation are investigated in this section. Hespenheide (1971) has indicated that for logarithmic data the variances, i.e. niche breadths, should be equal regardless of the mean log size of prey. For Swallows and Sand Martins in the present study (data for this analysis were too few for House Martins and Swifts), no correlations were found between mean daily log prey size and niche breadth (standard deviation, Swallow $r = -0.403$, $n = 17$, $p > 0.05$, Sand Martin $r = 0.004$, $n = 17$, $p > 0.1$). Therefore, an investigation into the variation in niche breadth was appropriate.

Analysis of data proceeded by the initial construction of correlation matrices to establish the inter-relationships of several possible variables likely to influence prey size selection. These same variables were then entered into a multiple regression analysis in a step-wise manner to create a series of equations. The ranking of variables for inclusion in the expanding equation was based upon how much of the residual variance in the dependent variable each could explain. The level of significance chosen was five percent. Environmental variables selected for inclusion in the analyses were maximum and minimum daily temperatures (°C), total amount of rainfall in 24 hours (mm) and, for each 24 hour insect catch (12.2m, 1.8m and ground level), the total number, mean size and range (standard deviation) of sizes available.

Mean Prey Size

For the Sand Martin four variables had significant correlations with mean daily prey size (Table 2.8.2a). When the variables were included in the regression analysis, insect abundance and mean size at 1.8m were not significant and were replaced in rank by the significant insect abundance at 12.2m and size range at 1.8m. The total variation in the data accounted for by all the variables was 89.2% with minimum temperature explaining the largest part. The correlations for all variables presented in the multiple regression analysis (Table 2.8.2b) were negative.

No variables were correlated with the mean prey size taken by Swallows. In a multiple-regression only insect abundance at 12.2m was significant in the equation, the data having a negative trend but accounting for only 6.7% of the variation in mean prey size.

These results suggest that the mean prey size selected on good days, i.e. high numbers of aerial insects, high air temperature, etc, at least by Sand Martins was smaller than that taken on bad days. This finding is discussed in relation to change in niche breadth below.

Prey size niche breadth

Variation in niche breadth of Sand Martins was significantly correlated with three variables (Table 2.8.3a) and that of Swallows with two variables (Table 2.8.4a). All correlation coefficients were positive except for rainfall in the Swallow multiple regression (Table 2.8.4b). Inclusion of all variables in the Sand Martin regression (Table 2.8.3b) explained 76.6% of the variance in niche breadth, with maximum temperature accounting for most of this and reducing the significance of insect abundance at 1.8m, which then accounted for only 36.7% of the variance if weather effects were excluded.

TABLE 2.8.2a

Environmental variables correlated with mean daily prey size selected by Sand Martins

	r	P
Minimum temperature	-0.725	< 0.01
Insect size range at 1.8m	-0.638	< 0.01
Mean insect size at 1.8m	-0.603	< 0.02
Insect abundance at 1.8m	-0.597	< 0.02

TABLE 2.8.2b

Multiple regression analysis of the effect of environmental variables on mean daily prey size selected by Sand Martins

Variable	Multiple Regression Coefficient b	Standardised Partial Regression Coefficient B.Wt	Cumulative Coefficient of Determination $r^2 \times 100$	F	P
Minimum temperature	-0.026	-1.296	52.6%	33.7	< 0.001
Insect size range at 12.2m	2.031	0.928	71.3%	16.5	< 0.001
Insect size range at 1.8m	-1.897	-0.861	79.5%	22.9	< 0.001
Insect abundance at 12.2m	0.106	0.429	87.4%	5.9	< 0.01

Constant = 1.387

Multiple r = 0.93

for all above variables

TABLE 2.8.3a

Environmental variables correlated with daily prey size niche breadths of Sand Martins

	r	P
Maximum temperature	0.725	< 0.01
Insect abundance at 1.8m	0.639	< 0.01
Minimum temperature	0.549	< 0.05

TABLE 2.8.3b

Multiple regression analysis of the effects of environmental variables on daily prey size niche breadths

	Multiple Regression Coefficient	Standardised Partial Regression Coefficient	Cumulative Coefficient of Determination		
Variable	b	B.Wt.	$r^2 \times 100$	F	P
Maximum temperature	0.013	0.821	52.5%	13.0	< 0.001
Insect abundance at 12.2m	0.082	0.478	59.3%	3.6	< 0.05
Insect abundance at ground level	-0.096	-0.371	64.3%	1.5	N.S.

Constant = 0.152

Multiple r = 0.80

TABLE 2.8.4a

Environmental variables correlated with daily prey size niche breadth of Swallows

	r	P
Insect abundance at 12.2m	0.552	< 0.05
Mean insect size at 12.2m	0.469	< 0.05

TABLE 2.8.4b

Multiple regression analysis of the effect of environmental variables on prey size daily niche breadths of Swallows

Variable	Multiple Regression Coefficient b	Standardised Partial Regression Coefficient B.Wt.	Cumulative Coefficient of Determination r^2 x100	F	P
Insect abundance at 12.2m	0.128	0.541	30.5%	4.06	< 0.05
Insect size range at ground level	0.537	0.511	46.3%	3.97	< 0.05
Rainfall	0.004	0.500	56.8%	4.77	< 0.05
Mean insect size at 12.2m	-0.082	-0.198	58.5%	0.40	N.S.

Constant = -0.164

Multiple r = 0.77

For the Swallow the total variance in niche breadth accounted for by all variables amounted to 71.5%, with insect abundance at 12.2m explaining the major part and mean insect size at 12.2m contributing only 1.7% to explain further variance. Hence, for both species there was an apparent increase in niche breadth with increase in air temperature and insect abundance, i.e. on good days. This increased generalization in prey size selection with greater food abundance is the apparent converse of the prediction that increase in selectivity results from increase in food abundance. Two additional findings further this impression. One is that there was no relationship between the mean size of insects available and their absolute abundance in the air (12.2m $r = 0.182$, 1.8m $r = 0.113$, ground level $r = -0.279$, $n = 26$, $P > 0.1$ for all). This means that an increase in aerial insect density would not necessarily imply an increase in numbers of larger types and could equally be caused by an increase in abundance of smaller, swarming insects. Furthermore, that feeding on these smaller, swarming types is a more profitable strategy for Sand Martins than taking larger items is indicated by the lower mean prey size observed on good days (Figure 2.8.3a). The major contribution of minumum temperature to the decrease in mean prey size may be effected through a lower incidence of take-off for swarming insects with lower morning temperatures.

The confounding effect of difficulty in sampling scarce prey is illustrated by calculating the mean prey size of Sand Martins from only those taxa which are also represented in the suction trap samples. The observed lower mean prey sizes (Figure 2.8.3b), particularly for the days with the previous high means (in Figure 2.8.3a), indicates that on bad days Sand Martins are out of necessity selecting larger prey items not generally available, i.e. not represented in the suction

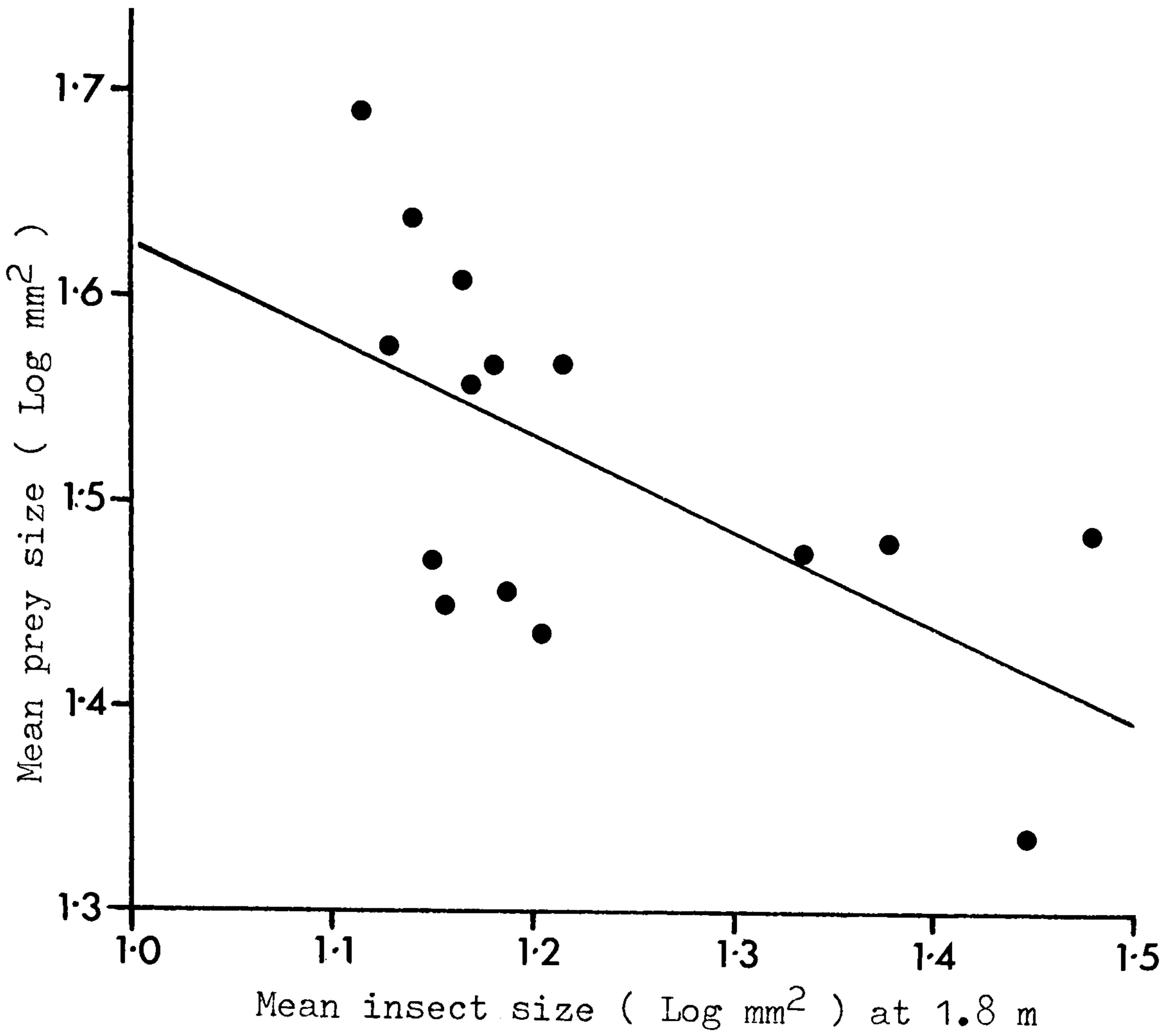


Figure 2.8.3.a. The relationship of mean prey size selected by Sand Martins to the mean size of aerial insects available (1.8m suction trap samples). $y = 0.4564x - 2.0821$, $r = -0.603$, $P<0.02$.

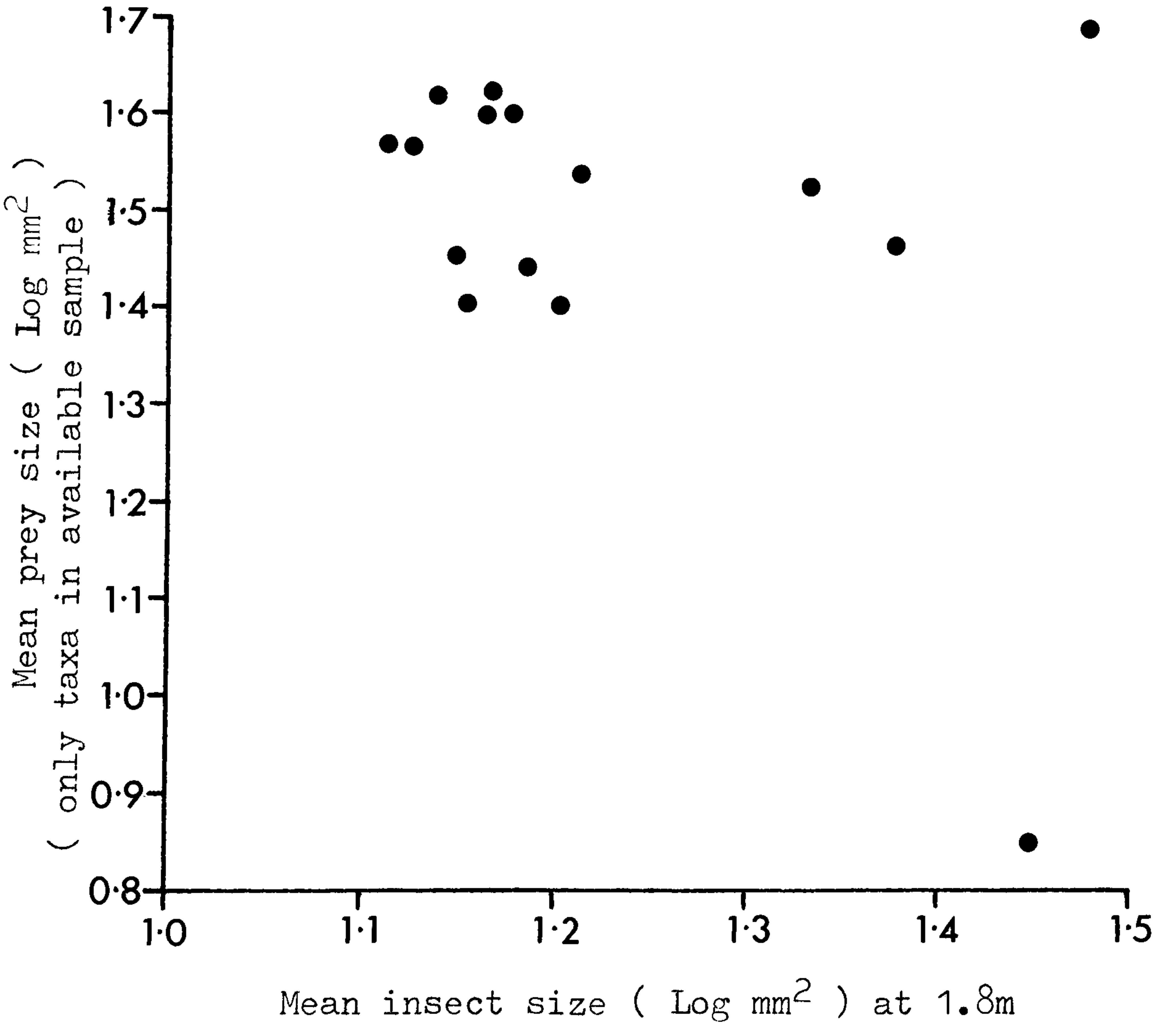


Figure 2.8.3.b. The effect of excluding prey types not represented in the 1.8m suction trap samples from calculation of mean prey size for Sand Martins.

trap, and likely to be concentrated behind shelter belts, over water surfaces, etc.. The lack of a demonstrable relationship for the Swallow lends weight to the argument that this species is far less dependent on swarming insects for prey.

Predator body size

In using body weight or wing length to represent body size it is apparent that the size sequences for both criteria are the same, the single inequality being the larger difference between the mean weight of the heaviest hirundine and that of the Swift (Table 2.8.5). It was found that these aerial-feeding birds were not selecting particular mean prey sizes on the basis of body weight (semi-log plot, $r = 0.456$, $n = 4$, $P > 0.1$), and no relationship was apparent for the hirundines alone. This result differs from that of Hespenheide (1971) where progressively larger mean prey sizes (again log transformed values) were taken by larger swallows in North America, including *R. riparia*

TABLE 2.8.5

Biometrical data of aerial-feeding birds

Species	Body weight (g)	Wing length[1] (mm)	Bill size[2] (mm)	Functional bill shape[3]
Swift	42.25	172.17	7.16	2.06
Swallow	20.24	125.55	8.61	2.34
House Martin	19.55	108.71	7.24	2.07
Sand Martin	13.70	105.77	6.8	2.21

1. Maximum chord
2. Exposed culmen length
3. $\frac{(\text{Width} \times \text{depth})\text{mm}^2}{\text{Exp. Cul. length mm}}$

and H. rustica. Hespenheide's data were based on beetle prey only (from Beal 1918), but again no correlation was determined for body weight and mean beetle prey size in the present study (semi-log plot, $r = 0.004$, $n = 4$, $P > 0.1$). It is notable that no sub-specific variation is recognised between North American and European R. riparia, and the respective mean lengths of beetle prey taken by these geographical isolates are approximately 3.00 mm (Hespenheide 1971, figure 5, untransformed data) and 3.05 mm. It may therefore be unwise not to include all prey types when comparing prey sizes to predator size, and the accuracy of faeces analysis lends support to this.

Bill size and shape

In cases where differences in body size fail to illustrate differences in food niche, it may be found that varying sizes of feeding apparatus correlate well with differences in prey size. Hutchinson (1959) established that for two species to co-exist at the same level of a food-web, the ratio of longer bill (length of culmen) to shorter bill should usually be between 1.1 and 1.4, and he demonstrated this difference for several pairs of sympatric congeneric species. Amongst other studies correlating bill length with food niche, Holmes and Pitelka (1968) showed that similarity in prey size of arctic waders was predicted more accurately by similarity in bill size than by body size.

However, Hespenheide (1971) found bill size (using width) in swallows poorly correlated with prey size, and in the present study bill length of the birds (Table 2.8.5) was similarly found not to be correlated with mean prey size ($r = 0.853$, $n = 4$, $P > 0.05$).

Hespenheide (1966), Johnson (1966) and again Ashmole (1968) have pointed out the neglect of other characters likely to predict food

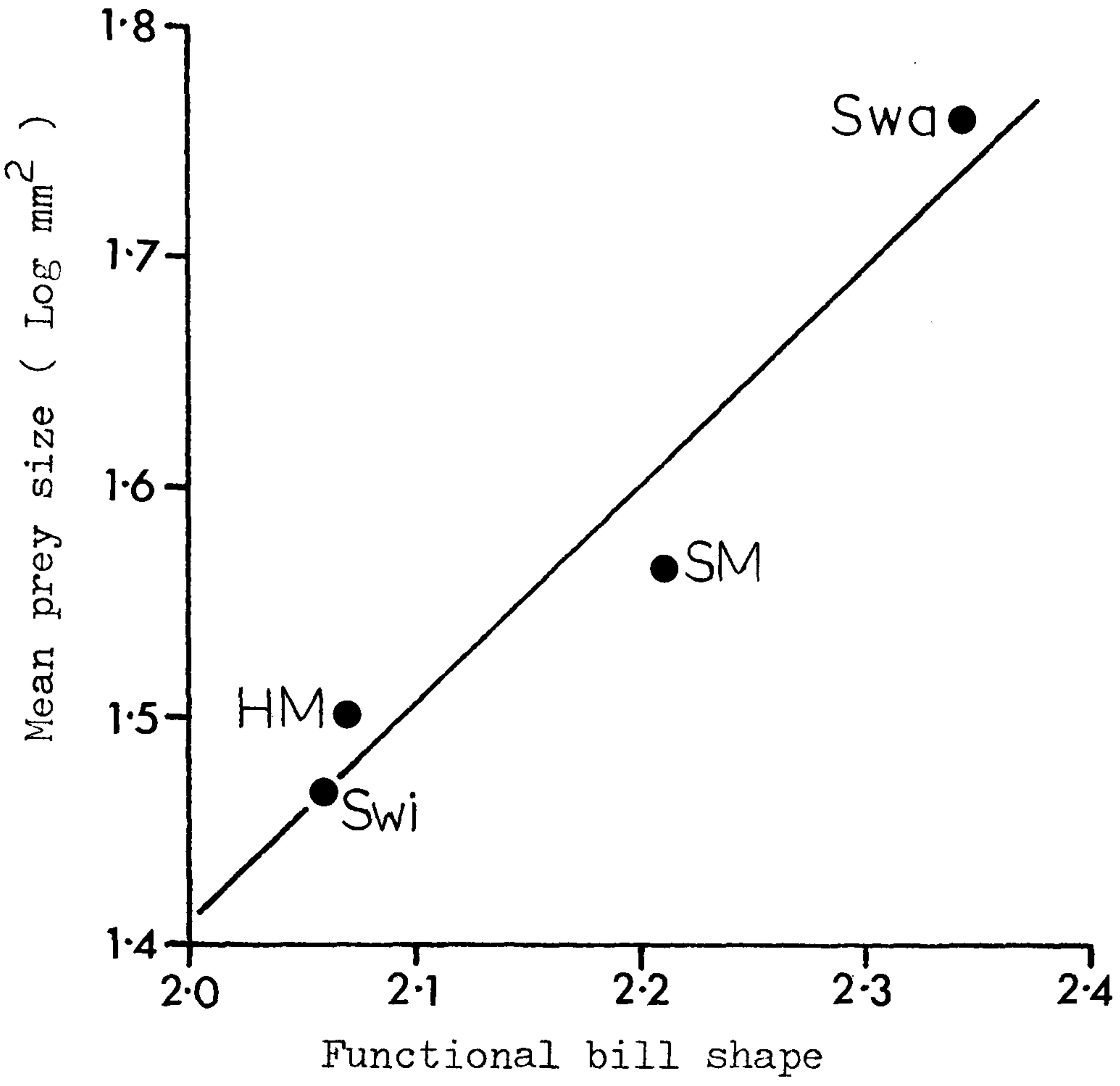


Figure 2.8.4. The relationship between bill morphology and size of prey taken by the four study species. Log y = 0.9753x - 0.5419, r = 0.97, P<0.01.

niche differences due to over-emphasis on bill length. They have argued that variation in bill width and depth between congeners can effectively alter bill shape and function when bill length is constant. If different bill shapes have been evolved by aerial-feeding birds in relation to time spent in handling prey items, then it may be expected that those species taking larger prey would have evolved an intrinsically stronger shape. A higher ratio of cross-sectional area of the bill to bill length, i.e. the functional bill shape (Table 2.8.5) was expected to impart greater strength, and indeed this character was found to be highly correlated with mean prey size (Figure 2.8.4). Hence, these bill shapes may have been evolved, together with other characters, to minimize handling time costs.

2.8.2 Predator manoeuvrability and prey mobility

Several studies have established links between characteristics of the habitat and behaviour patterns, and between these behaviour patterns and morphological adaptation (e.g. Root 1967, Caccamise 1974, Gaston 1974, Feinsinger and Chaplin 1975, Partridge 1976). The air space as a feeding habitat is characterised by the distribution of aerial insect types, e.g. fewer larger items at higher levels, and the related feeding behaviours of the predators are likely to be associated with their own flight capabilities. As with handling time, attempted minimization of time spent in pursuit (to the point of capture) of prey items is a realistic expectation, and each predator should therefore display a morphology best adapted to ease of capture of its preferred prey types.

Prey mobility

For each predator species the energy and time costs of pursuit of prey will rise in direct proportion (although the gradients should differ) to the flight speed and evasive action of the insect type. The theoretical flight speeds determined for a variety of taxonomic groups (Table 2.8.6) compare well with values determined from direct flight experiments by Ewing (1938) and, for heavy-bodied Diptera and Hymenoptera, by Lewis and Taylor (1967). In the theoretical formulations it was not possible to compensate for the effect of trailing appendages (e.g. long legs) in increasing drag, and therefore flight speeds derived for smaller, slender-bodied groups should be regarded as maxima.

It is apparent that considerable variation in flight speed exists between different taxa, which remains detectable even when these are plotted against size (Figure 2.8.5). Hence, for any given size an insect type occurring above or below the slope will be respectively faster or slower than expected.

Flight speed values were assigned to each taxonomic group occurring in the diets of the aerial-feeding birds (see Table 2.8.13) and frequency distributions were derived from these data (Figure 2.8.6a). The same procedure was undertaken for taxonomic groups occurring in the suction trap samples (see Table 2.8.14, Figure 2.8.6b), and mean values were calculated for both the prey and available insect food (Table 2.8.7). Insect types occurring in the diets and suction trap samples without a calculated theoretical flight speed were assigned the value of the most similar taxonomic group (Table 2.8.6) with regard to weight and wing-length ratio. The mobility distributions of insect prey showed a displacement pattern similar to that shown by

Figure 2.8.5. The relationship of insect size to flight speed (mobility), $r = 0.701$, $P<0.001$.

Key:

●Tipulidae

○Muscidae

□Cordilurinae

■Acalypterate Schizophora

◊Syrphidae

♦Lonchopteridae, Phoridae (P), Empididae, Stratiomyidae, Tabanidae, Rhagionidae

|Nematocera, B = Bibionidae, C = Chironomidae

△Hymenoptera

▽Coleoptera

—Hemiptera, A = Aphidoidea

XTrichoptera, Ephemeroptera (E), Plecoptera, Lepidoptera (L)

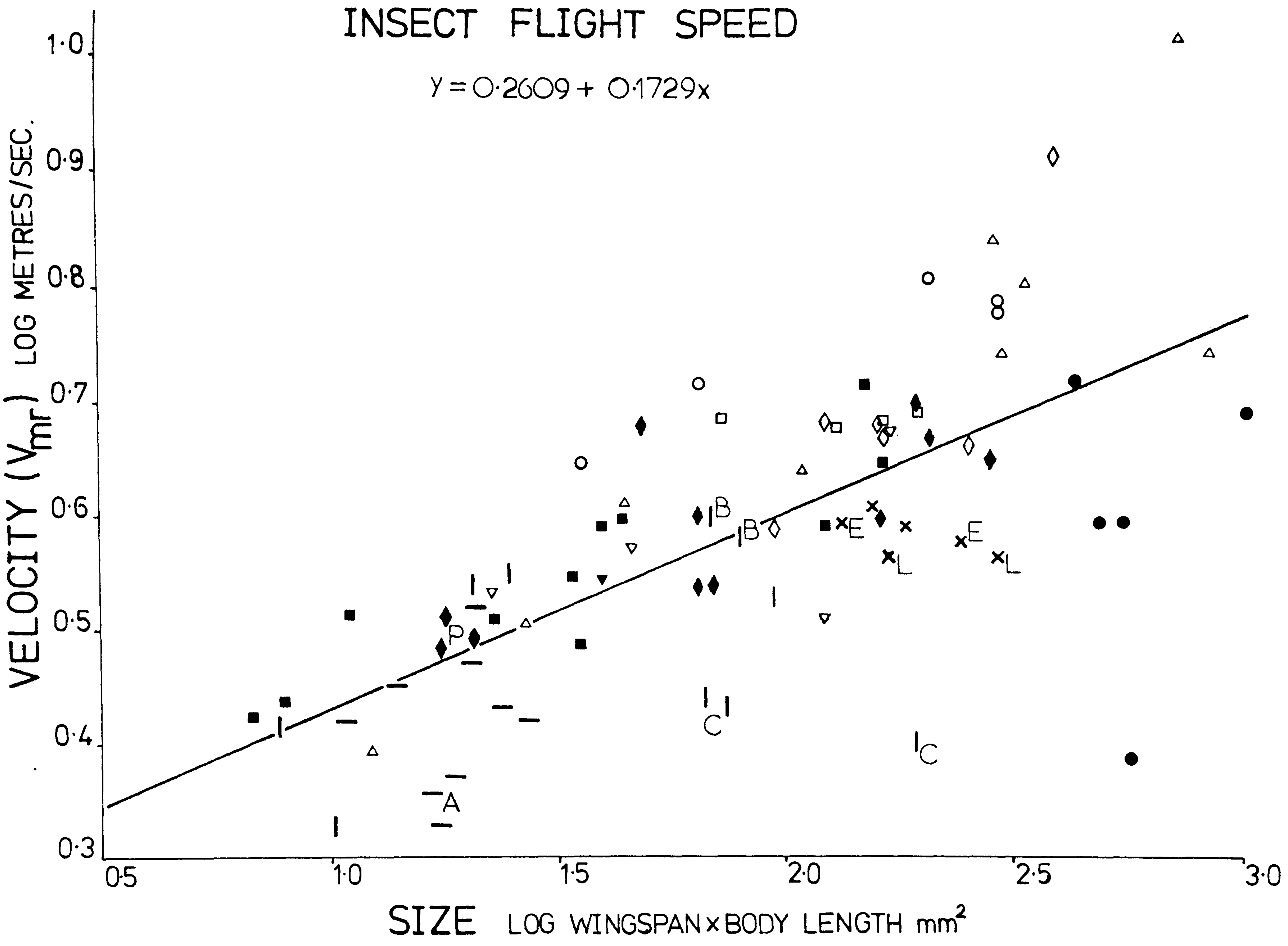

INSECT FLIGHT SPEED
y = 0·2609 + 0·1729x
VELOCITY (V_{mr}) LOG METRES/SEC.
1·0
0·9
0·8
0·7
0·6
0·5
0·4
0·3
SIZE LOG WINGSPAN × BODY LENGTH mm²
0·5
1·0
1·5
2·0
2·5
3·0
P
A
B
B
C
C
E
E
L
L
8

TABLE 2.8.6

Insect mobility: flight speeds of different insect types

Taxon	V_{mr} (m/s)	Taxon	V_{mr} (m/s)
Ephemeroptera	3.896	Tabanidae	5.020
Plecoptera	3.924	Empididae	3.765
Psocoptera	2.673	Lonchopteridae	3.136
Heteroptera	3.028	Phoridae	3.172
Homoptera	2.660	Dolichopodidae	3.760
Aphidoidea	2.348	Syrphidae	5.196
Psyllidae	2.838	Sepsidae	3.427
Neuroptera	3.952	Borboridae	2.987
Lepidoptera	3.685	Chloropidae	3.992
Trichoptera	4.037	Muscidae	5.374
(Diptera)	(3.940)	Cordilurinae	4.885
(Nematocera)	(3.400)	(Hymenoptera)	(4.723)
(Brachycera)	(4.378)	Symphyta	5.537
Acalypterate Schizophora		(Parasitica)	(3.471)
> 6mm	4.515	Ichneumonoidea	4.091
< 6mm	3.326	Chalcidoidea	2.851
Tipulidae	4.314	Vespidae	6.928
Trichoceridae	3.860	Apidae	6.415
Anisopodidae	3.063	Bombus spp.	10.417
Psychodidae	2.709	Coleoptera	3.826
Simuliidae	3.572		
Mycetophilidae	2.824		
Cecidomyiidae	2.709		
Chironomidae	2.657		
Bibionidae	3.972		
Stratiomyidae	4.123		

Groups in parentheses were derived from several sub-groups.

Acalypterate Schizophora were put into two categories to compensate for grouping of very similar taxa. All Borboridae contributing to the diets were small.

Figure 2.8.6. Distributions of flight speeds of insects taken as prey by aerial feeding birds (a.) and of available insects at three sample heights in the air (b.). The means are indicated.


Swift.
House Martin.
Sand Martin.
Swallow.
%
40
30
20
10
0
60
X̄
0·610
0·3
0·4
0·5
0·6
0·7
0·8
Log Vmr m/s
a.
12·2m.
1·8m.
Ground Level.
80
0·032
0·233
0·005
0·035
0·01
0·124
0·002
0·128
0·467
0·012
0·013
0·012
0·9
1·0
b.

TABLE 2.8.7

A comparison of mean flight speeds of insect prey taken by aerial-feeding birds and mean flight speeds of available insects

Species	Mean speed Log Vmr.m/s	Suction trap height (m)	Mean speed Log Vmr.m/s
Swift	0.543		
		12.2	0.489
House Martin	0.553		
		1.8	0.482
Sand Martin	0.579		
		Ground level	0.502
Swallow	0.648		

TABLE 2.8.8

Niche breadths along the insect prey flight speed continuum, and ranges of available insect flight speeds (both index B)

Species	B	Suction trap height (m)	B
Swift	3.416		
		12.2	1.706
House Martin	3.534		
		1.8	1.341
Sand Martin	4.170		
		Ground level	1.867
Swallow	2.998		

the size distributions, i.e. with the Swallow taking the fastest prey, the Swift taking the slowest and the House and Sand Martins intermediate. Similarly, it is evident that the mean prey flight speeds selected by all four predators were greater than the mean flight speed of available insects at any sampling height. Additionally, the prey distributions for all predators were significantly different from the insect distributions at all sampling heights (χ^2 test, $P < 0.001$ for all comparisons). These log-transformed distributions were all significantly non-gaussian (negative skew for Swallow, positive for all others) and therefore niche breadth was expressed as B (Table 2.8.8, see Section 2.5.3), and not standard deviation. They show that Sand Martins were the most generalised aerial feeders with respect to slow and fast flying insect prey, whilst Swallows were the most specialised by selecting mainly fast flying types. To be consistent and to illustrate the increase in faster flying insect types at ground level (due to an expansion of the range), the range of insect flight speeds at each sampling height was also expressed as B (Table 2.8.8, and see Figure 2.8.6b).

Since insect flight speed has been derived from weight and wingspan, it is important to relate weight to size class ($\log_{10}$ mm^2). In the present study data on weight and size are too few for separate correlations of different taxa, and the good correlation ($r = 0.939$, $n = 75$, $P < 0.001$) for all taxa combined undoubtedly obscures differences between insect types in increment of weight for a given size increase. The different ratios of body to wing length are of limited use for indicating taxonomic differences in weight increase relative to size increase (from Log_{10} mg + 1 = 1.2421 $\log_{10}$ mm^2 - 0.9588). However, the good agreement between theoretical and actual insect flight speeds shows this limitation to be minor.

Factors influencing selection of prey of different mobilities

As with size selection of prey, the possibility of environmental factors causing variation in the selection for mean insect mobility (flight speed) and the range of mobilities taken in the prey was investigated. The niche breadth index, B, represented range of mobilities in this analysis.

Mean prey mobility

Significant correlates with mean daily prey mobility selected are detailed in Tables 2.8.9 and 2.8.10 for Sand Martin and Swallow respectively. The only variable in both species analyses producing a negative correlation was rainfall. These results are in contrast to the negative relationships derived for prey size selection by Sand Martins. It is apparent that both species selected faster flying insect types on days of high insect abundance, and with faster flying insects available in the case of the Swallow.

A multiple regression analysis for the Sand Martin data (Table 2.8.9b) confirmed the dominant effect of insect abundance, with numbers at 1.8m and ground level explaining 49.7% of the variance in prey mobility and only a further 8.7% being explained by all other variables combined. No other variables were significant in the regression equation and separate analyses for individual effects of mean daily insect mobility and weather factors showed them to be of lesser importance. The results of a similar analysis for Swallows (Table 2.8.10b) showed that all the variables together accounted for 90.1% of the prey mobility variance, the mean insect mobility at 12.2m for much of this. Variables additional to those listed were non-significant in the regression equation and separate analyses for individual effects of insect abundance and weather variables again demonstrated their lesser influence.

TABLE 2.8.9a

Environmental variables correlated with mean daily prey mobility selected by Sand Martins

	r	P
Insect abundance at 1.8m	0.595	< 0.01
Minimum temperature	0.548	< 0.01
Maximum temperature	0.563	< 0.01
Insect abundance at 12.2m	0.447	< 0.05

TABLE 2.8.9b

Multiple regression analysis of the effect of environmental variables on mean daily prey mobility selected by Sand Martins

	Multiple Regression Coefficient	Standardised Partial Regression Coefficient	Cumulative Coefficient of Determination		
Variable	b	B. wt.	$r^2 \times 100$	F	P
Insect abundance at 1.8m	0.069	0.818	35.4%	6.03	< 0.01
Insect abundance at ground level	-0.090	-0.786	49.7%	4.44	< 0.05
Minimum temperature	0.003	0.615	54.9%	4.53	< 0.05

Constant = 0.603

Multiple r = 0.74

TABLE 2.8.10a

Environmental variables correlated with mean daily prey mobility selected by Swallows

	r	P
Mean insect mobility at 12.2m	0.796	< 0.001
Rainfall	-0.612	< 0.01
Insect abundance at 1.8m	0.602	< 0.01

TABLE 2.8.10b

Multiple regression analysis of the effect of environmental variables on mean daily prey mobility selected by Swallows

Variable	Multiple Regression Coefficient b	Standardised Partial Regression Coefficient B. wt.	Cumulative Coefficient of Determination $r^2 \times 100$	F	P
Mean insect mobility at 12.2m	0.260	0.643	63.3%	20.8	< 0.00
Rainfall	-0.004	-0.0277	73.2%	4.7	< 0.05
Insect abundance at 12.2m	-0.059	-0.522	81.1%	11.3	< 0.01
Insect abundance at 1.8m	0.051	0.402	85.6%	4.1	< 0.05

Constant = 0.524

Multiple r = 0.93

Prey mobility niche breadth

The correlation analyses (Tables 2.8.11 and 2.8.12) show for both Sand Martin and Swallow that niche breadth along the prey mobility axis increases on good days. Although the index, B, used in this analysis does not discriminate which section of the resource axis is utilized, to accord with the corresponding increase in mean prey mobility taken on good days presumably the expansion of the niche must be to incorporate more faster-flying items. It has been previously demonstrated that prey size niche breadths also expand on good days for both species but, with the Sand Martin, to include the lower end of that axis.

TABLE 2.8.11

Environmental variables correlated with daily prey mobility niche breadths of Sand Martins

	r	P
Insect abundance at 1.8m	0.506	< 0.05
Mean insect mobility at 12.2m	0.488	< 0.05
Minimum temperature	0.472	< 0.05
Insect abundance at 12.2m	0.493	< 0.05

TABLE 2.8.12

Environmental variables correlated with daily prey mobility niche breadths of Swallows

	r	P
Minimum temperature	0.532	< 0.02
Insect abundance at 12.2m	0.487	< 0.05

Multiple regression analyses of the data resulted in only insect abundance at 1.8m being significant ($F = 5.5$, $P < 0.05$) in the Sand Martin equation and accounting for 25.6% of the variance in niche breadth with a cumulative total explanation of 41.8% for all variables. Only minimum temperature was significant ($F = 6.3$, $P < 0.05$) in the Swallow regression accounting for 28.3% of explained variance out of a total of 54.6% for all the variables. Separate analyses of other variables confirmed their relative meagre contribution to the explanation of niche breadth variance.

Predator manoeuvrability

In terms of an evolutionary response to differences in insect prey size and mobility within the air-space, it was not possible to demonstrate adaptations of wing-length, weight and tail-length measurements in isolation. However, these measurements in combination, as flight speeds and manoeuvrability indexes (Figure 2.8.7), indicated less obvious forms of adaptation to niche. It may be expected that faster flying predators should be able to catch faster flying insect prey, however no correlation between predator and prey flight speeds could be demonstrated to this effect ($r = -0.630$, $P > 0.1$). Indeed it was apparent that the fastest prey were selected by the two slower predators.

So how are the Sand Martin and, in particular, the Swallow adapted to catch more mobile prey than the House Martin and Swift? Observations of feeding birds show the species to differ in the relative amounts of twisting and turning that are used to secure prey. At one extreme the Swallow demonstrates habitual rapid turning movements as it feeds, whilst at the other the Swift approaches prey items with minimum deflection of the flight path. The Sand Martin

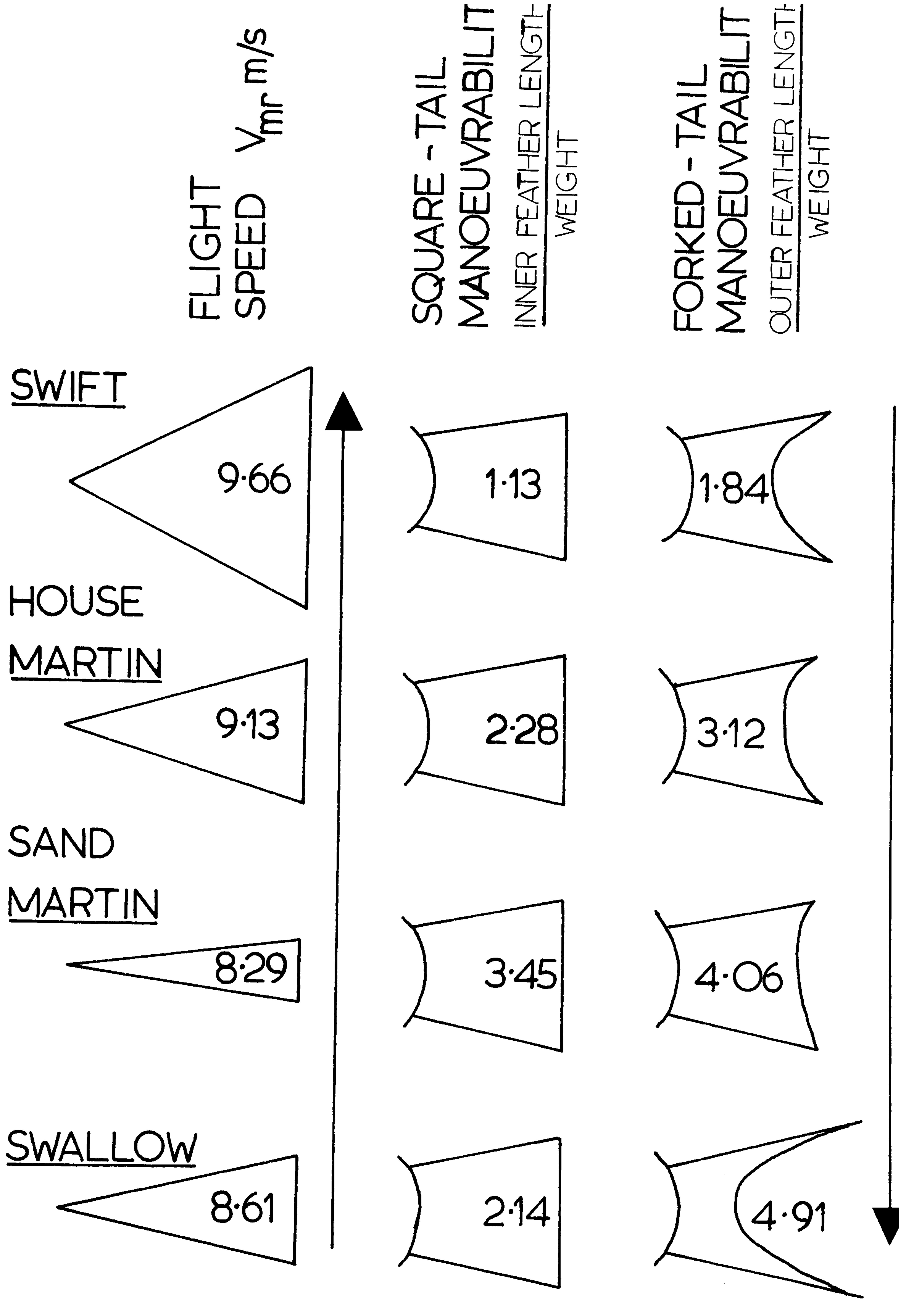


Figure 2.8.7. Flight speeds and manoeuvrability indexes of aerial feeding birds.

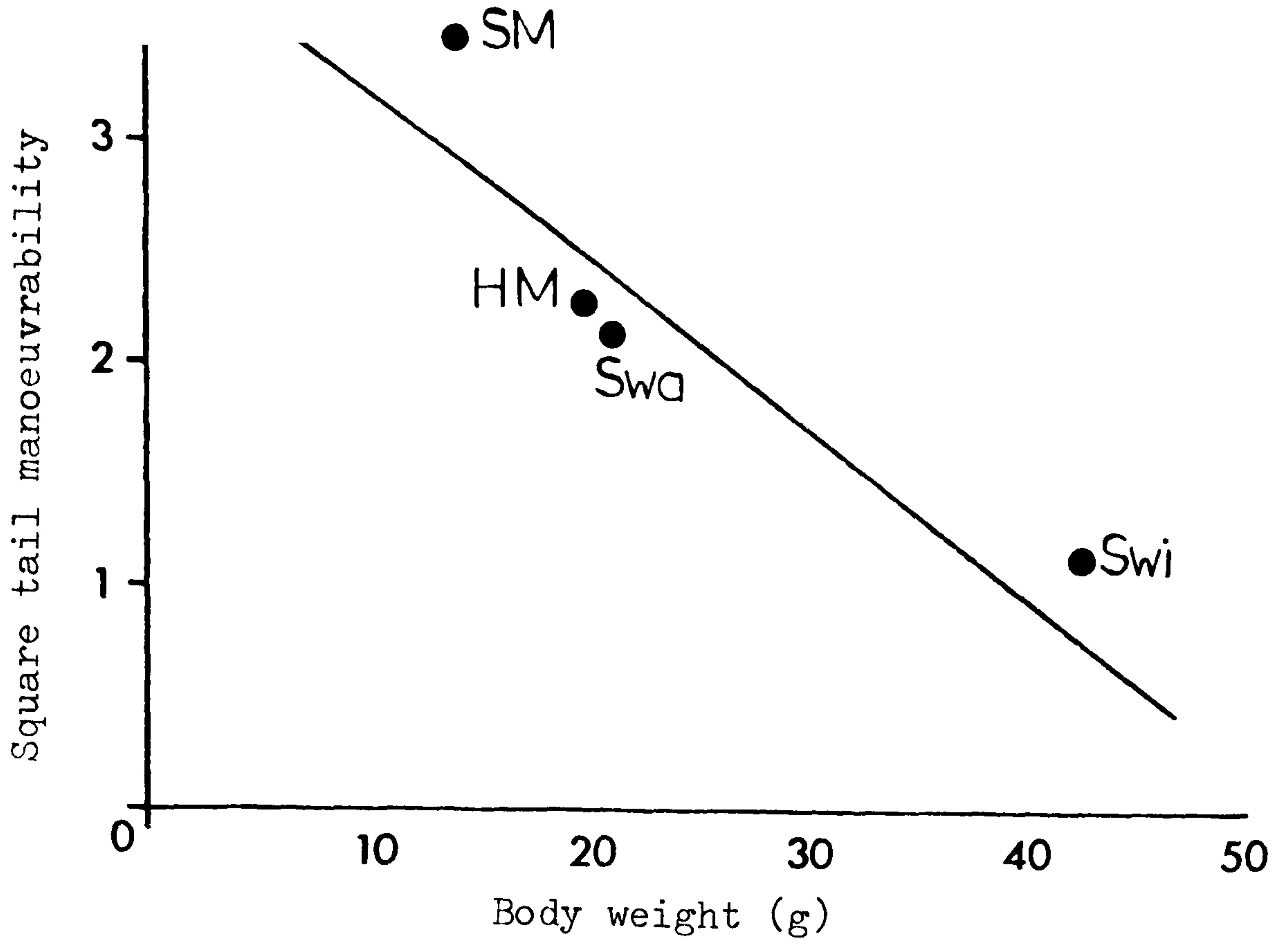


Figure 2.8.8. A hypothetical situation where all aerial feeding birds have square tails shows the larger species to be less manoeuvrable. $y = 0.069x - 3.905$, $r = -0.911$, P 0.05

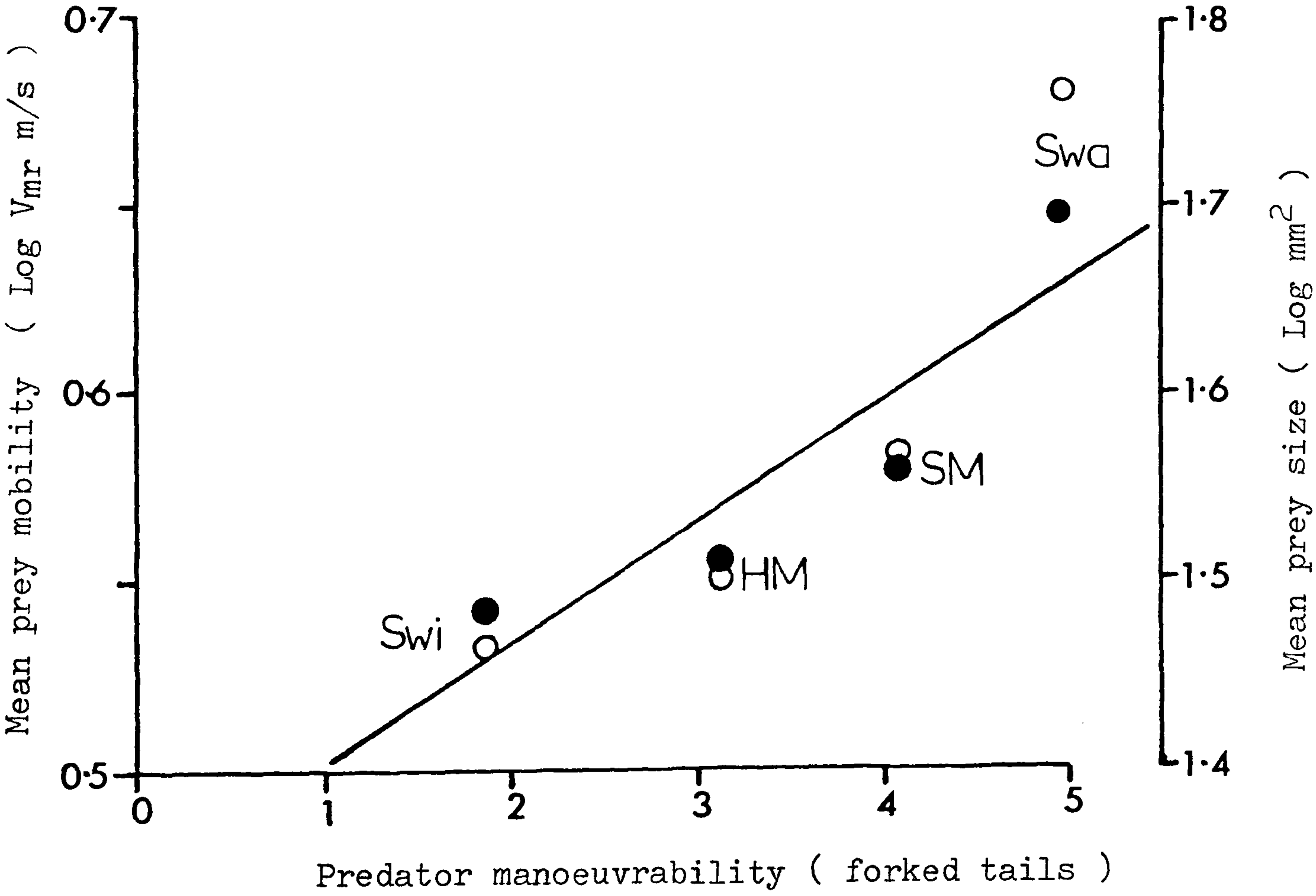


Figure 2.8.9. Relationship between the real manoeuvrability index and characteristics of the prey. More manoeuvrable predators catch larger, more mobile prey. ● = prey mobility, ○ = prey size. The slope has been calculated for prey ~~mobility,~~ Log $y = 0.0321x + 0.4690$, $r = 0.902$, $P<0.05$.

and House Martin are intermediate with the former more like the Swallow. (For all four species capture of prey items is by active selection and none fly with the mouth open, simply acting as a "scoop".) To test the importance of tail-shape as an adaptation to increase manoeuvrability, and hence the capture of more mobile prey, the hypothetical square tail manoeuvrability indexes were compared to the mean flight speeds of prey taken. No relationship between the two could be demonstrated ($r = 0.238$, $n = 4$, $P > 0.1$), and the Swallow in particular would be capturing disproportionately faster-flying prey than expected. In this hypothetical situation, predator manoeuvrability would actually depend on relative body weights (Figure 2.8.8). It was evident, from a comparison of the hypothetical manoeuvrability indexes and the indexes calculated from the real tail shapes, that the longer, forked tails increase manoeuvrability for all species, but by proportionately different amounts. These latter indexes were compared to the mean flight speeds of prey taken by each species, and it was found that the more manoeuvrable predators were capturing more mobile prey (Figure 2.8.9). The evidence therefore is consistent with the idea that the relative elongations of the outer tail-feathers are adaptations for increasing the ability to turn rapidly and capture faster-flying insect prey.

The mean size of prey selected by the different species shows an almost identical pattern to that of prey mobility (Figure 2.8.9). Both indicate that above a certain predator manoeuvrability, prey of all mobilities and sizes are catchable and the respective constraints will then be the upper limit to the flight-speed of insects and the handling time for each item, this being dependent on bill morphology.

It is realised that although the above analysis does not quantify the effect of prey mobility, extra to that of prey size, on segregation between the aerial-feeding species, and is therefore not a critical test of relative selection pressure, the results do point encouragingly in the right direction. A more refined analysis may be able to quantify the apparent differences in the mean prey sizes and mobilities shown in Figure 2.8.9. At present it is indeterminate whether these are real differences or simply the effects of scaling. A more detailed analysis of this problem appears in Chapter 3.

2.8.3 Selection of different prey types: taxonomic identity of the food items

In discussing the prey taken by birds it is important to attempt an assessment of the particular attributes of different taxonomic groups which cause them to be selected differentially by the different predator species. Some previous studies have centred on the problem of whether size or taxonomic identity of the prey is the more important characteristic. Schoener and Janzen (1968) have shown that different taxonomic groups of insects have different average sizes within the same habitat with the implication that birds foraging in the same habitat should show distinct proportions of taxonomic groups in their diets in relation to their preferred prey size. Hespenheide (1975), in a study of two swifts and a swallow in a tropical area, found that different proportions of taxonomic groups in the diets could not be accounted for by size selection alone. He found that insect flying ability was important in the exclusion of some prey types, particularly Diptera, and that density and taxon-characteristic aggregation, notably of Hymenopteran sub-taxa, was an additional influence on selection of particular types. Support for the importance of prey size in relation to taxonomic preference comes from positive correlations of overlap of size and overlap of prey type in the diets of birds feeding in the same habitats (Schoener 1968). For all four aerial-feeders the correlation between prey size and prey type overlaps is good for the entire breeding season (Figure 2.8.10). However, a separate analysis of the diets of Swallow and Sand Martin throughout the season failed to support this relationship. Hence, although some differences in taxonomic preference of prey may be accounted for by differences in size selection, there remains further variation which may be explained by other attributes of the prey, e.g. mobility.

In the present study the proportions of different taxonomic groups occurring in the diets of the four aerial-feeding species were compared to the availability of particular prey types caught in the suction traps (Tables 2.8.13 and 2.8.14). The most important groups available together with those selected by the birds are summarised in Table 2.8.15. The House Martin diet (data from Bryant 1973) is included for comparative purposes and the proportional similarity of a number of prey types is notable, although they cannot strictly be compared against the suction trap data collected for this study (see Bryant 1973 for availability data). The high values for Acalypterate Schizophora (Diptera) result from grouping of several families difficult to identify. These are all very similar in body-plan and are similar in size, thereby compensating for the grouping procedure. The proportions of different taxa taken by Swallows accord with those noted for boluses removed from adults trapped at one site for several successive years (Thomas 1933-39), except for a higher incidence of Bibionids which probably resulted from a feature of the immediate environment in that study. Lack and Owen (1955), in a detailed study of the diet of the Swift, found Hemiptera, most of which were Aphids,

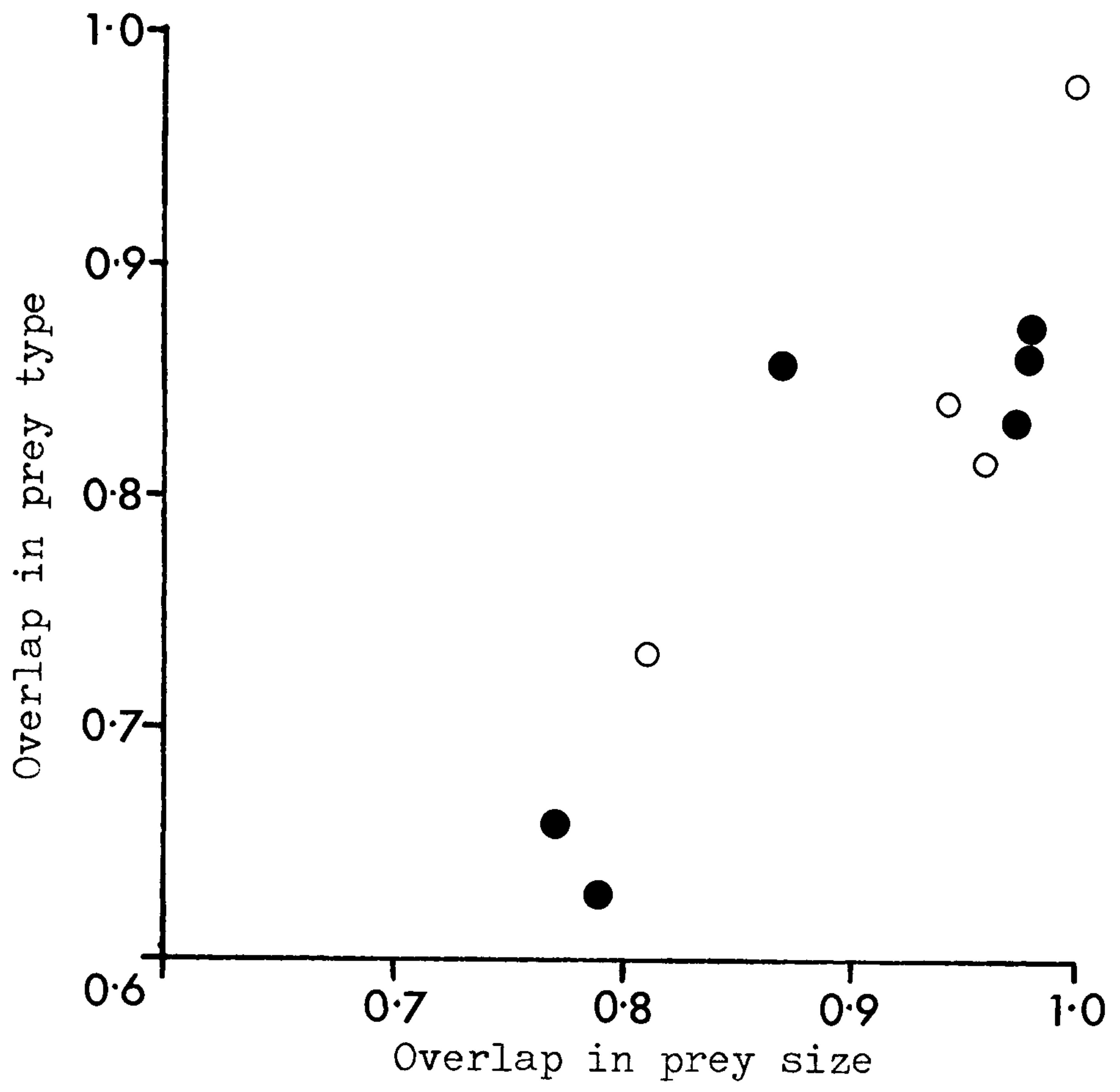


Figure 2.8.10. A comparison of dietary overlap in aerial feeding birds indicates how a varying proportion of preference for certain insect prey types may be accounted for by size selection of prey. ● = pairwise overlap, ○ = diffuse overlap for the complete breeding season. $r = 0.88$, $P < 0.001$. (Refer to Tables 2.8.21. and 2.8.23., and Appendix I).

TABLE 2.8.13

Mean percentage occurrence of taxonomic groups of insects in the faecal samples for the complete breeding season (1975)

	Swallow	Sand Martin	House Martin	Swift
Ephemeroptera		1.05		
Zygoptera				
Plecoptera		0.11		
Leuctridae		0.07		
Orthoptera	0.04			
Psocoptera	0.08	0.45	0.20	2.67
Heteroptera	0.03	0.12	0.20	0.80
Homoptera	0.05	0.04	0.22	
Psyllidae		0.19		9.29
Aphidoidea	0.32	12.18	17.80	17.74
Thysanoptera				
Neuroptera				0.10
Sisyridae				
Hemerobiidae		0.10	1.00	
Chrysopidae			0.80	0.07
Lepidoptera	0.50			
Trichoptera	0.05	0.40		3.46
Psychodidae		0.01	0.10	
Tipulidae	1.66	1.41	0.04	0.32
Trichoceridae	1.39	1.02		
Culicidae	0.71	0.33	0.10	
Anisopodidae	3.18	0.62		0.46
Simuliidae	0.47	2.06		0.57
Cecidomyiidae				
Mycetophilidae	0.42	2.23	2.50	1.19
Chironomidae	4.21	7.14	2.40	3.34
Bibionidae	0.51	7.29	20.00	3.95
Scatopsidae		0.04	0.30	
Proctotrupoidea	0.32	1.41		0.49
Platygasteridae	0.05	0.02		0.17
Formicoidea	0.45	0.02	2.70	1.53
Vespidae				
Apoidea				
Bombus spp.				

TABLE 2.8.13 (cont.)

	Swallow	Sand Martin	House Martin	Swift
Coleoptera	10.45	7.99	5.02	4.88
Staphylinidae	1.38	2.69		1.11
Araneae				0.35
Brachycera	4.17	5.04	0.30	1.98
Tabanidae	0.05			
Stratiomyidae	1.35	0.68	2.10	0.52
Empididae	2.54	2.22	1.00	0.75
Dolichopodidae	0.17	0.05		0.81
Phoridae		0.28	0.20	0.21
Lonchopteridae	2.66	4.50	1.50	4.40
Syrphidae	3.42	1.15	1.00	0.49
Acalypterate Schizophora	44.11	22.00	26.80	17.47
Sepsidae	0.08	1.18		0.21
Opomyzidae	1.35	2.90		0.52
Borboridae	0.09			3.23
Agromyzidae		0.21		0.07
Chloropidae	0.22	4.40		5.52
Muscidae	7.73	1.87		0.60
Cordilurinae	1.93	0.63		0.33
Hymenoptera		0.02		0.70
Symphyta	0.04	0.12		
Diprionidae				
Apocrita	0.57	0.21		
Parasitica	0.63	0.21	10.60	
Ichneumonidae	2.28	1.81		3.87
Braconidae	0.24	1.12		0.88
Cynipidae	0.10	0.04		0.57
Chalcidoidea		0.03		1.51
Pteromalidae		0.01		0.73

Data for the House Martin from collections in 1968 and 1969
(from Bryant 1973)

TABLE 2.8.14

Mean percentage occurrence of taxonomic groups of insects in the suction trap catches for the months April to September, 1975

	12.2m	1.8m	Ground Level
Ephemeroptera	0.062	0.030	
Zygoptera			0.001
Plecoptera			
Leuctridae			
Orthoptera			
Psocoptera	0.395	0.468	0.028
Heteroptera	0.070	0.127	0.312
Homoptera	0.030	0.038	0.255
Psyllidae	0.183	0.708	0.178
Aphidoidea	4.882	2.552	1.762
Thysanoptera	0.292	0.032	0.052
Neuroptera		0.008	
Sisyridae			0.005
Hemerobiidae	0.005		
Chrysopidae	0.008	0.012	
Lepidoptera	0.027	0.107	0.423
Trichoptera			
Psychodidae	11.458	26.087	26.953
Tipulidae	0.127	0.242	0.448
Trichoceridae	0.527	0.016	0.209
Culicidae	9.823	0.435	0.088
Anisopodidae	0.321	0.020	0.152
Simuliidae	0.467	0.015	0.363
Cecidomyiidae	1.360	5.100	16.308
Mycetophilidae	3.153	2.170	6.260
Chironomidae	50.115	47.519	13.909
Bibionidae	0.093	0.135	0.082
Scatopsidae	7.663	0.012	0.117
Proctotrupoidea		0.053	0.530
Platygasteridae	0.222	0.225	1.002
Formicoidea	0.030		0.130
Vespidae	0.035	0.128	0.013
Brachycera	0.472	0.052	0.023
Tabanidae			
Stratiomyidae			0.002
Empididae	0.422	0.067	0.102
Dolichopodidae	0.005		0.063
Phoridae	0.473	3.037	3.493
Lonchopteridae	0.013		0.578
Syrphidae	0.032	0.042	0.085
Acalypterate) Schizophora)	1.147	1.290	2.993
Sepsidae	0.002	0.065	0.260
Opomyzidae			0.070
Borboridae	0.225	0.567	2.432
Agromyzidae	0.170	0.270	0.360
Chloropidae	1.240	2.845	8.028
Muscidae	0.185	0.452	0.643
Cordilurinae		0.082	0.322
Hymenoptera			
Symphyta	0.047		0.063
Diprionidae			0.002
Apocrita		0.002	0.003
Parasitica			0.003
Ichneumonidae	0.395	1.048	2.370
Braconidae	0.440	0.392	1.755
Cynipidae	0.210	0.155	0.865
Chalcidoidea	0.489	0.268	1.358
Pteromalidae	0.242	0.118	0.577
Apoidea	0.005	0.002	0.012
Bombus spp.	0.013		0.012
Coleoptera	0.527	0.945	1.918
Staphylinidae	1.213	1.927	1.633
Araneae	0.387	0.135	0.395

TABLE 2.8.15

Frequency of major prey taxa occurring in the diets and amongst those flying during the same season

	SELECTED				AVAILABLE		
	Swallow	Sand Martin	House Martin	Swift	12.2m	1.8m	Ground Level
Aphidoidea/Psyllidae	0.32%	12.37	17.80	27.03	5.06	3.26	1.94
Nematocera	12.55	22.15	25.44	9.83	85.10	81.76	64.89
Brachycera/Cyclorrhapha	69.87	47.11	39.50	37.11	4.50	8.77	19.46
Hymenoptera	4.68	4.93	13.30	10.45	2.13	2.39	8.70
Coleoptera	11.83	10.68	5.02	5.99	1.74	2.87	3.55
Others	0.75	2.76	5.54	9.59	1.47	0.957	1.55

to contribute almost 67%, whilst Diptera were far less important at 16.1%, proportionately less Hymenoptera than in this study at 5.8%, but partly compensated for by Coleoptera with 8.4%.

2.8.4 Spatial segregation: the measurement of feeding station

It has been shown how the four aerial-feeding species partially segregate by selecting prey of different sizes and mobilities. From what is known of the distribution of different insect types in the air, together with the different diets of the predators, an observable difference in preferred feeding stations may be expected. The results of observations, which continued throughout the breeding season in all weather conditions, do in fact show differential utilization of particular patches in the air-space by the different species (Figure 2.8.11a, b).

The mean heights of the high, mid and low levels were respectively 43.4m, 12.5m and 2.2m, these being calculated from the combined observations for all species. Although aerial insects display a log density to log height relationship it was not expected that the mean feeding heights of the birds should similarly conform to a log series. The mean feeding heights differed between species within each level (see Appendix I), but as a cause of error in predicting overlap in air-space (see below) these differences were considered negligible.

Factors influencing feeding station

The patterns of air-space use are discussed here in relation to the principal environmental factors effecting changes in the feeding stations of each species. The niche breadth index B, although useful for describing the extent of air-space use for feeding by each species, was inappropriate for identifying which environmental conditions

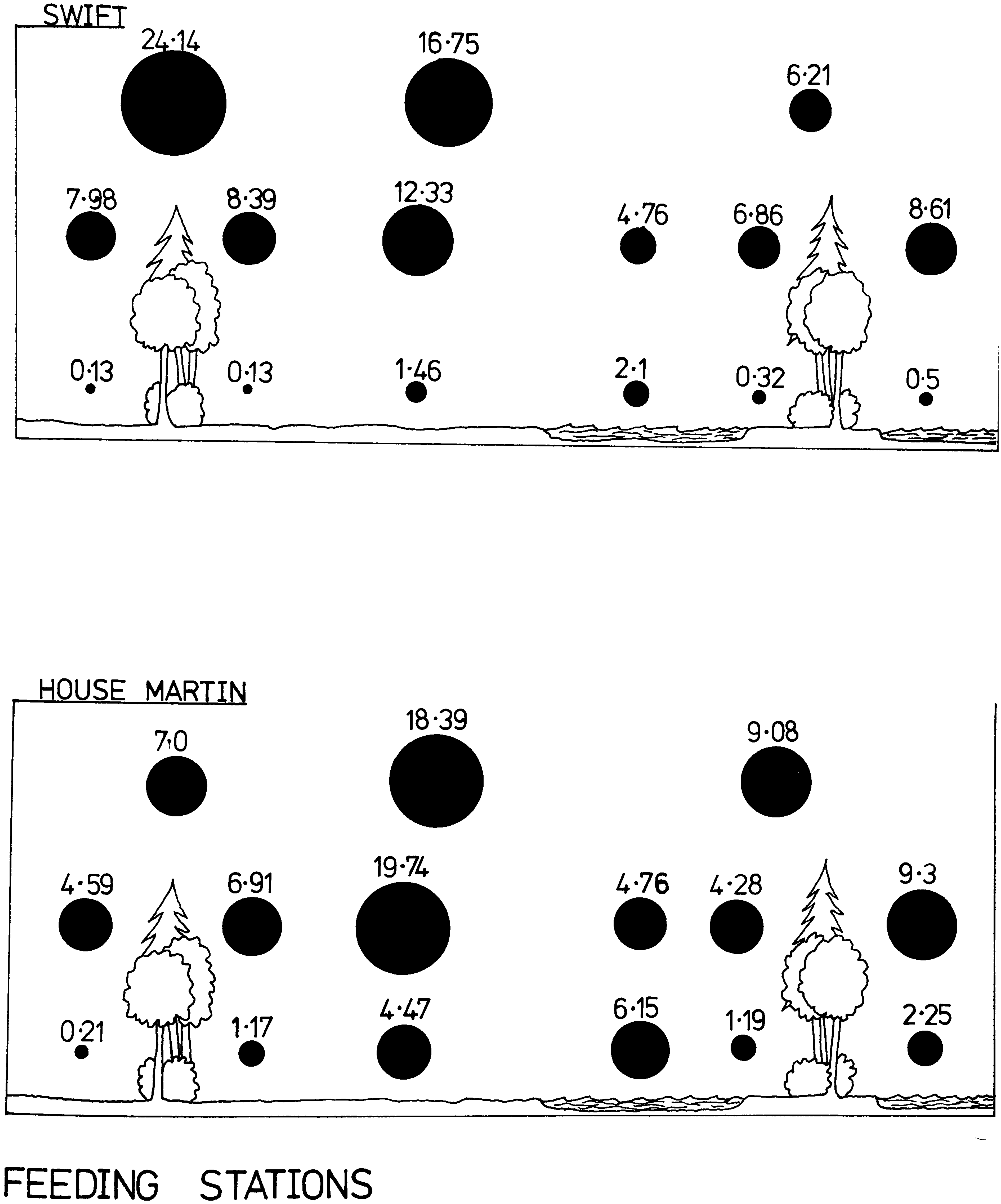
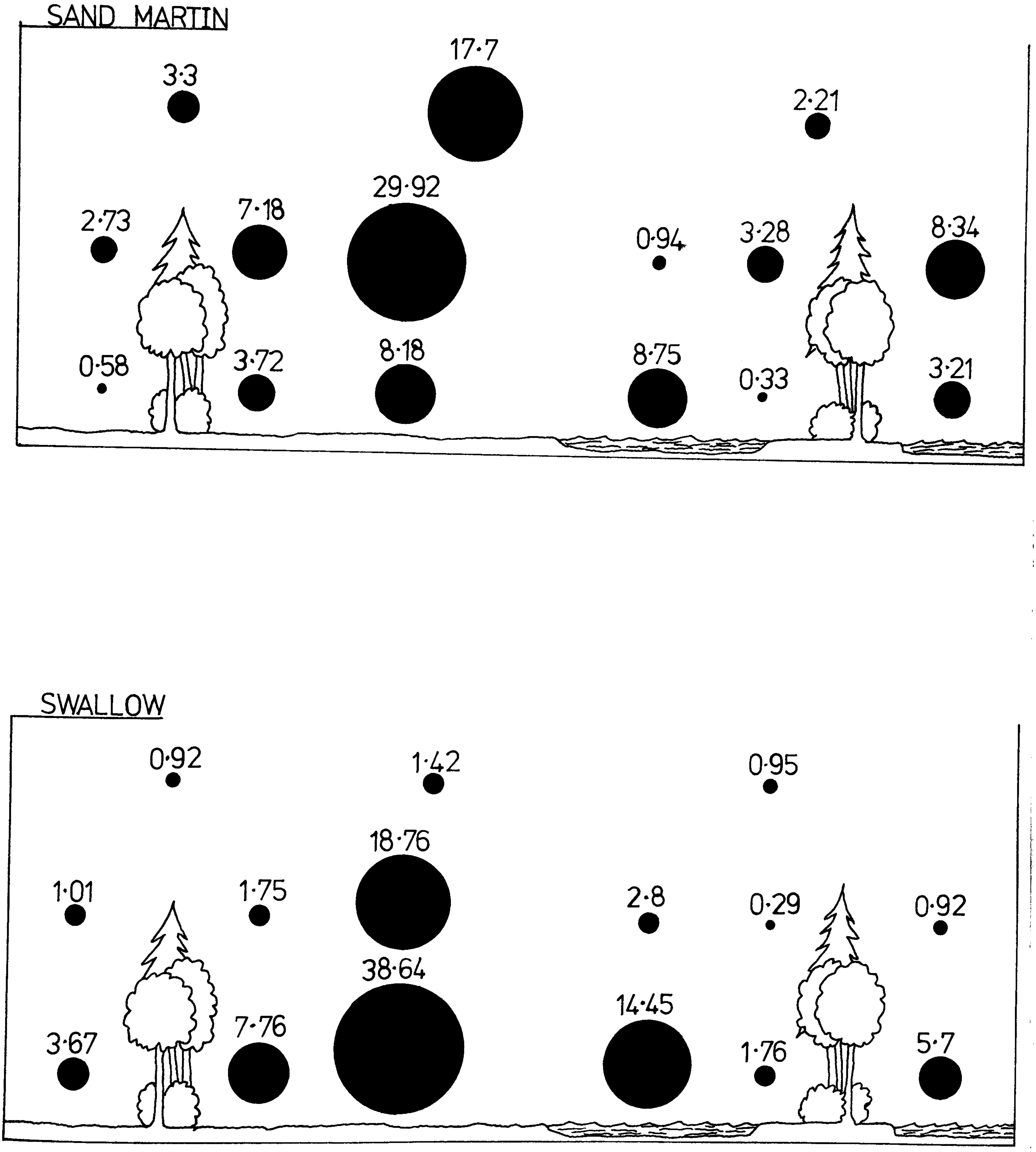


Figure 2.8.11.a. Partitioning of the air-space: preferred feeding areas (as percentages of total patches) of aerial feeding birds in all conditions during the breeding season.



FEEDING STATIONS

Figure 2.8.11.b.

caused the birds to switch from one patch to another. Hence, when total niche breadth contracted, only separate analyses for each patch could determine to which sector of the air-space birds were confined. The subjective weather categories proved to be reliable when tested against standard meteorological data (Table 2.8.16) and

TABLE 2.8.16

Correlation matrix for subjective observational weather categories and 24 hour meteorological station data

Weather Observations	METEOROLOGICAL STATION DATA		
	Maximum temp °C	Minimum temp °C	Total Rainfall mm
Wind speed	-0.203***	0.021 NS	0.172**
Air temperature	0.536***	0.232***	0.163**
Sunshine	0.225***	-0.105 NS	-0.200***
Cloud cover	-0.323***	0.108 NS	0.252***
Rainfall	-0.272***	0.029 NS	0.334***

** = $p < 0.01$, *** = $p < 0.001$, N.S. = Not significant, $n = 220$

these categories were therefore used in the subsequent multiple regression analysis of air-space usage.

The Swift (Figs 2.8.11a and 2.8.12a) as predicted, concentrated its feeding effort in the upper layer of the air column predominantly above vegetation and over open topography. These are the patches to which small, weaker flying insects are carried upwards in a passive manner by convection currents and other air movements. Mass insect take-off from fields would account for the observed numbers feeding in open situations at a mid-level although this was only common when the temperature was low. When temperature and insect abundance were high then more birds fed higher, although on rainy

FIGURE 2.8.12

Principal factors influencing the feeding distributions of the four aerial feeding species. Patch enumeration as in Figure 2.5.1. T = Air temperature, W = Wind speed, S = Sunshine, C = Cloud cover, R = Rainfall; I, II and III = insect abundance at ground level, 1.8m and 12.2 m respectively. First column figures refer to r, the simple correlation coefficient, and second column to β, the standardised partial regression coefficient. For the significance of F ratios in the multiple regressions:- * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$. For significant regression equation variables numbering over three refer to Appendix I. All correlation coefficients are significant.

(a) SWIFT

n = 144

<table>
<tr><td colspan="2">1 r β
T 0.53 *** 0.514
I 0.28 ** 0.208
II 0.15 ** -0.189</td><td colspan="2">4
S 0.38 *** 0.401
R -0.30 *** -0.211
T 0.31 *** 0.192</td><td colspan="2">7
R 0.22 ** 0.220</td></tr>
<tr><td>2W
T -0.22 ** -0.148</td><td>2L
T -0.21 *** -0.166
W 0.41 * 0.147</td><td>5
T -0.36 *** -0.298</td><td>8
T -0.40 *** -0.380
R 0.36 *** 0.332
III-0.28 ** -0.199</td><td>10W
T -0.48 *** -0.426
I -0.25 *** -0.305
S -0.33 *** -0.166</td><td>10L
T -0.46 *** -0.414
W 0.20 *** 0.251
I -0.29 *** -0.325</td></tr>
<tr><td>3W
W 0.19 * 0.190</td><td>3L
W 0.19 * 0.190</td><td>6
II -0.17 * -0.145</td><td>9
T -0.38 *** -0.374
R 0.35 *** 0.317</td><td>11W
T -0.23 * -0.193</td><td>11L
T -0.24 *** -0.253
W 0.21 *** 0.224</td></tr>
</table>

(b) HOUSE MARTIN

n = 200

<table>
<tr><td colspan="2">1 r β
T 0.45 *** 0.349
S 0.35 *** 0.226
R -0.21 * -0.108</td><td colspan="2">4
T 0.37 *** 0.297
W -0.20 *** -0.215</td><td colspan="2">7
I -0.24 *** -0.249
T 0.14 *** 0.214
II -0.21 ** -0.185</td></tr>
<tr><td>2W
II 0.21 ** 0.192
R -0.14 ** -0.125</td><td>2L
W 0.20 ** 0.200</td><td>5
W -0.20 *** -0.190</td><td>8
III-0.32 *** -0.333
R 0.16 ** 0.136
T -0.20 * -0.104</td><td>10W
T -0.21 ** -0.183</td><td>10L
W 0.28 *** 0.301
T -0.24 *** -0.182
R 0.17 * 0.120</td></tr>
<tr><td>3W
W 0.14 ** 0.146</td><td>3L
W 0.25 *** 0.248
T -0.13 * -0.124</td><td>6
III 0.16 ** 0.152
C 0.16 * 0.138</td><td>9
T -0.34 *** -0.237
R 0.28 *** 0.183
III-0.28 *** -0.283</td><td>11W
W 0.23 *** 0.215
T -0.19 ** -0.151</td><td>11L
W 0.30 *** 0.283
T -0.26 *** -0.227</td></tr>
</table>

(c) SAND MARTIN

n = 324

<table>
<tr><td colspan="2">1 r β
T 0.45 *** 0.458
I 0.11 *** -0.192
R -0.22 ** -0.109</td><td colspan="2">4
T 0.53 *** 0.538
II 0.27 *** 0.344
R -0.25 *** -0.114</td><td colspan="2">7
III 0.26 *** 0.378
T 0.24 *** 0.171
II 0.14 *** -0.234</td></tr>
<tr><td>2W
W -0.30 *** -0.255
R -0.20 *** -0.113</td><td>2L
W 0.27 *** 0.279
T -0.23 *** -0.306
R -0.13 *** -0.232</td><td>5
III -0.37 *** -0.394
W -0.21 *** -0.217
R 0.10 ** 0.097</td><td>8
II 0.23 ** 0.209</td><td>10W
W -0.30 *** -0.249
III 0.18 *** 0.237
C -0.24 *** -0.237</td><td>10L
W 0.26 *** 0.248
T -0.17 ** -0.135</td></tr>
<tr><td>3W
T -0.21 *** -0.186</td><td>3L
W 0.45 *** 0.419
T -0.19 *** -0.276
III 0.14 *** 0.270</td><td>6
T -0.26 *** -0.155
III -0.19 * -0.168</td><td>9
R 0.20 *** 0.176
III 0.15 *** 0.221
T -0.12 *** -0.153</td><td>11W
T -0.16 ** -0.141</td><td>11L
W 0.40 *** 0.339
T -0.21 *** -0.285
R 0.17 * 0.080</td></tr>
</table>

(d) SWALLOW

n = 220

<table>
<tr><td colspan="2">1</td><td colspan="2">4
T 0.22 *** 0.223</td><td colspan="2">7
S 0.20 * 0.171</td></tr>
<tr><td>2W</td><td>2L r β
II -0.14 * -0.116
W 0.12 * 0.084</td><td>5
C -0.30 *** -0.232
W -0.24 *** -0.157</td><td>8
W -0.16 *** -0.194
III -0.11 ** -0.154</td><td>10W</td><td>10L</td></tr>
<tr><td>3W
T -0.16 * -0.155</td><td>3L
W 0.28 *** 0.269</td><td>6
III 0.46 *** 0.285
T 0.42 *** 0.261</td><td>9
III -0.42 *** -0.590
C 0.28 *** 0.334
II -0.31 *** 0.341</td><td>11W
III -0.28 *** -0.184</td><td>11L
W 0.35 *** 0.265
T -0.34 *** -0.247
R 0.30 *** 0.160</td></tr>
</table>

days it is apparent that they resorted to feeding over water. Few Swifts were observed feeding low down and only did so when temperature or insect abundance were low. Predictably the numbers feeding in the shelter or vicinity of vegetation were greater on windy days but observations also indicated that the proportions feeding around tree-tops were increased in the late evening. This crepuscular feeding was observed for the Swift alone and remains the single example of temporal segregration on a diurnal basis.

The patches fed in most by House Martins (Figs. 2.8.11a and 2.8.12b) were those over open ground at mid and high levels, with substantially lower numbers than the Swift over vegetation. Good days again were reflected by an increase in numbers feeding higher as indicated by the weather correlates, but a lowering of insect abundance caused more to feed over water, and particularly low down with an increase in rainfall. More House Martins flew lower down than Swifts and were affected more by high winds, utilizing patches mainly to the leeside of shelter belts under those conditions.

At a mid level over open ground the Sand Martin (Figs. 2.8.11b and 2.8.12c) was the dominant species with almost a third of all feeding observations contributing to this patch. Surprisingly, greater numbers feeding in this patch did so under conditions of lowered food abundance and on calm but rainy days. An increase in food abundance and temperature were responsible for a corresponding increase in numbers feeding at higher levels, although here the proportions over vegetation and water were much smaller compared to those of House Martin and Swift. As for the previous two species it is evident that Sand Martins fed in higher numbers in the shelter of obstructions in windy conditions with an associated drop in temperature.

This latter factor was also a part cause of increased utilization of the lowest air-spaces over open water and open ground.

The consistently lowest feeding station was adopted by the Swallow (Figures 2.8.11b and 2.8.12d) which dominated all patches close to the ground or water. Almost 40 percent of feeding occurred at a low level over open ground, demonstrating the specialisation of this species for the air-space in which large, fast-flying prey types occur with the greatest frequency. An increase in insect abundance and temperature caused more feeding to take place here, apart from extremely few observations at high levels. Swallows fed over open water proportionately more than the other species, increasingly so on days of limited insect abundance. The proportion feeding at a mid-level over open ground was similar to that for House Martin and likewise they increasingly did so in generally favourable conditions. As for the other species, more feeding in the lee of shelter belts was apparent with an increase in windspeeds, particularly at low levels for this species. That flying insects do accumulate more to the leeward side of shelter belts (such as trees), both near and distant from water, has been well demonstrated although the concentrations of different taxa vary in association with the height and permeability of the obstruction, and the velocity and angle of the wind impinging upon it (Lewis 1965, 1966; Lewis and Stephenson 1966). It is evident that all four aerial-feeders utilized these concentrations to different extents whenever they occured, either when food in other patches became scarce and/or in windy conditions.

The results of separate observations carried out on days with high wind speed and high rainfall corroborate the above findings where various proportional shifts in feeding station were related to the

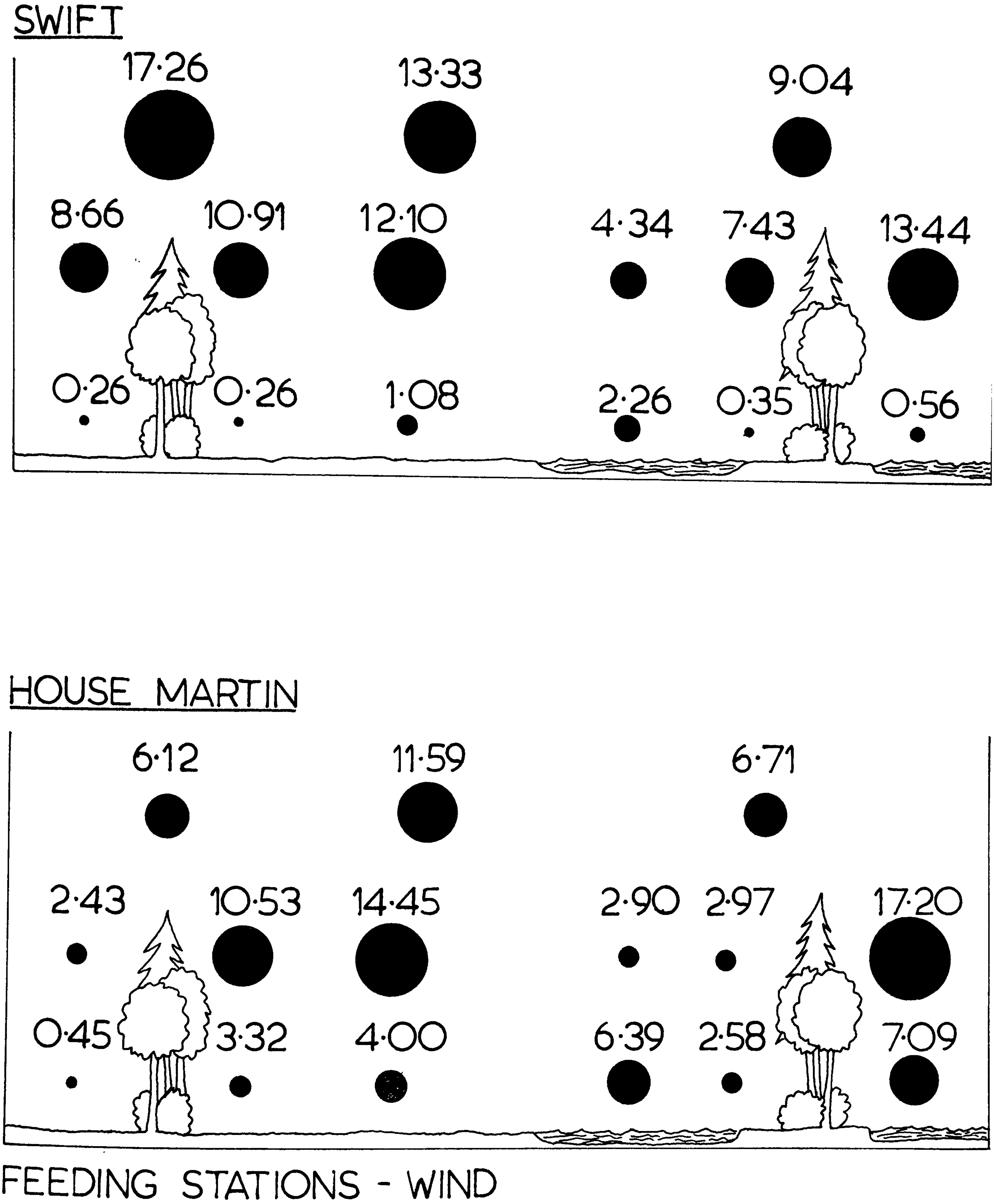
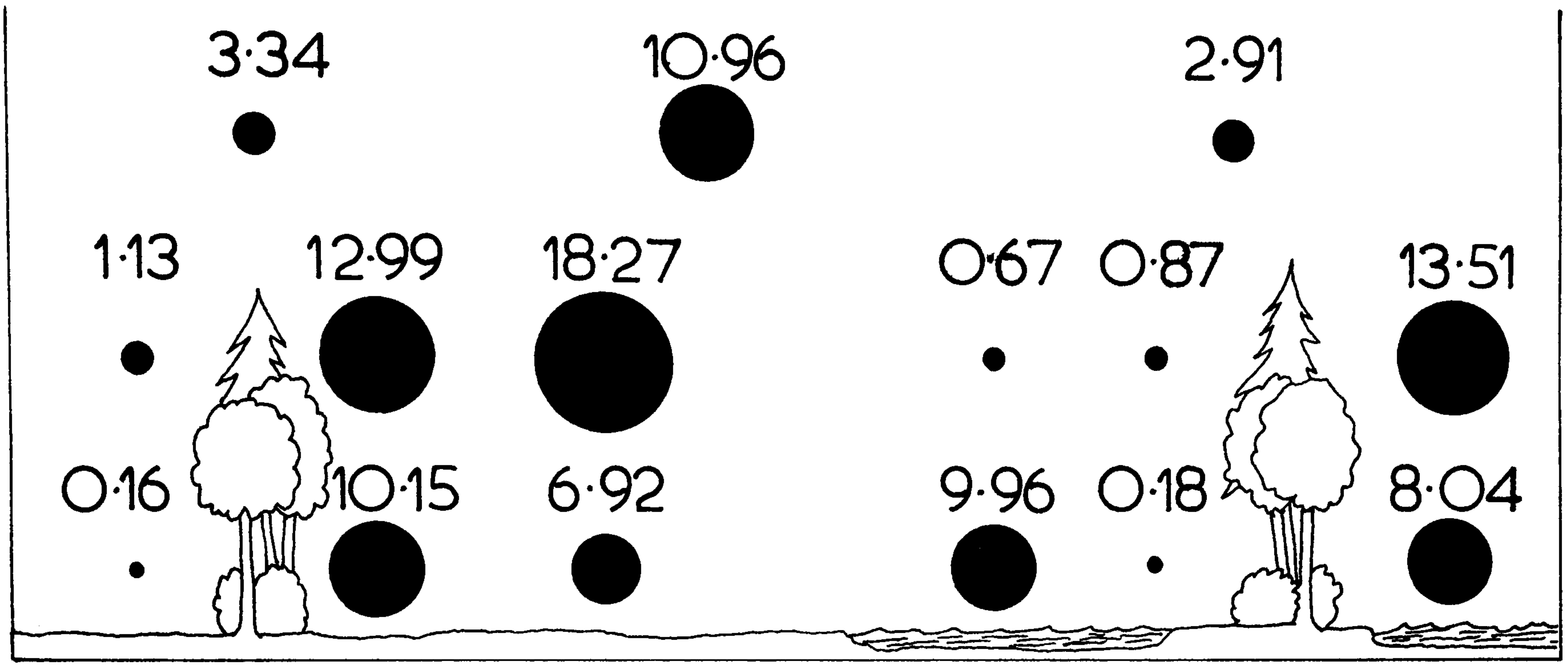


Figure 2.8.13.a. Feeding stations of aerial feeding birds on days with high wind speed.

SAND MARTIN



SWALLOW

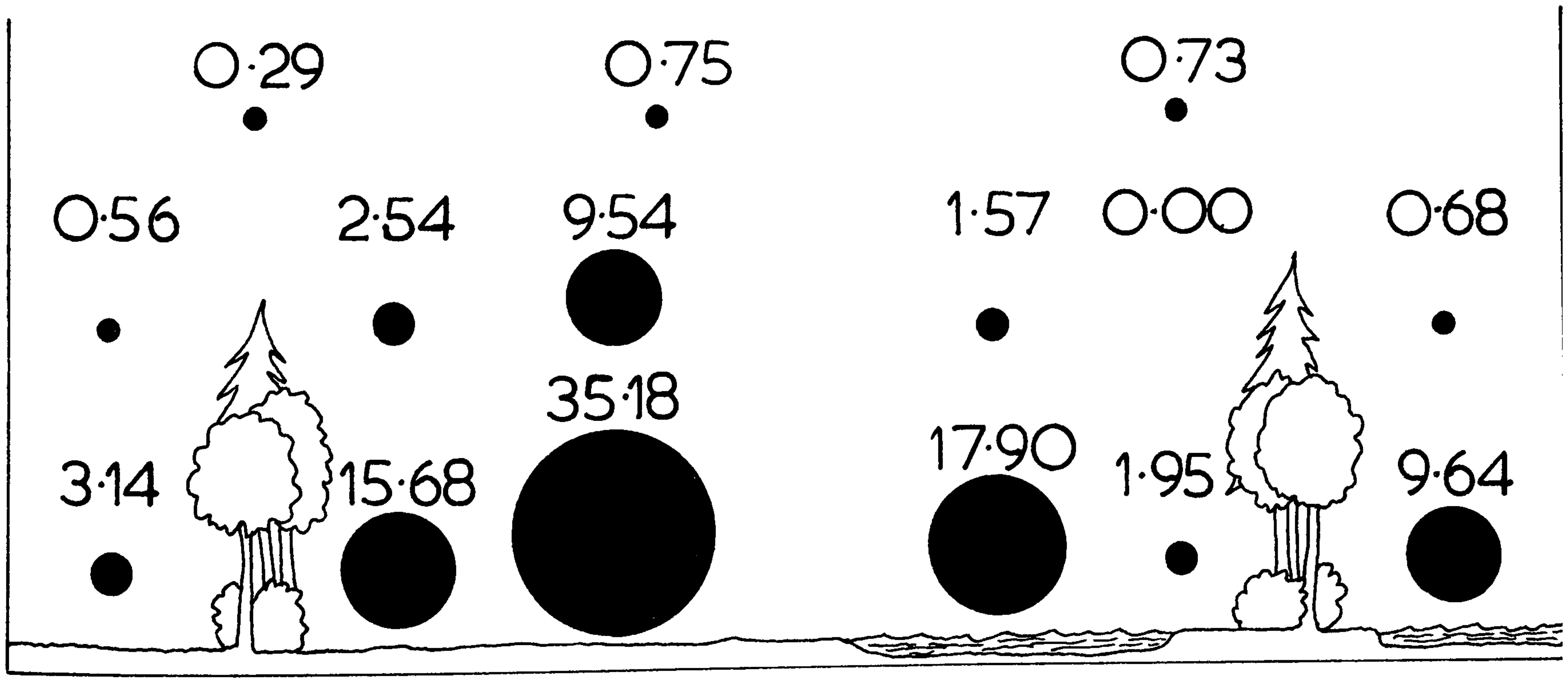


Figure 2.8.13.b.

influence of these two environmental factors. The proportion of birds feeding in the lee of obstacles (usually vegetation) increased with an increase in wind speed, and a corresponding decrease in the proportion feeding at higher levels was notable (Figure 2.8.13). The decrease in higher level feeding was also marked during conditions of persistent rain, at which times a parallel increase in the proportion of birds feeding low occurred (Figure 2.8.14).

Apart from the House Martin, these shifts in relative patch use effectively increased the overall niche breadth in conditions of greater rainfall and higher winds, i.e. on bad days (Table 2.8.17).

TABLE 2.8.17

Air-space utilization by aerial-feeding birds

Species	N	Mean height ± SD (m)	B_1	B_2	B_3
Swift	146	29.2 ± 44.3	7.470	8.626	9.842
House Martin	211	21.5 ± 33.2	8.918	10.199	7.584
Sand Martin	328	15.0 ± 15.0	6.525	8.754	6.652
Swallow	152	7.4 ± 15.7	4.588	4.969	4.826

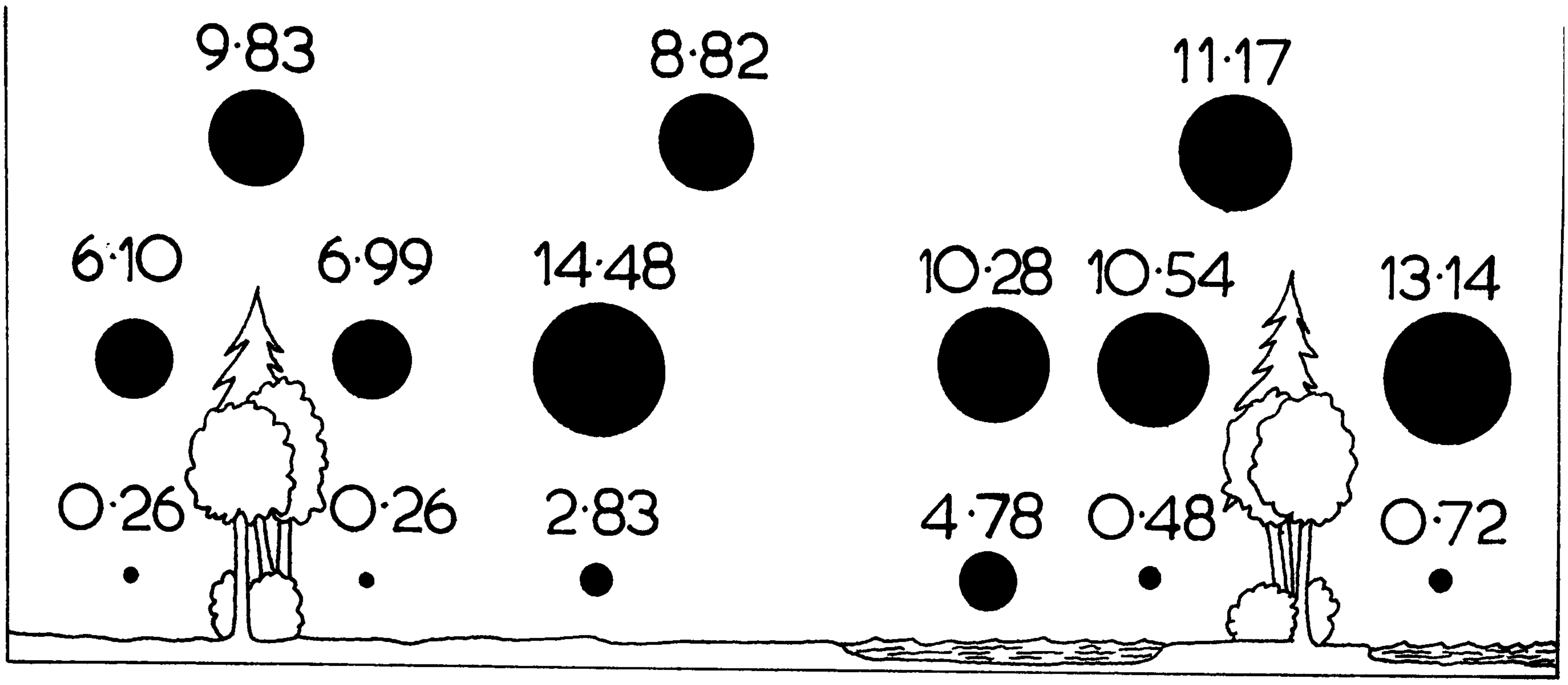
Niche Breadth B_1 = All weather conditions niche breadth

B_2 = High wind speed niche breadth

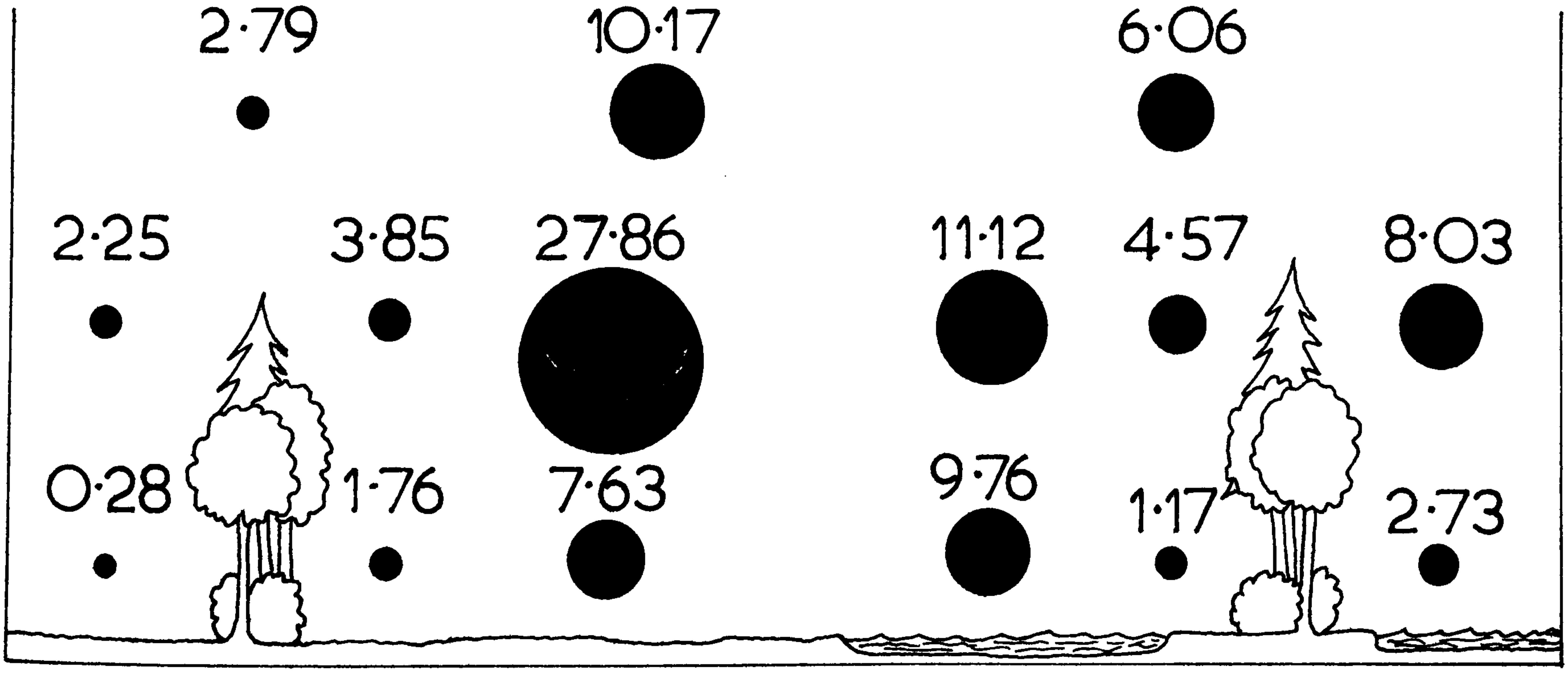
B_3 = Persistent rain niche breadth

For both conditions the increases for three species were a result of birds expanding from the concentration of favoured feeding areas to other areas where prey abundance had been less reduced or prey accumulated. So, for rainy days the shift was generally downward except that the proportion of House Martins at mid-level was increased which therefore led to a niche breadth decrease for this species.

SWIFT



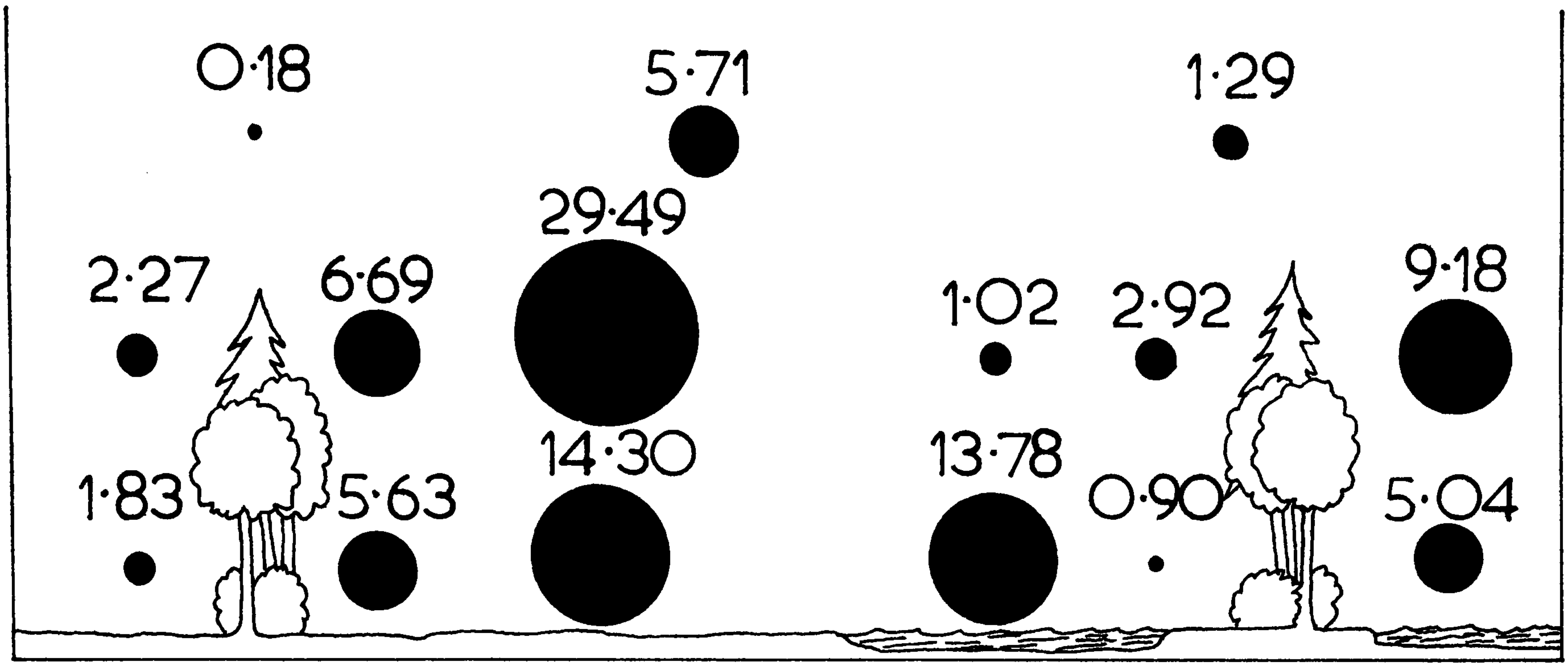
HOUSE MARTIN



FEEDING STATIONS - RAIN

Figure 2.8.14.a. Feeding stations of aerial feeding birds on days with persistent rain.

SAND MARTIN



SWALLOW

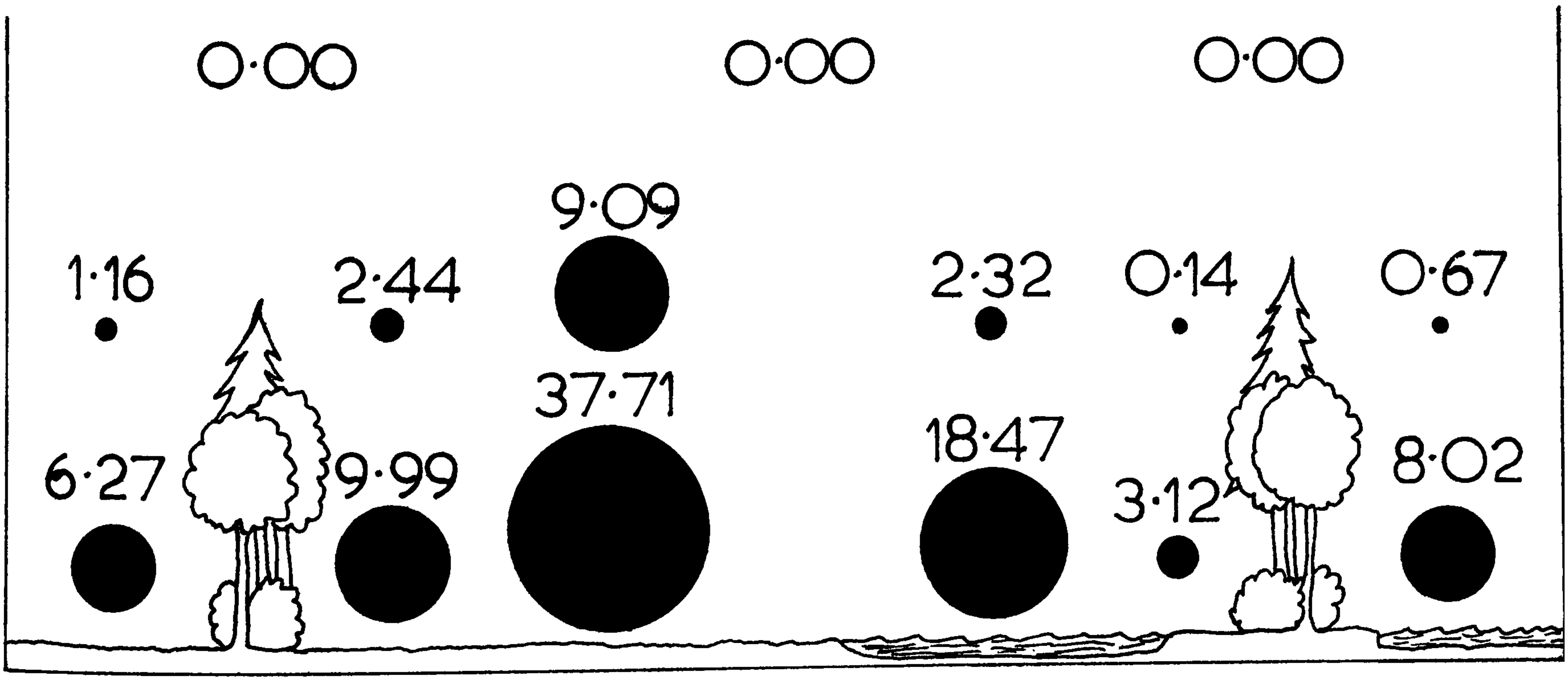


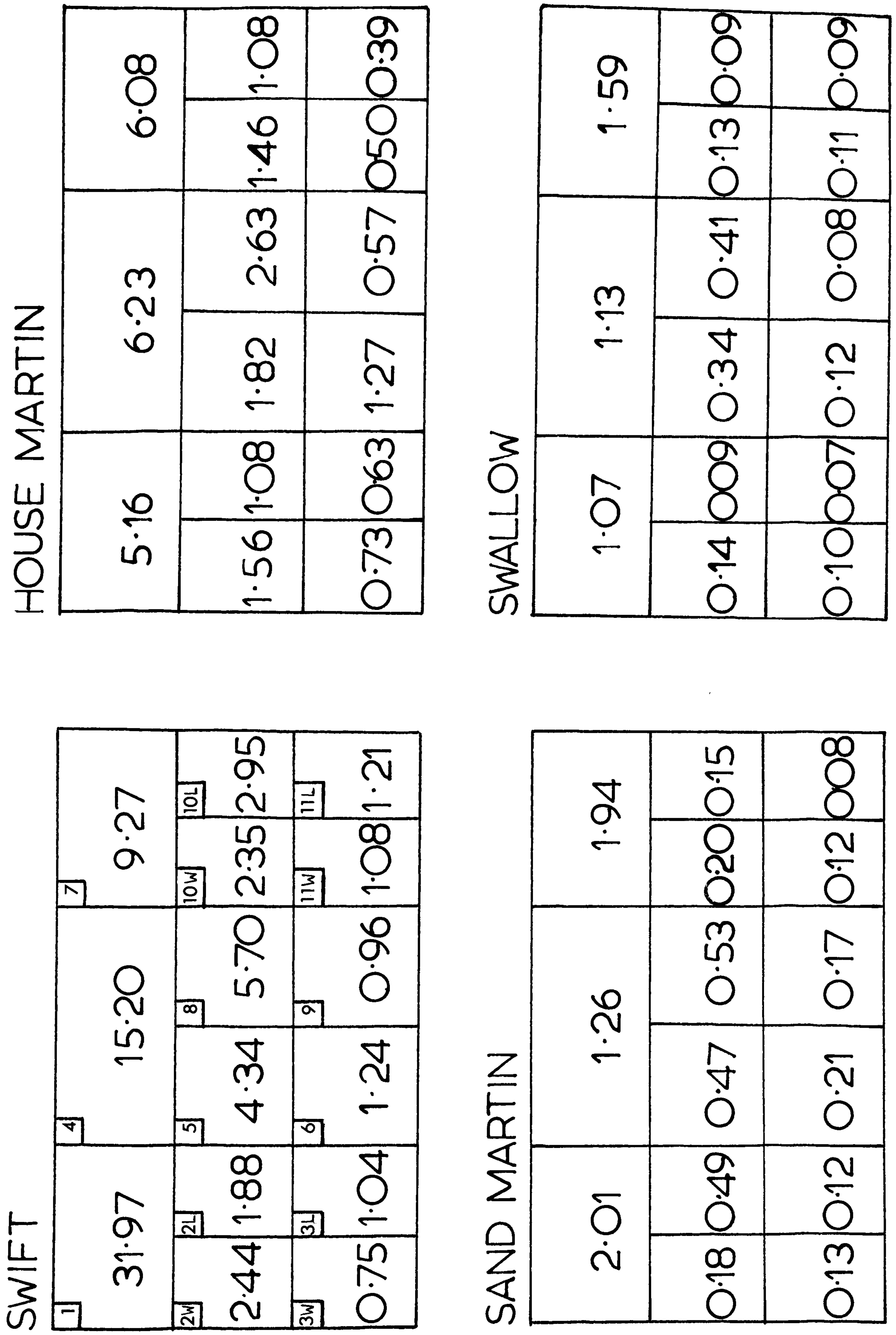
Figure 2.8.14.b.

However, increased incidences of high winds and rainfall are often simultaneous and, since House Martin niche breadth expanded in windy conditions, on unfavourable days the overall niche breadth for this species would probably show an increase. Although a downward shift was noted for the Swallow, the more even distribution of feeding at a low level contributed more to the niche breadth expansion of this species. On windy days the shift in feeding distribution was primarily to the leeward side of vegetation.

The mean heights of feeding for the complete breeding season showed a regular interval between the different species (Table 2.8.17). All height distributions were non-gaussian.

2.8.5 The association of flight mode with feeding station

The gliding/active flight ratios revealed considerable differences in mode of flight between the species (Figure 2.8.15). The high values for the Swift demonstrated the extent to which this species is morphologically adapted for a gliding mode of flight and, of the hirundines, the House Martin showed the highest values, again indicating adaptation for extended gliding flight. The Sand Martin and Swallow exhibited considerably reduced ratios, the latter using more active flight than all other species. Within each species considerable variation in the gliding/active flight ratios were observed, the general pattern being a decrease in ratio with a corresponding decrease in height of feeding (Figure 2.8.15). Relating flight ratios of particular patches to the proportional utilization of the same patches for feeding (from Figure 2.8.11) emphasised the essential difference in foraging strategy and associated morphological adaptation between two pairs of aerial feeding birds (Figure 2.8.16). The Swift and House Martin both showed significant correlations between



SWIFT

1 31·97		4 15·20		7 9·27	
2W 2·44	2L 1·88	5 4·34	8 5·70	10W 2·35	10L 2·95
3W 0·75	3L 1·04	6 1·24	9 0·96	11W 1·08	11L 1·21

HOUSE MARTIN

5·16		6·23		6·08	
1·56	1·08	1·82	2·63	1·46	1·08
0·73	0·63	1·27	0·57	0·50	0·39

SAND MARTIN

2·01		1·26		1·94	
0·18	0·49	0·47	0·53	0·20	0·15
0·13	0·12	0·21	0·17	0·12	0·08

SWALLOW

1·07		1·13		1·59	
0·14	0·09	0·34	0·41	0·13	0·09
0·10	0·07	0·12	0·08	0·11	0·09

Figure 2.8.15. Patterns of gliding/active flight ratios associated with different feeding stations for all weather conditions combined. Patch enumeration as in figure 2.5.1.

Figure 2.8.16. The association of air-space utilization with mode of flight.

a. Swallow $r = -0.255$, $P>0.1$

b. Sand Martin $r = 0.053$, $P>0.1$

c. House Martin $y = 1.5519x + 3.4058$, $r = 0.55$, $P<0.05$

d. Swift $y = 0.7163x + 2.7759$, $r = 0.866$, $P<0.001$.


a. Swallow
Percent feeding in patch
Gliding/active flight ratio
40
30
20
10
0
0·5
1·0
1·5
2·0
b. Sand Martin
30
20
10
0
0·5
1·0
1·5
2·0
c. House Martin
20
10
0
1
2
3
4
5
6
d. Swift
30
20
10
0

the level of patch use and the extent to which gliding flight was employed for feeding; the Sand Martin and Swallow did not. An increase in the proportion of gliding flight is energetically economical and, for the House Martin and Swift, it is suggested that this is an adaptation to moving over greater distances at higher levels where insect prey are smaller and relatively sparse. In favourable environmental conditions when these two species resort to feeding in patches of least preference they increase the proportion of active flight and necessarily increase energy expenditure in a situation to which they are relatively morphologically maladapted. The rather low glide/flap ratio observed for the House Martin at the open mid-level station could result from the limited data and/or could indicate a change of strategy at this station to pursuit of larger or more mobile prey items.

Although the Sand Martin and Swallow show increases in gliding flight on the few occasions when feeding at high levels (and the proportionate increases are of a similar magnitude to those of House Martin and Swift), they are primarily strategists for relatively larger, more mobile prey at lower levels and the morphological adaptations they have evolved reduce energy costs accordingly.

2.8.6 Niche size and the extent of overlap within the aerial-feeding guild

The fore-going results have detailed the ways in which the four aerial-feeding species partition resources whilst in the breeding area, but the limits to the use of these resources by each species remains to be quantified. The following section investigates the relationship of niche breadth to extent of overlap for each resource, and the intensity of competition, if any, that results from this overlap.

Niche breadth and niche complementarity

For the complete breeding season the niche breadths along the separate resource dimensions showed considerable variation between species, whilst total feeding niche sizes were relatively uniform (Table 2.8.18). With respect to overall feeding niche the Swallow was apparently more specialised than the other species. It is evident that for this species feeding was concentrated in fewer patches and, although a large range of prey sizes occurred in the diet, this was comprised primarily of fast flying insect types. The Swift is apparently not so specialised as may have been considered elsewhere although some specialist features may have been obscured in this analysis. Faeces analysis on a broad temporal and spatial basis would not reveal the Swift's habit of often feeding on single species insect swarms (Lack and Owen 1955, Hespenheide 1975). Additionally, the higher air-space niche breadths observed for this species and the House Martin may be partially accounted for by the necessity to lower their mean feeding heights in bad weather. On good days it would not be essential for the Sand Martin and Swallow to feed higher and they therefore had lower values for air-space niche breadth.

The House Martin had the smallest prey size niche, the gradation of niche breadths for all the species reflecting the occurrence of progressively larger prey items in the diet. The niche breadth of the Swift was not so restricted along this dimension and that of prey mobility, even though it selected a larger proportion of slow-flying aphids than the House Martin. This was due to the inclusion of Trichoptera, Neuroptera, larger Chironomids and Ichneumonids, and more Tipulids into the Swift diet. The broad prey size niche of the Sand Martin, coupled with the fact that it is the least specialised with respect to prey mobility bears out the earlier finding of

TABLE 2.8.18

Summary of separate resource dimension niche breadths and total feeding niche size

Species	Niche Breadth B			Total niche size ΣB
	Prey size	Prey mobility	Air-space	
Swift	4.665	3.565	7.470	15.70
House Martin	3.636	3.216	8.918	15.77
Sand Martin	4.724	4.540	6.525	15.79
Swallow	6.915	2.371	4.588	13.87

TABLE 2.8.19

Niche complementarity: co-efficients of correlation between niche breadths of separate resource dimensions

	Air-space/ prey size	Air-space/ prey mobility
Sand Martin	- 0.27	0.04
Swallow	- 0.09	0.14

$n = 16$, $p > 0.1$

Seasonal data unavailable for House Martin and Swift divergence in prey size and mobility selection under given environmental conditions.

In accordance with the Hutchinsonian (1957) model of the niche, it may be expected that a set of resources will at any one time effectively limit the ultimate total niche size of a particular guild, together with limits on total niche sizes of the constituent species members. Fluctuation in availability of a set of resources, such as seasonal variations, may be paralleled by increases and decreases in total niche size. Additionally, some guild members may expand the required range of resource states, to the detriment of other member species if these latter show corresponding contractions of total niche size. Stability in total niche size of a particular species may be achieved if expansion along one resource dimension is complemented by contraction along another. Such niche complementarity would be manifest as negative correlations between different resource niche breadths and Ulfstrand (1977) found this situation pertaining to two member species of the pariform guild. In the present study, over the extent of the breeding season, no correlations between prey size, prey mobility and air-space were significant (Table 2.8.19). However the negative correlation between air-space and prey size for the Sand Martin suggests potential niche complementarity and further investigation may confirm this trend. The problem remains of deciding how low aerial insect abundance has to be before niche changes and complementarity occur. It is possible that insect abundances on the days during which these data were collected were not low enough for these inter-relationships to be evident.

Prey size differences between adults and nestlings: relevance to niche size

Analysis of faeces collected at the same times throughout the breeding season showed, for both Sand Martin and Swallow, that when young were in the nests the mean size of prey fed to them was significantly larger than the mean size of items ingested by the adults (Table 2.8.20). The possibility of this difference resulting from fewer large items surviving intact in adult faeces is weakened in the light of other studies where similar results were obtained without faeces analysis, e.g. with the Great Tit, Parus major (Royama 1970) and Blue-grey Gnatcatcher, Polioptilus caerulea (Root 1967). It is also apparent that these mean sizes selected by adults for self-maintenance were significant reductions on the mean sizes of prey taken prior to the broods hatching. Additionally, comparing these early season adult diets with those for the complete season shows the narrower niche breadths of the former. Root (1967) made the observation that adult birds with offspring foraged such that they

TABLE 2.8.20

Average prey size ($\log_{10}$ mm^2) and range of sizes selected by breeding Sand Martins and Swallows for self-maintenance and to feed nestlings

	Swallow	Sand Martin
	Mean ± S.D.	Mean ± S.D.
Adult diet: pre-hatching	1.772 ± 0.227	1.602** ± 0.289
Adult diet: post-hatching	1.696 ± 0.342	1.497 ± 0.280
Nestling diet	1.890 ± 0.323	1.548** ± 0.322

** Sand Martin pre-hatching adult mean and nestling mean significantly different at $P < 0.01$ (t-test). All other within-species differences significant at $P < 0.001$ (t-tests).
Note: first broods only.

broadened the niche, and postulated that self-maintaining adults were conserving energy by pursuing less energy-expensive items. This postulate stemmed in part from the fact that larger prey items were found to be less abundant, and a similar lower abundance of larger aerial insects has been demonstrated in the present study. Hence, adult Sand Martins and Swallows may be conserving energy in this way at the time of peak demand on their foraging capabilities.

Although the niche breadths are broadened by this differential selection, the capture of smaller prey for self-maintenance shifts the niches towards the more abundant prey items and away from the scarcer larger types. The implication of this scale shift for Sand Martin and Swallow is that overlap between the two would be reduced (although not directly measurable in this form). It is probable that the smaller the insect types in the diet the less this effect will be manifest, for example in the House Martin and Swift. The availability of different insect taxa within different periods during the breeding season will have some effect on the mean prey size selected and may explain the elevation of the pre-hatching mean size for adult Sand Martins over the mean size fed to nestlings.

Species packing and prey size

How closely a number of species can be packed when supported on one major resource axis has been the subject of considerable theoretical interest (MacArthur and Levins 1967, MacArthur 1972, May and MacArthur 1972, May 1973). The minimum distance, (d) between the means of the utilization curves of two species on one resource axis was determined by MacArthur and Levins (1967) to be 1.56σ, while May and MacArthur (1972), by a different approach, demonstrated a typical minimum packing distance (= d/σ) for a guild of co-existing species

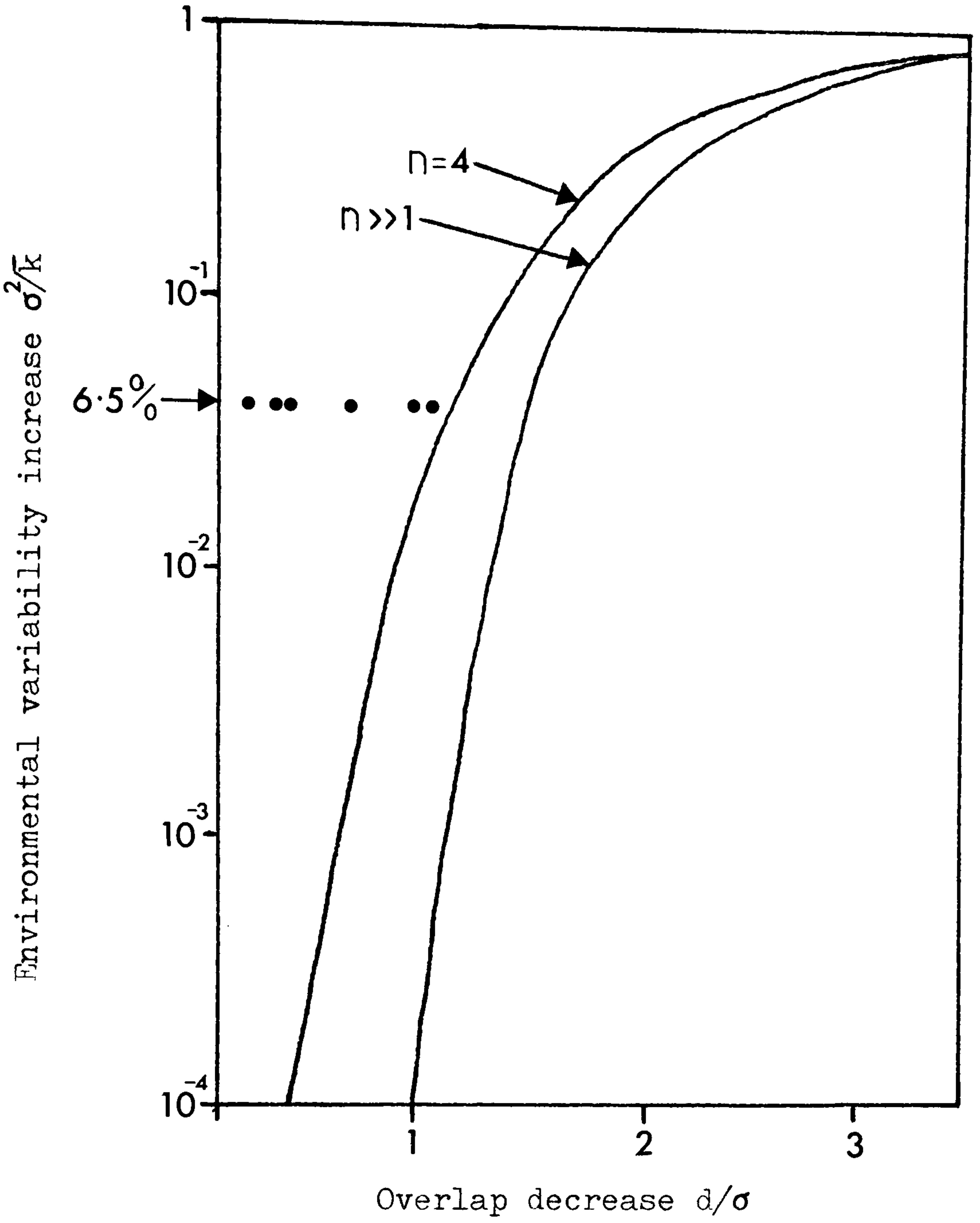


Figure 2.8.17. The theoretical minimum packing distance for a guild of species coexisting along one resource dimension: n equals the number of species. If the resource dimension is prey size then the points show that aerial feeding birds cannot coexist along this continuum alone (modified from May and MacArthur 1972). Refer to text for details.

to approximate to 1. May and MacArthur also showed that this minimum niche separation was relatively insensitive to environmental fluctuations over a wide range, and was appreciably enlarged only when these variations approached arctic equivalent conditions, i.e. at $\simeq$ 30%. These predictions are dependent on the species utilization curves approximating to Gaussian form thereby allowing niche breadth to be expressed as the standard deviation. In the present study the birds have been shown to exploit prey size in this way but the utilization functions for other resource dimensions show typically non-Gaussian distributions and are therefore not accessible to such analysis.

Figure 2.8.17 represents a modification of May and MacArthur's (1972) presentation of minimum packing distance, (d/σ) relative to environmental variability (as characterised by a mean, $(\bar{k})$ derived from summation of all species utilization curves, and the variance about this mean, i.e. $\sigma^2/\bar{k}$); in this case the single dimension is prey size. The level of variability for this axis was found to be 6.5% and, at this level, the distribution of the points to the left of the four-species guild limit indicates that the aerial-feeding birds are too closely packed to co-exist on prey size separation alone. As would be expected, d is nearest to 1 (i.e. permitting co-existence) for the Swallow/House Martin and Swallow/Swift separations.

Since these four species do not separate on prey size alone these must be other co-ordinates of the niche which assume an importance in segregation, the most probable dimension being that of air-space. The greater ease of dividing space relative to that of dividing food size is suggested by the preponderance of lower overlap values for habitat or geographical distribution. For example within the Formicariidae (ant-birds) separation of mean foraging heights approximates to one standard deviation (J. Terborgh in MacArthur 1972). It was not possible in the present study to show that the height separations were more or less than the theoretical minimum. It may be that the additive effect of partitioning the separate resource dimensions is responsible for permitting co-existence.

Diffuse niche overlap

Diffuse overlap describes the situation where a portion of any particular resource being used by one guild member is also utilized by not just one, but all other guild members. Within the aerial-feeding bird guild the diffuse overlaps for the entire breeding season were mostly high for all resource dimensions (Table 2.8.21).

TABLE 2.8.21

Diffuse niche overlaps for the separate resource dimensions

	Prey size	Prey mobility	Air-space	Mean diffuse overlap
Swallow	0.812	0.520	0.453	0.595
Sand Martin	0.996	0.805	0.869	0.890
House Martin	0.943	0.826	0.888	0.886
Swift	0.961	0.834	0.630	0.808

It is apparent that the Swallow overlapped least with the other guild members for all resource dimensions and this reflects the distinctness of the niche breadth values scored for this species (Table 2.8.18). The Sand Martin had an extremely high overlap in prey size, this value again according with a broad niche breadth along this axis. Although the Swift overlapped considerably in prey size and had the highest value for prey mobility, these were partly compensated for by the reduced sharing of air-space. The average effects of overlap in the different dimensions (equivalent to Cody's (1974) "summation α") clearly show that the two species habitually utilizing the extremes of the resource spectra do not share these resources with other guild members to the extent that the Sand Martin and House Martin do by being positioned in the middle.

The nature of the relationship between diffuse overlap and total niche size is obscure (Figure 2.8.18). A reasonable expectation would be that overlap should increase as niche size increases until a certain threshold co-existence level, at which point the curve would flatten out, allowing no further increase in overlap (Ulfstrand 1977). Possible reasons for this expectation not being fulfilled are, (i) that the relative population sizes of individual species members of the guild could not be assessed and the total niche sizes could not be adjusted accordingly, (ii) that a four species guild is simply not large enough to significantly demonstrate this relationship in a graphical representation, (iii) that there is in fact no limit to the co-existence of these four species when all resource dimensions are taken into account.

The effect of separate resource niche breadths on the amount of diffuse overlap observed for the same dimensions could not be assessed due to lack of seasonal Swift and House Martin data, and simple pair-wise overlap values for the Sand Martin and Swallow were not correlated with expansion or contraction of the appropriate resource niche breadth. With no limit to the co-existence of these species during the breeding season, the implications are that the food supply would always be super-abundant and that the characteristic resource separations would not alter under different environmental conditions.

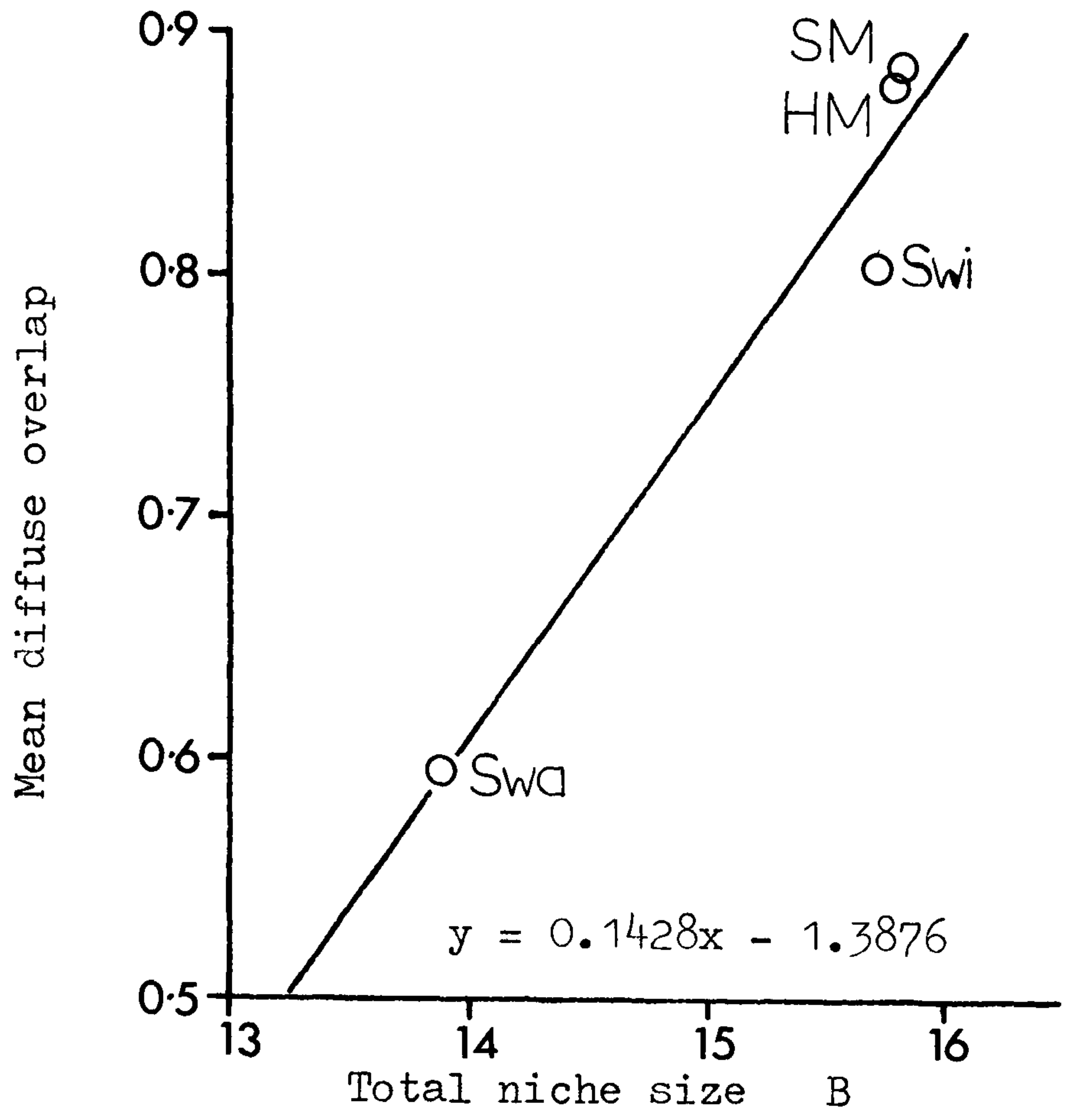


Figure 2.8.18. The relationship of diffuse overlap in all resource dimensions to the total feeding niche size, r = 0.972, P<0.

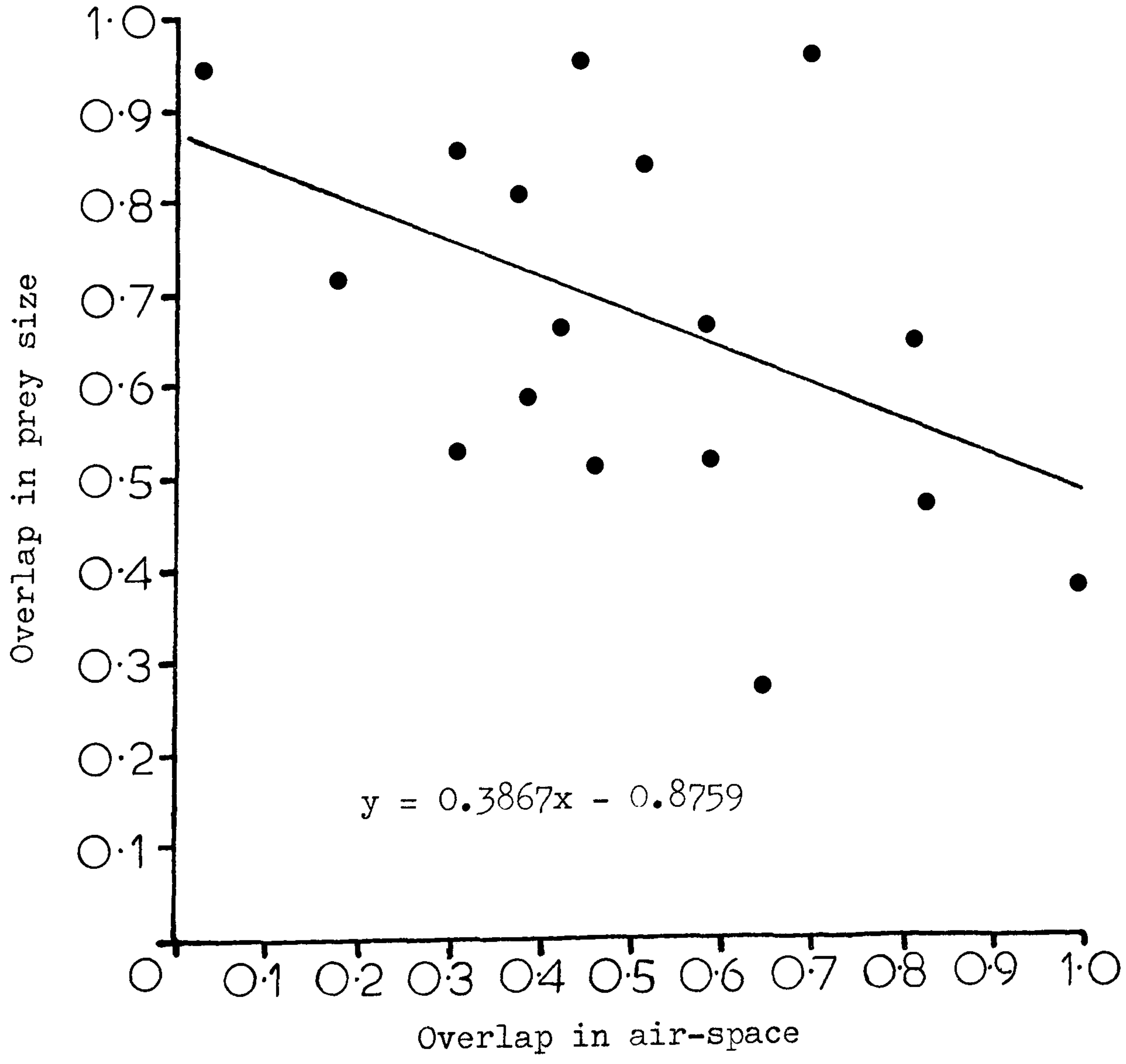


Figure 2.8.19. Resource overlap between the Swallow and Sand Martin. The

Additionally, density-dependent regulation would not operate during the breeding season, although it is by no means certain that it would function even with demonstrable competition between the species relative to fluctuations in the environment. Again the possibility remains that no days for which data were collected were sufficiently poor to demonstrate an effective limit to co-existence. However, much of the data presented above evidences alterations in resource utilization under different environmental conditions and, in particular, the increases in diffuse overlaps during windy and rainy conditions showed increases (Table 2.8.22) which reflect the niche breadth expansions for all species (Table 2.8.17).

TABLE 2.8.22

Diffuse niche overlaps in air-space on days with high winds and high rainfall

Swallow	0.454
Sand Martin	0.900
House Martin	0.922
Swift	0.634

Pairwise niche overlap

The extent of resource use overlap between species pairs within the aerial-feeding guild varies with resource and species (Table 2.8.23). Consistently high overlaps were evident between Sand Martin and House Martin, and between the latter species and Swift in all dimensions except air-space. For all species pairs it is apparent that segregation in feeding air-space would be more effective than segregation in prey size as evidencedby the greater overlaps within the latter resource dimension. The lowest overlaps in all resource dimensions were exhibited by the Swallow thus endorsing the specialisation of this species.

TABLE 2.8.23

Pair-wise overlap values for the separate resource dimensions

	Swallow	Sand Martin	House Martin	Swift
		Prey size		
Swallow	1.000	0.867	0.771	0.790
Sand Martin		1.000	0.980	0.978
House Martin			1.000	0.973
Swift				1.000
		Prey mobility		
Swallow	1.000	0.583	0.299	0.392
Sand Martin		1.000	0.838	0.936
House Martin			1.000	0.812
Swift				1.000
		Air-space		
Swallow	1.000	0.600	0.450	0.240
Sand Martin		1.000	0.920	0.680
House Martin			1.000	0.830
Swift				1.000

The varying influences of environmental factors on changes in niche breadth, together with shifts along the resource dimensions and the possibility of resulting complementarity have been demonstrated above. Intra-specific niche complementarity functions to prevent increase in total niche size, and hence limits overlap and extent of possible competition with other guild members. Therefore the earlier intimation that the Sand Martin at least might complement an increase in air-space utilisation, notably on a bad day, with a corresponding decrease in prey size niche breadth might be reinforced by determination of overlap change under the same conditions. Sand Martin and Swallow overlaps in air-space and overlaps in prey size showed a negative correlation (Figure 2.8.19). Therefore the more these two species overlapped in feeding patches, by broadening this aspect of the niche, the less overlap was observed for prey size due to mutual contraction along this dimension.

The conclusion is that compensation for increased overlap of one resource, by reducing overlap in another dimension of the niche, does occur and it may be the possibility of competitive exclusion that maintains this situation.

Overlap in bad weather: an extreme case?

Further evidence to support the existence of active competition during the breeding season emerges from observations of feeding behaviour and the results of diet analysis for birds mist-netted on the 2nd June 1975. Environmental conditions of extreme adversity for aerial-feeding, with prolonged rain, low air temperature and strong wind, prevailed from the previous evening through to early afternoon (Table 2.8.24). The magnitude of the difference between conditions on this day and the average for May and June is somewhat

TABLE 2.8.24

Comparative environmental conditions for a "bad" feeding day and the average early to mid season day in 1975

		2nd June	May/June
Insect abundance (log number)			
	at 12.2m	2.4654	3.0145
	at 1.8m	2.7513	3.7749
	ground level	3.5824	4.0622
Maximum temperature °C		12.20	17.05
Minimum temperature		-0.50	4.87
Total rainfall (mm)		7.7	
Number of days with rain over 5.0mm			4

obscured by the fact that the daily insect abundances and maximum temperature were affected by the amelioration in conditions during the afternoon. Suffice to say that the data resulting from these conditions were possible only because the birds were restricted to feeding low around vegetation near water, and were presumably intent on feeding and therefore catchable. Hirundines and Swifts are difficult to mist-net whilst feeding and indeed a similarly extreme adverse situation occurred on only one other day (in 1976) but no House Martins were caught on this second occasion. Although Swifts do feed lower and over water in poor conditions they are also known to fly round and away from local storms and have been shown to make large-scale movements to avoid adverse conditions associated with approaching cyclones (Koskimies 1950). Because no Swifts were observed during the bad weather of the day in question it can only be assumed that they either remained in nest-holes or circum-navigated the frontal system. Whatever the situation, this species was not present alongside the hirundines and therefore not consuming prey items in the area in question.

The area in which the hirundines were feeding corresponded to one patch as defined in the section dealing with feeding stations. The obvious anomaly is that in this situation the niche breadths (air-space dimension) evidence contraction rather than broadening as observed for poor days throughout the breeding season, but since the birds were restricted to the same patch the overlap in air-space was effectively complete. The numbers of birds in the catching area were in the proportion; Swallow = 43% (75), Sand Martin = 34% (60), House Martin = 23% (40).

The relative frequency of occurrence of different prey types available within the patch was compared to the selection of different taxonomic groups by the predators (Table 2.8.24). It is apparent that the most prominent group available was selected with almost the same frequency by the hirundines, the lower value for the Sand Martin being accounted for by a conspicuous inclusion of Curculionid beetles in the prey. The small sample size of the birds (Swallow = 14, Sand Martin = 2, House Martin = 3), and the possible inadequacy of the insect sampling method deserve a cautionary note when attempting to assess further real instances of selection by the birds. Selection of Psychodids by House Martins is probably genuine but the net sampling would undoubtedly have under-estimated Ephemeroptera. This does not detract however, from the remarkable parity of the Chironomid proportions in the net sample and those actually taken by the birds. The mean size of prey taken by the Sand Martins was not significantly different with exclusion of the beetle prey ($t = 0.84$, $p > 0.1$).

The prey sizes selected by the hirundines (Table 2.8.26) compared to the normal diet (Table 2.8.1), show that each species captured a smaller average size of prey and the ranges (except for the House Martin) were more restricted. This was not surprising however, given the distribution of prey sizes available (net sample mean = 1.435 ± 0.253). Tests of difference between the mean sizes selected proved significant for all combinations (Swa/Sm, $P < 0.02$; Sm/Hm, $P < 0.05$; Swa/Hm, $P < 0.001$). The most distinct difference from the normal situation is the manifest reduction in overlap values (cf Table 2.8.23), particularly that between Swallow and Sand Martin, caused by diminution of the niche breadths. This result appears to be a substantiation of the earlier prediction (see Figure 2.8.19) that an increase in air-space overlap would lead to a reduction in overlap along another resource dimension, notably prey size.

TABLE 2.8.25

Foraging in bad weather: Percentage occurrence of different taxonomic groups in a net sample* and in faeces of the three hirundines

	AVAILABLE	PREY		
		Swallow	Sand Martin	House Martin
Ephemeroptera		6.39		1.70
Aphidoidea		0.38		
Psychodidae	0.74	0.38		8.33
Chironomidae	81.48	82.33	70.21	84.97
Brachycera		0.38		
Empididae	2.22	1.51	2.13	
Acalypterate Schizophora	15.56	6.02	4.26	5.00
Coleoptera		0.38		
Curculionidae		2.26	23.40	
N	135	266	47	60

* A butterfly net sweeping through the feeding area between the ground and 3.0m.

TABLE 2.8.26

Foraging in bad weather: the mean size ($\text{Log}_{10}\ \text{mm}^2$) and range of prey sizes taken, and the amount of overlap in size utilization

	PREY SIZE		OVERLAP		
	Mean	S.D.	Swallow	Sand Martin	House Martin
Swallow	1.598	0.245	1.00	0.38	0.41
Sand Martin	1.517	0.208		1.00	0.81
House Martin	1.432	0.245			1.00

It will be observed that in this situation the prey size niche separations were still less than the theoretical minimum ($d/\sigma < 1$). Although the severity of the adverse conditions just discussed was not sustained, the event was enough to stop egg-laying. It is postulated that prolonged spells of less severe (and therefore less noticeable), but adverse conditions involve the same effects, the subtlety of which may escape direct measurement but are manifested in a decrease in reproductive output at certain stages of the breeding cycle, i.e. reduction of clutch-size, increased nestling mortality (e.g. Bryant 1975a).

2.8.7 Resource partitioning and character difference

The four study species have been shown to differ systematically in bill shape and flight capabilities in relation to resource utilization. Given that a certain character state exhibited by a species is proportional to the particular section of a resource spectrum being utilized, it follows that the amount of overlap in the resource will decrease with increasing difference in the character states of two species. Brown and Wilson (1956) included morphological, ecological, behavioural and physiological features as being involved in character displacement and convergence. In redefining character displacement as convergent and divergent, Grant (1972) restricted the term character to morphological attributes of animals but considered the ecological behavioural and physiological aspects to be analogues. In the present study the gliding/active flight ratios are considered a behavioural character, and other characters derived from combinations of morphological measurements, since they vary in a predictable way, are considered valid expressions of difference between the birds.

TABLE 2.8.27

Ratios of character difference between the four aerial-feeding species derived from morphological measurements

	Swallow/ Sand Martin	Swallow/ House Martin	Swallow/ Swift	Sand Martin/ House Martin	Sand Martin/ Swift	House Martin/ Swift
Body size (weight g)	1.48	1.04	2.09	1.43	3.08	2.16
Bill size (length mm)	1.266	1.189	1.203	1.065	1.053	1.011
Functional bill shape	1.0588	1.1304	1.1359	1.0676	1.0728	1.0049
Forked tail manoeuvrability	1.2094	1.5737	2.6685	1.3013	2.2065	1.6957
Vmr (m/s)	1.0386	1.0604	1.1220	1.1013	1.1653	1.0581
Gliding.active flight*	0.166	1.708	5.123	1.542	4.957	3.415

* Observational measurement; mean values for all stations combined.

Character difference ratios (larger value/smaller value) were calculated (Table 2.8.27) and these included body size and bill size for comparative purposes only, since their difference ratios were not expected to be negatively correlated with any resource overlap. It is notable that only three bill ratios were within the expected 1.1 to 1.4 limits (Hutchinson 1959), the other three being smaller.

In relating resource overlap to character difference the variances, i.e. niche breadths, should be about the same whatever the magnitude of the mean resource utilizations, otherwise two pairs of species with respectively large and small character differences could conceivably show the same overlap. Equal variances for prey size utilization by insectivorous birds were found by Hespenheide (1971), but not in the present study. However, no correlation was found to exist between mean prey size and amount of variance, and variance ratios were very small, so overlap in prey size was considered suitable to compare against character differences. The above reasoning depends upon the utilization curves for any resource approximating to a normal distribution, and only prey size fulfils this requirement. Nevertheless, overlaps in air-space and prey mobility were included in a correlation analysis with character differences (excluding bill size and body size), since negative trends would indicate an effect on these overlaps by the different character states which a more refined analysis could clarify.

Only four negative associations emerged from the correlation analysis, and only one of these was significant (at the five percent level, Figure 2.8.20). The two clearest results were the association of difference in functional bill shape with prey size overlap (a), and of tail manoeuvrability difference with air-space overlap (c).

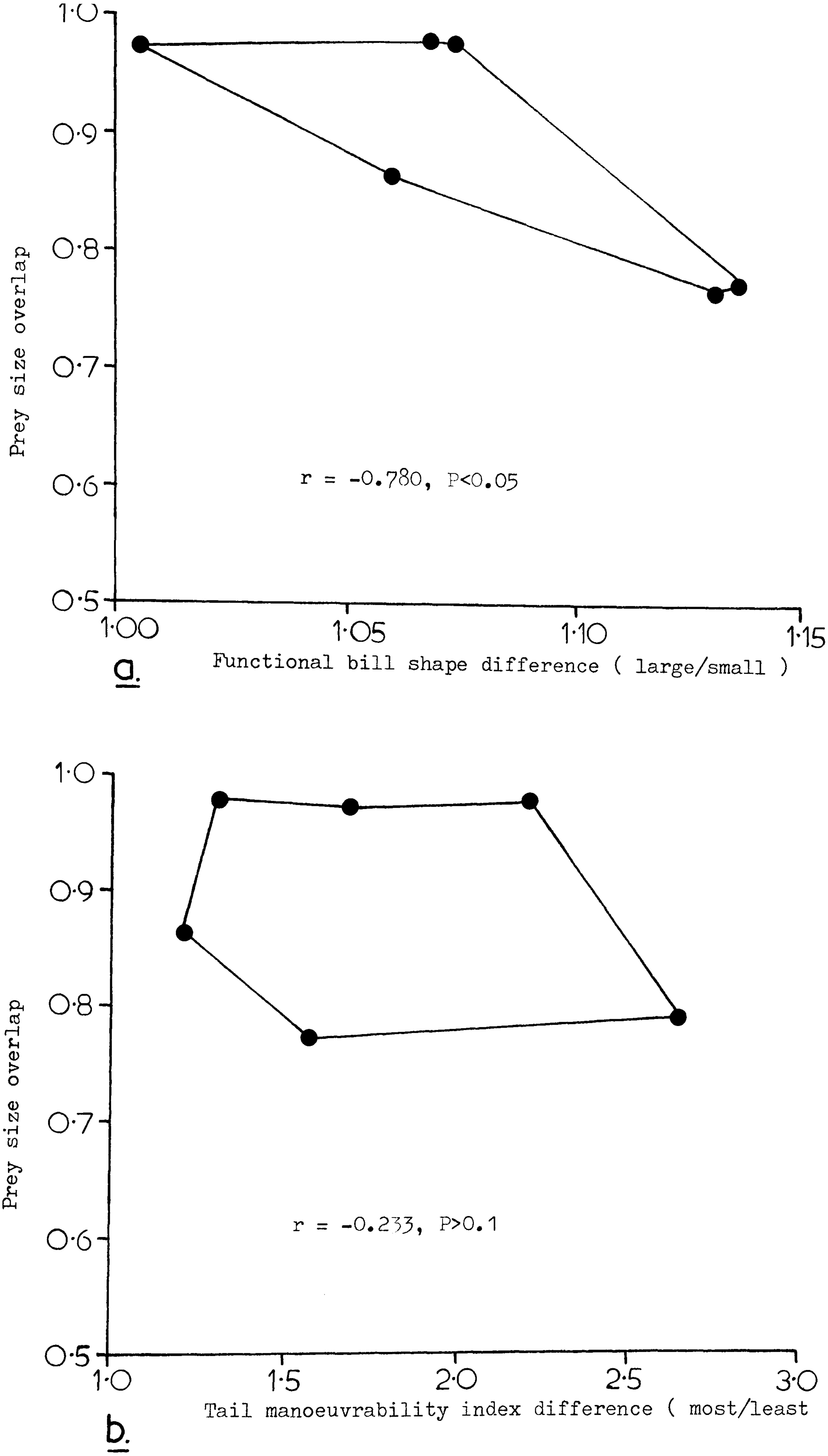


Figure 2.8.20. The association of character difference with separate resource overlap in four aerial feeding birds.

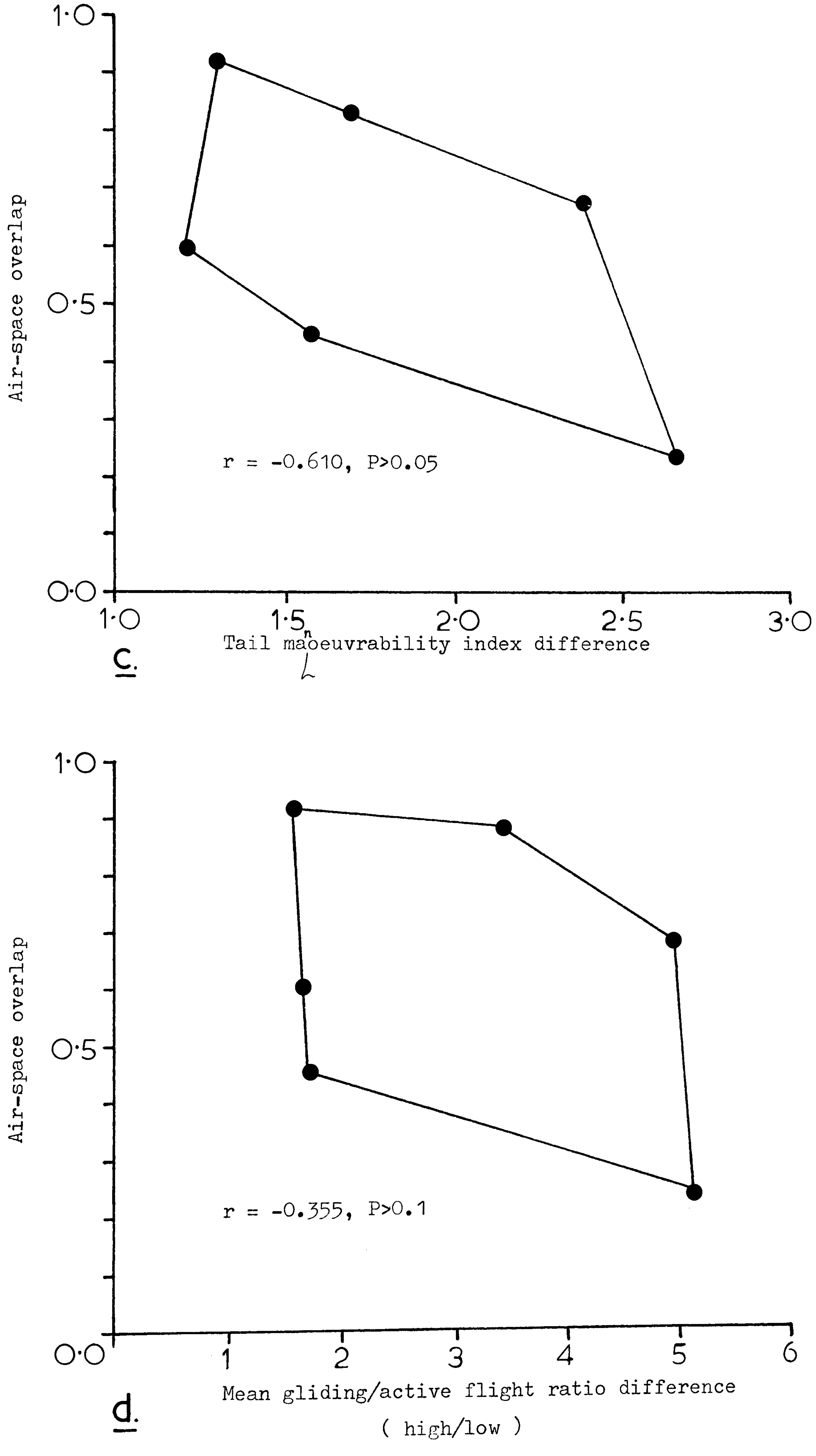


Figure 3.8.20 cont.

The lack of a negative correlation between tail manoeuvrability difference and prey mobility overlap was surprising, particularly when a slight negative trend was apparent with overlap in prey size (b). A similarly negative association was evident between overlap in air-space and difference in mean gliding/active flight ratios (d).

Reliably predictive character differences may therefore only be tail manoeuvrability and functional bill shape, to show respective alterations in air-space use and prey size selection.

It is recognised that selection of feeding patches and selection of different prey sizes and mobilities are not mutually exclusive and that natural selection will therefore not act on one character in isolation, but is likely to effect simultaneous changes on a combination of characters.

CHAPTER 3

SHORT TERM STRATEGY : THE INDIVIDUAL EXAMINED

3. SHORT-TERM STRATEGY : THE INDIVIDUAL EXAMINED

Recent theoretical models of prey choice have shown how predators could maximise their rates of food intake while foraging (MacArthur and Pianka 1966, Emlen 1966, Royama 1970, Schoener 1971, Charnov, 1973, Pulliam 1974, Werner and Hall 1974). Optimization of foraging behaviour will undoubtedbly involve interrelated decisions on where to feed and when to leave for another area, which prey to select and which mode of feeding to use. In an unpredictable environment, changes in feeding conditions should be mirrored by observable alterations of behaviour if optimality is being maintained.

Utter (1971) suggested that there are three levels for the existence requirements of predators: (a) a low level where the individual has only to forage long enough to satisfy its own daily energy requirements (i.e. when not breeding), and hence may have a large proportion of its time for rest, (b) a second level where the individual will need to spend more time foraging when using proportionately more energy during courtship, nest-building etc; resting time will be depleted both by extra foraging time and energy and time costs of breeding activity, (c) a high level where the individual spends most of its time foraging to raise off-spring and will have little or no resting time. Given a situation in which environmental conditions are static it may be expected that an individual which is foraging in an optimal manner at all of the three specified activity levels will devote more time to feeding with the increase in demand during reproduction. However this rather simplistic view ignores the important point that environmental conditions will rarely be constant and therefore an individual may need a longer time to forage at the non-breeding level because the existence demand may have been increased, for example indirectly by reduction in density of preferred prey types. Therefore time, although important, is not by itself a meaningful measurement without also assessing these changes in abundance and spatial distribution of potential prey, together with changes in foraging place and diet of the predator.

The present study examines the foraging behaviour of the Swallow, H. rustica, during the breeding season in relation to the above-mentioned influences. Because the mortality-related risks of two-way migration and over-wintering in Africa are probably great for this species, it is a reasonable prediction that Swallows will attempt to produce maximum numbers of off-spring at the first opportunity. This could be the summer after hatching but it appears that first-year birds, through lack of breeding experience, have smaller broods. Additionally, natural selection will favour those individuals able to sustain maximum output of offspring throughout the reproductive life-span, but also suffer least life-span curtailment as a result of this effort (Lack 1966, Kluyver in den Boer and Gradwell 1971, Stearns 1976). To achieve this maximum output the individuals involved should be expected to make the right decisions at the right times, and this includes choice of the most economical foraging behaviours. Optimal foraging theory assumes that the predator should maximise its net rate of gathering some critical factor. For Swallows in the present study, the critical factor is taken to be energy, in the absence of knowledge about specific nutrient requirements of the brood, although these are not likely to be limiting (A. Turner, unpublished data).

The Swallow was chosen as the study species because it nests in association with man and is therefore tolerant of interference, the fact that it nests in buildings allows use of equipment not normally extending to a field situation, and many aspects of its basic biology are well known (Stoner 1935, Boyd, 1935/36, Moreau and Moreau 1939, Purchon 1947, von Vietinghoff-Riesch 1955, Kuzniak 1967, Ricklefs 1967, Lohrl and Gutscher 1973, Snapp 1973, Møller 1974)

METHODS

There are two basic factors which will influence the foraging behaviour of adult Swallows feeding nestlings. The first is associated with demands of the brood in terms of age of the nestlings and the number of nestlings and/or collective brood mass. In this context the well-recorded phenomenon of clutch size decrease from first to second broods in Swallows (e.g. Kuzniak 1967, and shown for other hirundines, e.g. Petersen 1955 for R. riparia (Bank Swallows), Bryant 1975a for House Martins) will have an effect.

The second influence relates to fluctuations in the environment where the distribution and abundance of different prey types vary temporally and spatially, and may be directly correlated with changes in weather variables.

To assess the relative contributions of the above factors to alterations in foraging behaviour three fundamental measures were required; (a) the variation in available insect quantity and quality in space and time, (b) the quantity and quality of food brought back to the nest, (c) the duration, distance and number of feeding trips. To record all these variables simultaneously it was only possible to work with one pair of Swallows at any one time. Since most of the farms in the study area had very similar surrounding foraging terrain for the Swallows, several pairs at different sites could be used.

An outline of the day-long (most day-light hours) experimental routine would be, (a) observing the adults flying to and from the nest on feeding trips, (b) sampling flying insects at various stations around the nest site, (c) collecting food brought to the nest, (d) noting the weather conditions.

3.1 Energy available: the distribution of flying insects

Aerial insects were sampled in the time inverval between successive collections of food at the nest (90 minutes: see later). For any particular pair of Swallows, a number of stations (n = 4-8) around the farm nest site were chosen (Figure 3.1.1) with regard to varying distance from the nest and variation in topographical features, e.g. vegetation forming a shelter belt. At each station flying insects were collected by sweeping a fine-mesh (< 1mm) butterfly net back and forth for a standard 80 strokes. Sweeping was carried out between 0.3 and 2.0 metres from the ground, these limits being chosen because they encompassed the most frequent feeding station of Swallows (see Chapter 2), and because problems of standardisation occurred at higher levels. This method of sweep sampling was chosen because electrically operated suction traps were impractical in a temporary field situation (they may also provide an unmanageably large sample), and sticky traps mounted at certain heights biased samples towards weak-flying and wind-drifted insects, besides the samples being difficult to segregate into time periods throughout the day. Immediately following collection of a sample, the insects were quickly killed by placing the net into a vapour (ethyl acetate) jar. Each sample was deep-frozen and the insects eventually identified and measured (see methods in Chapter 2) before being freeze-dried for a total dry weight determination. Reference was also made to the

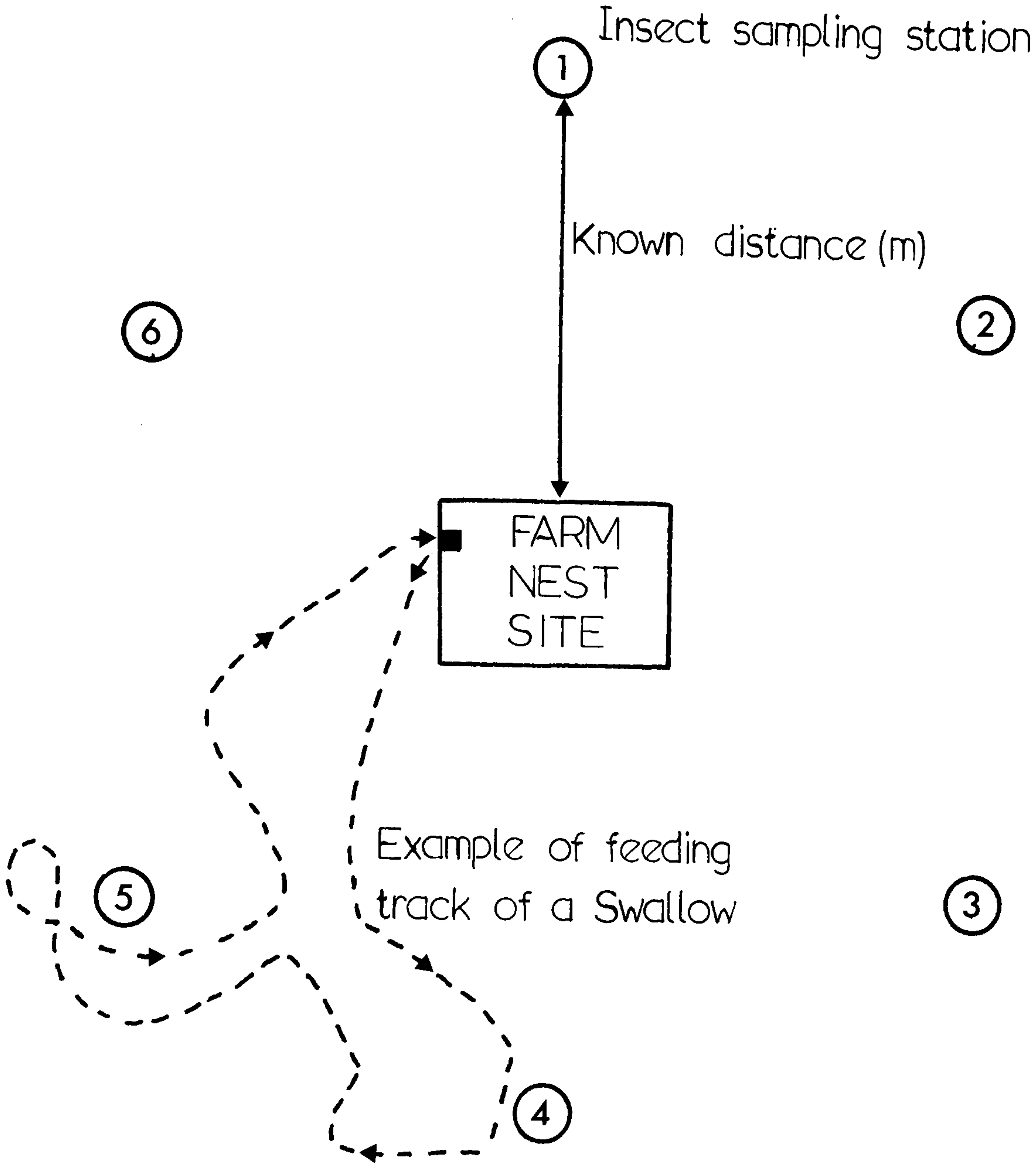


Figure 3.1.1. Diagrammatic representation of insect sampling stations and Swallow feeding areas in relation to the nest-site. In this example stations 4 and 5 are the "chosen" stations; 1,2,3 and 6 are the "rejected" stations.

suction trap catches (see Chapter 2) for those days on which experiments were performed to provide a more general description of the daily insect activity.

3.2 Energy harvested: analysis of the prey

Prey items were collected by using chokers around the necks of the nestlings which prevented them from swallowing any bolus delivered by the parent birds. The chokers were designed so as not to obstruct passage of air and to be of minimum discomfort to the nestlings; this method has been used successfully in other studies notably of aerial-feeding birds (Lack and Owen 1955, von Gunten and Schwarzenbach 1962). After initial experimentation a time interval of 90 minutes was chosen as suitable for the nestlings not to have altered their begging rate and for the adults not to have been disturbed too frequently from visiting the nest. In fact the adults invariably resumed feeding almost directly after their nesting site had been vacated. The procedure of changing the chokers after a period of observation took 20 minutes on average and involved removing all food boluses from the nestlings (plus those ejected into the nest and to the ground below). The chokers were then loosened to feed each nestling an artificial food (egg-yolk) roughly equalling the quantity of insects it would have received in 90 minutes (to maintain a constant begging rate); retightening the chokers then preceded replacing the brood into the nest.

The collected food balls were preserved in meths/glycerol mixture and subsequently each was dissected out and the constituent prey items identified and measured. After washing the insects each bolus was freeze-dried and a dry weight determined.

3.3 Energy expended: foraging excursion time

Each feeding excursion by the adults was considered to incorporate the summated search times, pursuit times and handling times for the items captured. To estimate the energy cost of feeding excursions a system was set up whereby visits to nests by parent birds were monitored with an automatic recording device. Fundamental to the design of this recording system was to place radioactive tags on the adult birds and record presence at the nest by detection of emission from these tags (Ward 1969). The most suitable tag for use in the field was found to be Iron-59 wire because the half-life of 45 days was of adequate duration for the experimental periods, and a relatively high emission allowed use of small amounts of material. High purity ("specpure") Iron wire was irradiated for 36 hours in a flux of 3×10^{12} n. cm^{-2} sec^{-1} in the nuclear reactor at the Scottish Universities Research Reactor Centre, East Kilbride. At this flux Fe^{59} attains a specific activity of 54 $\mu Ci.g^{-1}$. To differentiate between sexes two sizes of tag were used, these being 50 mg and 100 mg weights of irradiated wire, and giving emissions of 2.7 µCi and 5.4 µCi respectively. To prevent rusting the lengths of wire were sheathed in a shrink-fit plastic tubing and attached to the birds' leg with strips of heavy-duty self-adhesive tape, to be finally covered in polystyrene cement. The whole assembly was light (<200 mg), did not hinder the birds' activities and could be removed with little discomfort to the bird.

For recording activity a 1½" NaI crystal scintillation detector was place 20cm from the nest fixed to the adjacent beam or wall (Figure 3.3.1). Placing this in position 24 hours before experiments were to commence ensured that the birds were not affected by its presence. The detector was connected by 25m of co-axial cable to

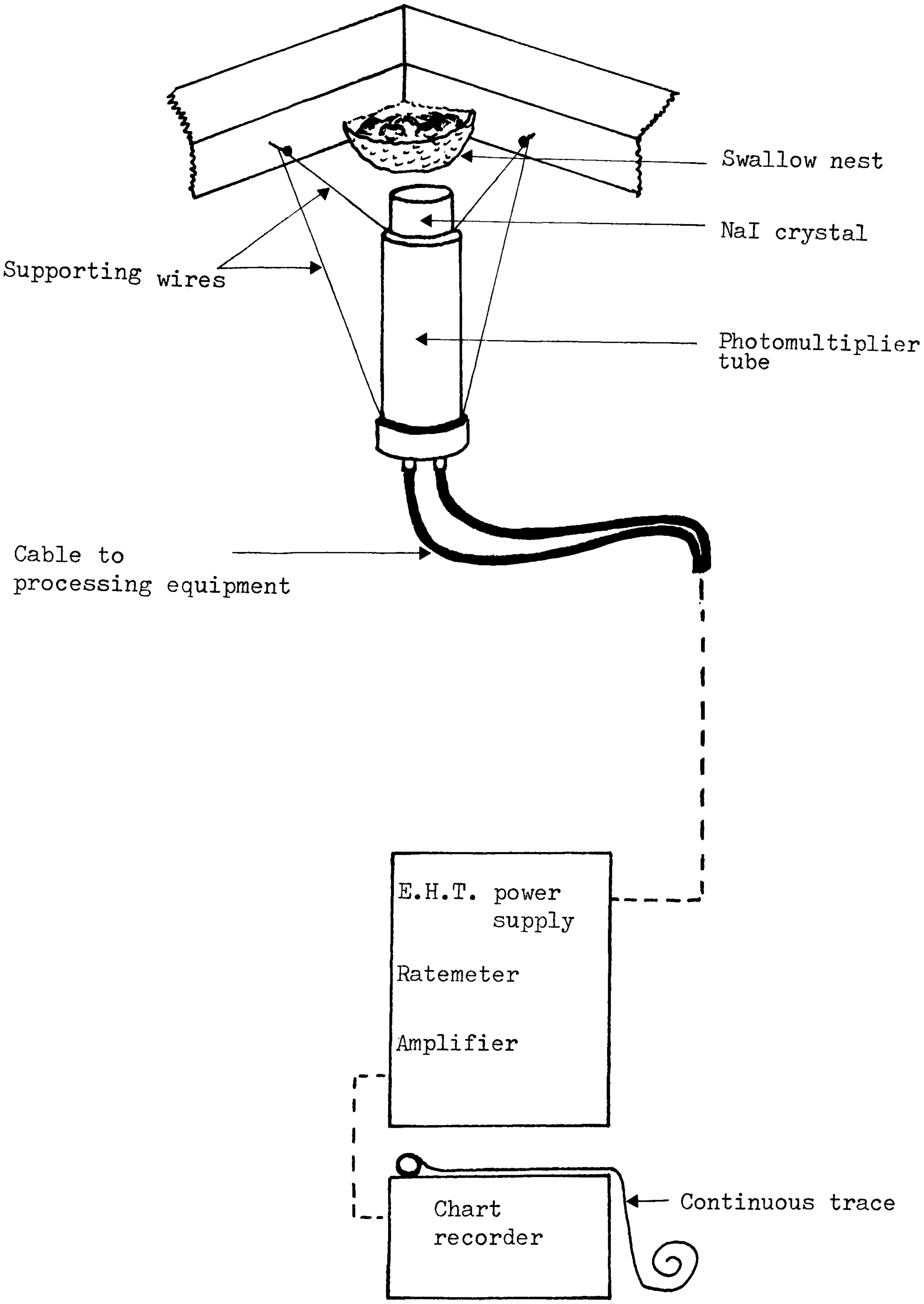


Figure 3.3.1. Diagrammatic representation of a Swallow nest with the automatic nest visit recording equipment in operation.

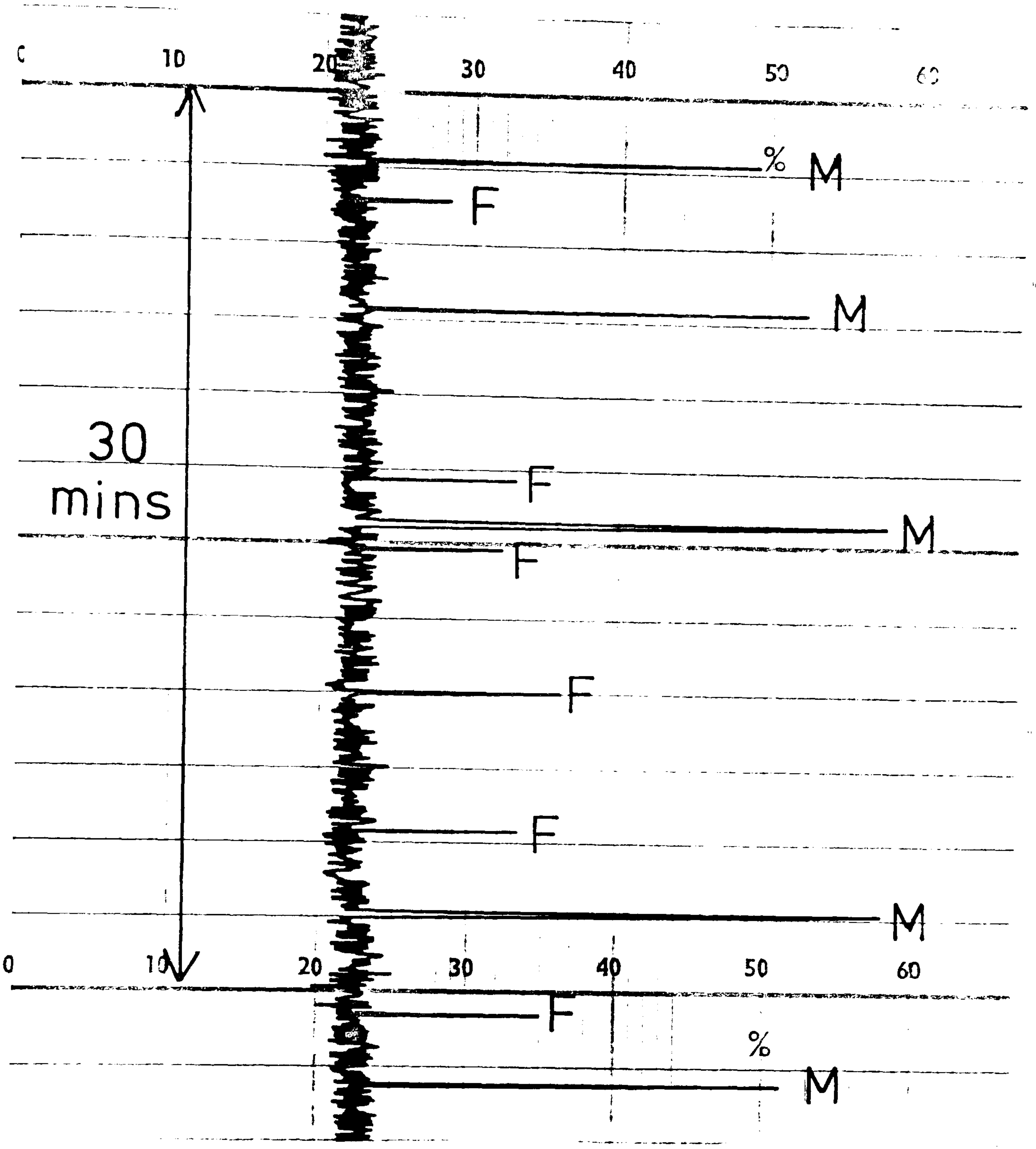


Figure 3.3.2. Section of a trace from the automatic nest visit recording device. M denotes male bird, F denotes female, (see text for explanation).

a combined E.H.T. power supply, ratemeter and amplifier unit together with a variable speed pen recorder. These were all out of sight of the nest and could be serviced without disturbance to the birds during the complete 24 hours of monitoring. A typical trace obtained by attaching a large and small tag to the male and female birds respectively is shown in Figure 3.3.2.

From the chart records mean foraging excursion times for each sex were calculated for 90 minute periods throughout the day (04.00 to 22.00 B.S.T.; periods 1 to 12). These foraging excursion times were then converted to energy expenditure values by using the flight cost derived for Swallows by Lyuleeva (1970) which was 0.065 Kcal $g^{-1}.h^{-1}$. This was for flight alone and its accuracy is supported by the figure derived for all swallow activities by Hails (1977) which was 0.059 Kcal $g^{-1}.h^{-1}$. It was not possible in practice to accurately record feeding activity and simultaneously conduct the choker experiments, therefore the average foraging energy expenditure derived from a number of undisturbed nests were applied to the untimed feeding excursions of adult birds in the choker experiments. The number of feeding excursions made by both sexes during each 90 minute period was equal to the number of boluses collected in each time period.

Travel distance and feeding area

To determine where the adult birds were obtaining food and how far they were travelling to the feeding area a system of observation was employed where the 360° radius around each nest-site was in view. The exact distance of each insect sampling station from the nest was measured and, by following the adults leaving the nest with binoculars, the approximate distance travelled for each trip could be estimated by noting to which station(s) the birds foraged closest (for convenience collectively called the "chosen" stations, those remaining being the "rejected" stations, Figure 3.1.1). Because the sweep sampling also had to be carried out during each 90 minute interval not every foraging excursion by each sex could be monitored but, since the feeding birds tended to forage in a particular sector over a series of excursions, the distances noted during a time period could reasonably be applied to all excursions within that period.

RESULTS

3.4 Prey availability: characteristics of the aerial insect population

The density and quality of the aerial insects varied in four ways; (a) diurnally, (b) seasonally, (c) between sampling stations, and (d) between days with different weather conditions. Although the weather conditions on the different sampling days were not uniform no extremes were encountered and any associated variations in the aerial insect populations were considered to be slight. Examination of the diurnal variation in the aerial insect population showed the fluctuation in total insect numbers throughout the day to be much greater than that for biomass, at least with this sampling method (Figure 3.4.1). The overall daily variation was nevertheless similar in both measures (co-efficient of variation; biomass = 74.5, numbers = 64.2). Biomass increased steadily from a morning low to peak in the mid-afternoon period and this curve reflected more accurately than insect numbers the expected diurnal insect activity for all taxonomic groups combined (Lewis and Taylor 1965).

The cause of the anomaly in the biomass and numbers curves lay with the variation in flight periodicities of different taxonomic groups. Lewis and Taylor (1965) have shown the main flight periods of larger Brachyceran and Cyclorhaphan Diptera to be during the mid-day and afternoon periods. Since Swallows have previously been shown

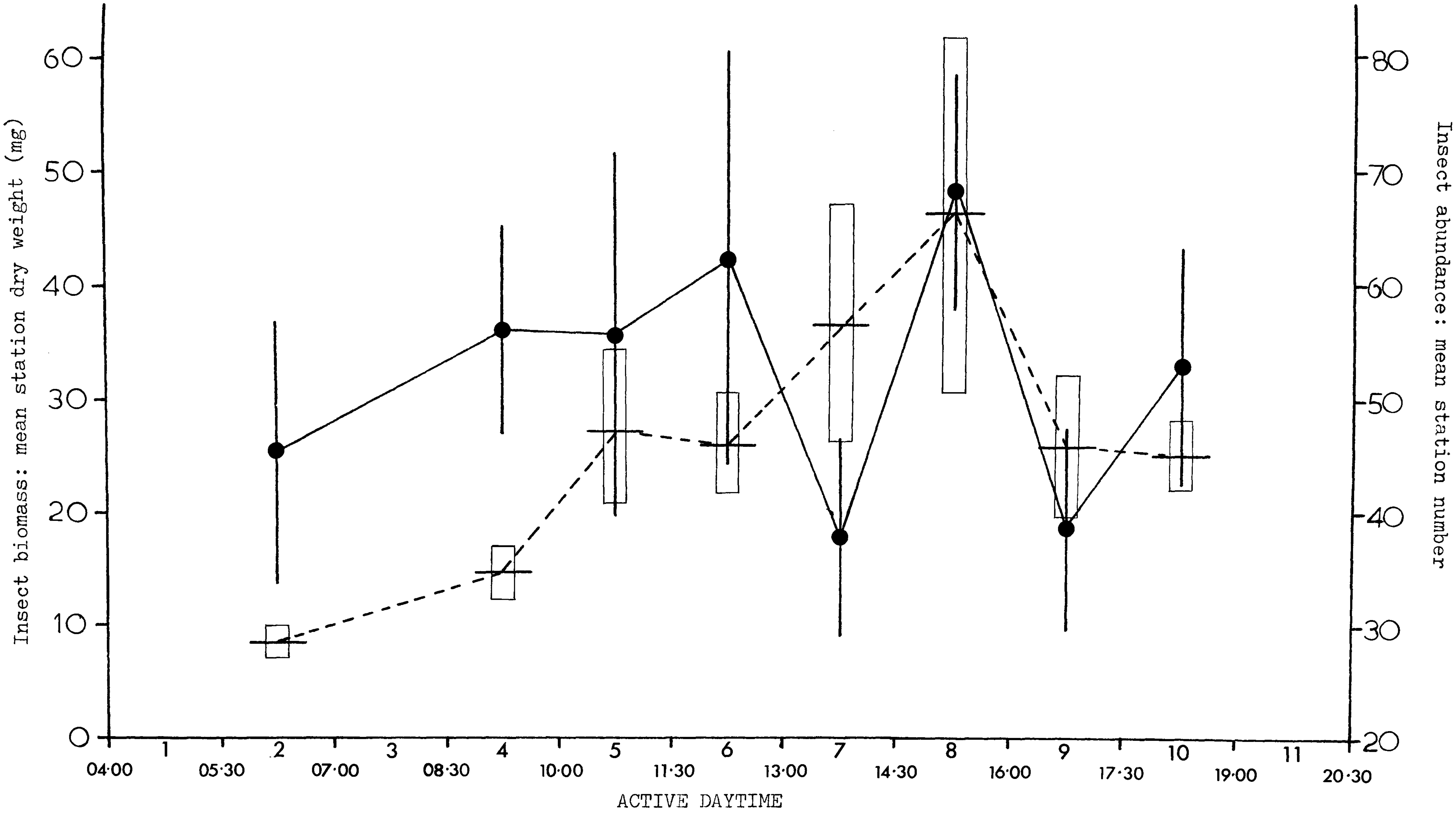


Figure 3.4.1. Diurnal variation in absolute insect abundance and insect biomass for early and late season combined. The points are means of all insect sampling stations. Circles = abundance, bars = biomass, both ± 1 standard error.

to be taking the larger of the insects available to them, particularly of the above taxa, it was of value to examine variation in prey quality. The numbers of larger insects (> 5mm body length) in fact did increase towards the mid-day and afternoon periods, both early in the season when first broods were being fed but more so during second brood feeding (Figure 3.4.2). Direct weight measurements of the insect samples confirmed the importance of variation in numbers of larger items because the average insect weight increased from morning to afternoon, despite the increased fluctuation observable for the late season. Again the average insect weights were higher during second brood feeding, (Figure 3.4.3).

3.5 The energy harvested

3.5.1 Energy value of the prey

The constant used for conversion of insect dry weight to an energy value was 5.3046 kcal/g. This composite figure was derived from groups listed in Bryant (1973) and certain groups in Cummins and Wuychek (1967). Variation in conversion values between taxonomic groups and with size within groups was considered small enough to allow use of a mean figure.

3.5.2 The effect of brood size

It would be expected that the collective demand of the brood for food would increase with increases both in the number of nestlings to be fed and the age of those nestlings. Bryant (1972) found the feeding rate to House Martin broods to be fairly constant along the section of the nestling growth curve encompassing nine to twenty days after hatching. Similarly for Swallows, Snapp (1973) found a plateau in the demand curve between eight and thirteen days.

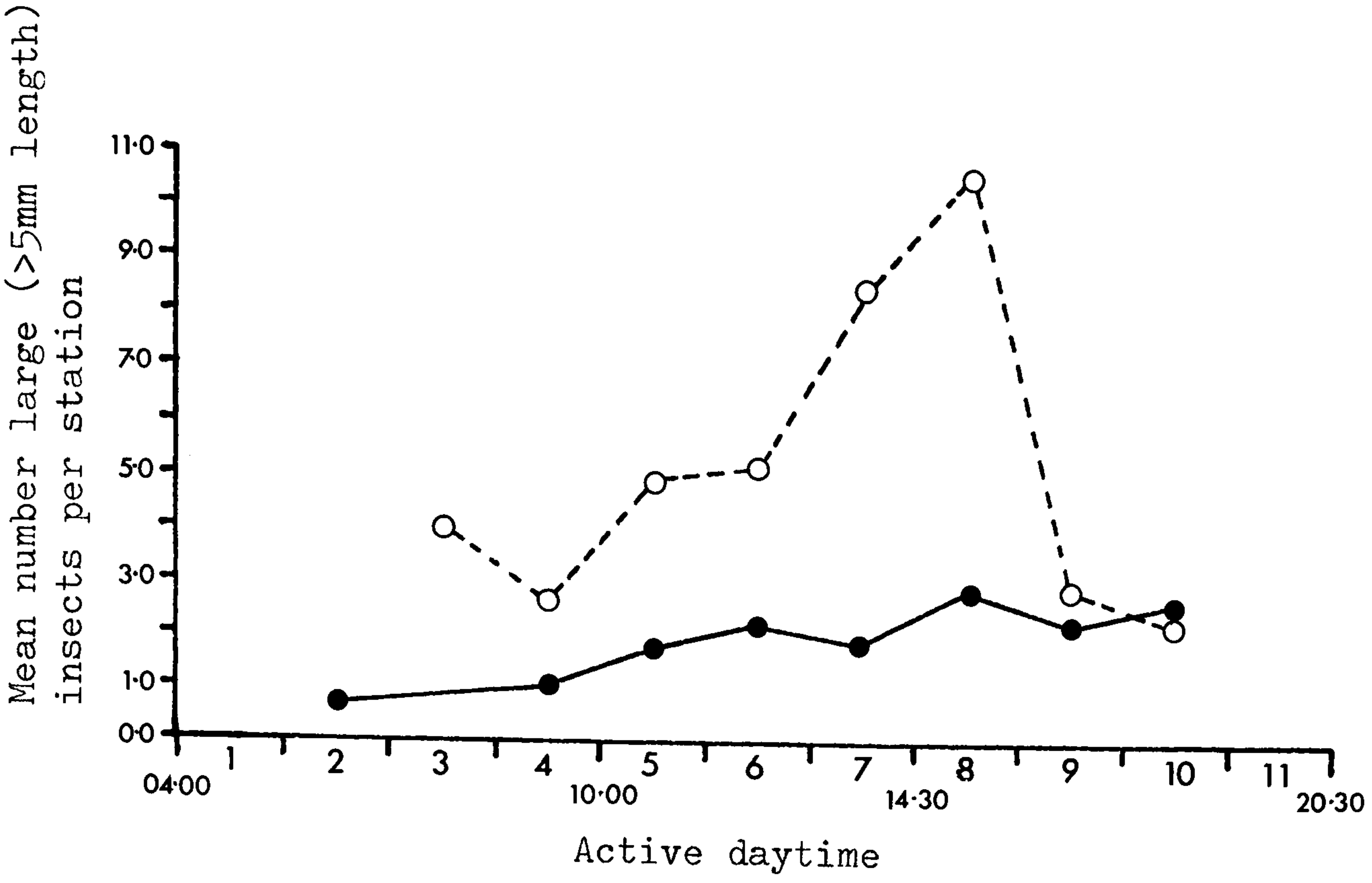


Figure 3.4.2. Diurnal and seasonal variation in the abundance of larger insects. Solid circles = early season (June, July), open circles = late season (Aug, Sept).

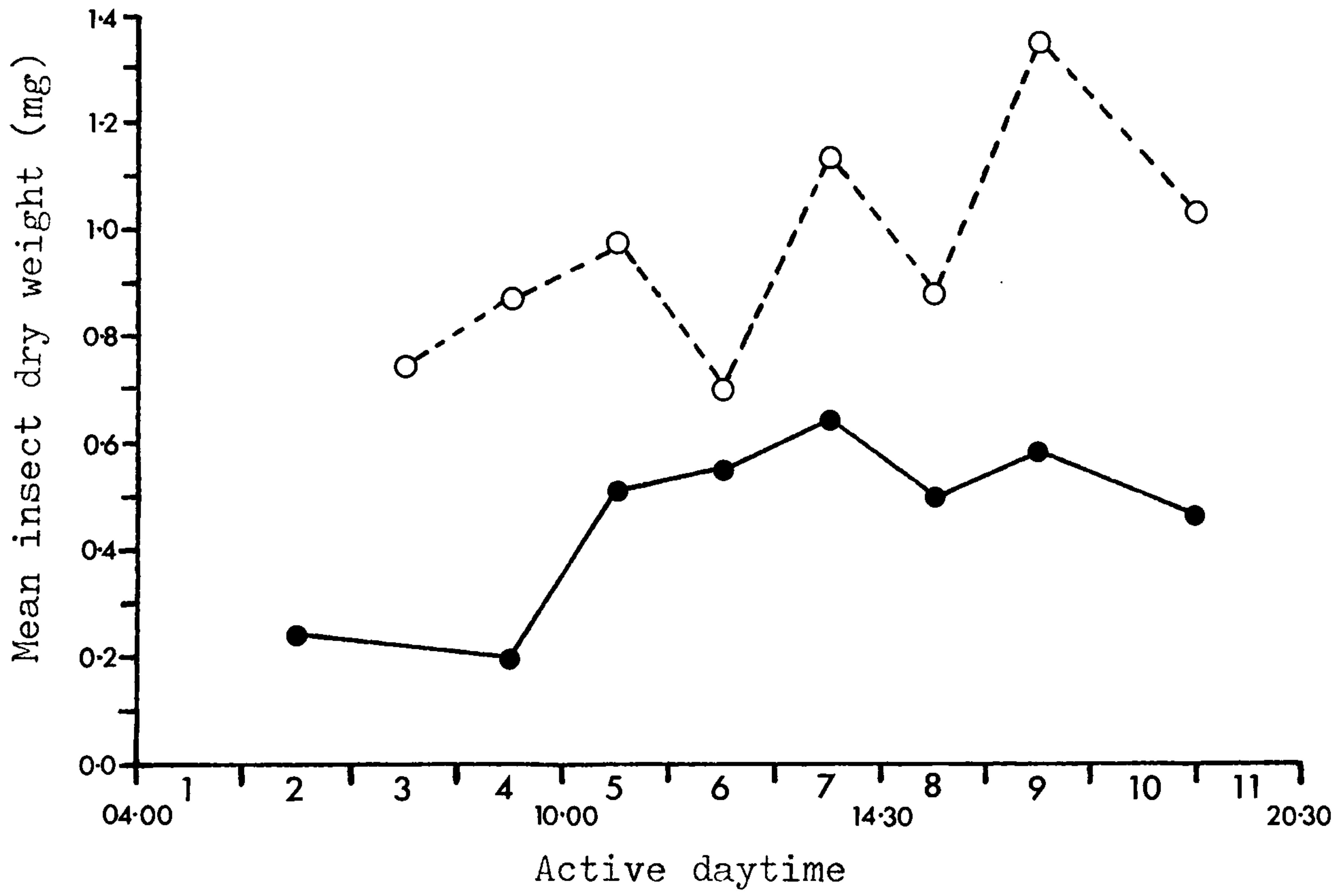


Figure 3.4.3. Diurnal and seasonal variation in the average weight of aerial insects at all sampling stations. Solid circles = early season, open circles = late season.

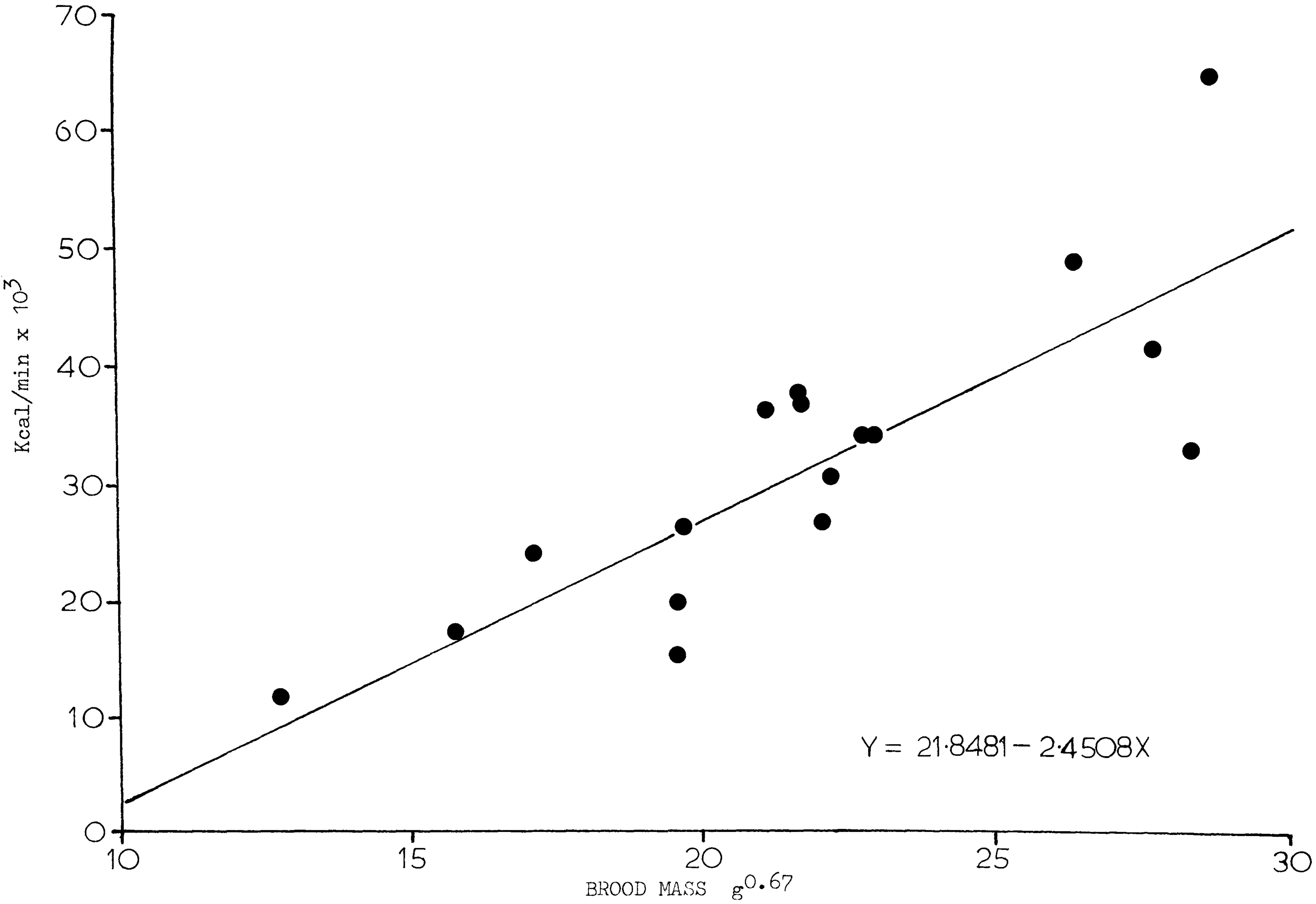


Figure 3.5.1. The amount of food per unit total time (time spent feeding nestlings + time spent on all other activities) delivered to broods of different size. r = 0.805, P 0.001.

Observations in the present study indicated a constant demand between nine and fifteen or sixteen days and therefore, to assess the food amounts delivered to each nestling in different sized broods, only those food collection data within these ages are included. For total food delivered however a more meaningful expression of brood demand, taking into account the effects of heat conservation by huddling (Royama 1966, Mertens 1969, Bryant and Hails 1975) is brood mass ($g^{0.667}$). From the choker experiments with first and second broods it was apparent that an increase in brood mass caused more food per unit total time (defined here as the sum of the time spent feeding nestlings and the time spent on all other activities) to be delivered to the nest (Figure 3.5.1). These experiments included artifically altered brood sizes (maximum 7) where the adults were not necessarily expected to be able to compensate but apparently did. The increase in food delivered was not due to an increase in the size of each bolus collected. There were no significant differences to be noted for bolus sizes collected for different first brood sizes (Table 3.5.1) and the mean bolus weight was 78.24 ± 32.05 mg (0.415 ± 0.170 kcal). There are insufficient accurate data to calculate second brood bolus weights. In a study of Barn Swallows, Snapp (1973) found that the number of feeds to the nest per hour

TABLE 3.5.1

Dry weights of boluses collected from nestlings of different sized first broods

No. nestlings	No. boluses	Weight (mg)	t	P
4	40	71.78 ± 22.85	1.958	> 0.05
5	48	84.09 ± 35.66	0.791	> 0.1
7	137	79.53 ± 32.55		

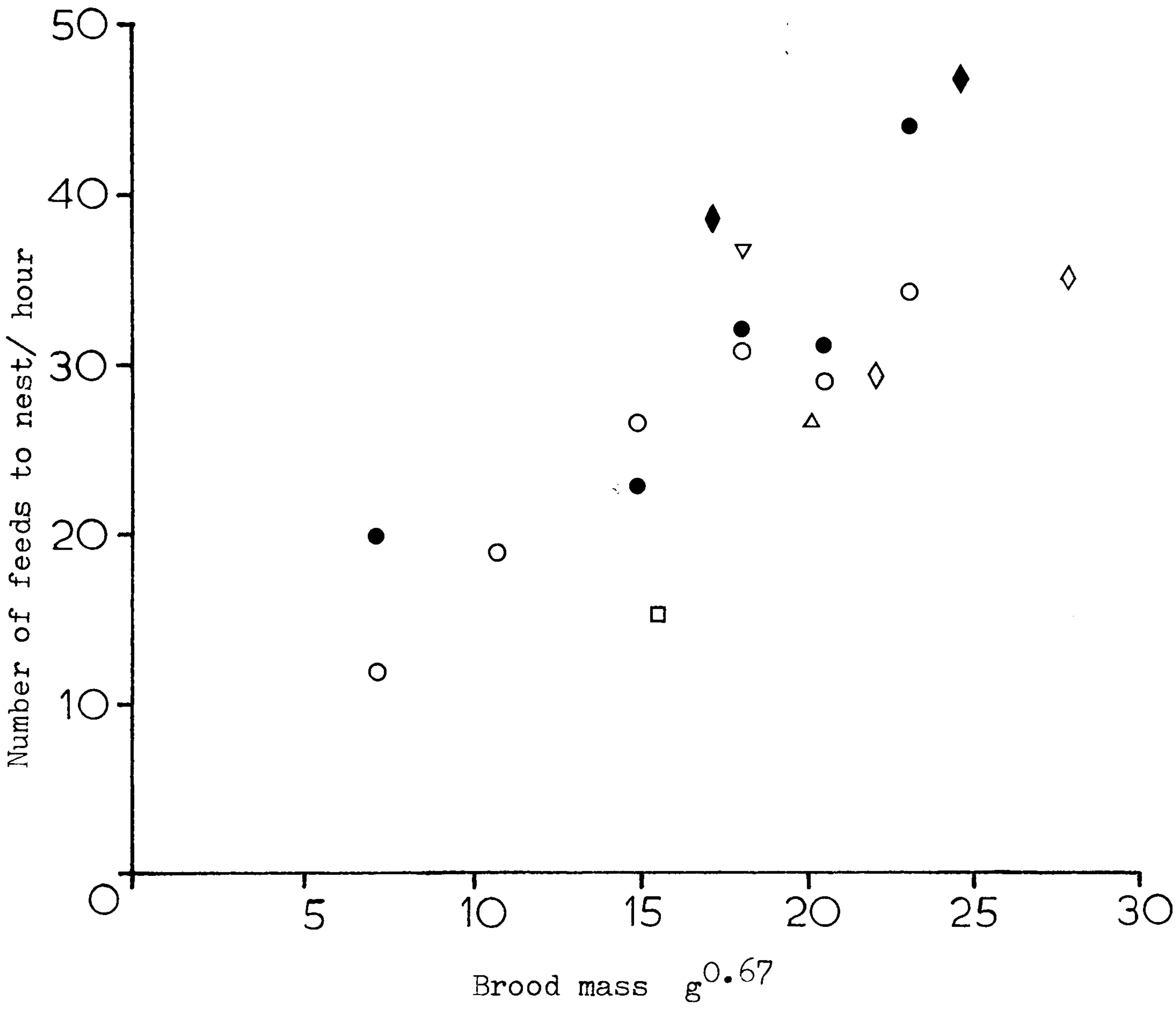


Figure 3.5.2. The effect of brood mass on the feeding rate of adult Swallows. Key: ◊ present study, ○ Snapp 1973, △ Brown 1940, □ Moreau and Moreau 1939, ▽ Purchon 1947. Open symbols = first broods, solid symbols = second broods.

increased in direct proportion to increase in brood size for both first and second broods, but the proportion of food received by each nestling was less in larger broods, at least for first broods. No account was taken of the reduced collective brood demand due to huddling effects however and, from Figure 3.5.2, it is again apparent that more food (feeding visits) was delivered to broods of higher mass. The first brood curve may level out at broods in excess of six nestlings and it is uncertain whether the adults could sustain such high feeding rates continuously to the date of fledging, particularly with regard to environmental fluctuations. The effect upon the adults in terms of loss of condition is also unknown. It was not possible to test these aspects in the present study. Certainly, a drop in individual nestling weight has been noted for broods artifically enlarged to number seven and eight (Snapp 1973). The feeding rates were higher for second broods and the significance of this will be discussed in the following section.

3.5.3 The effect of insect abundance and quality

The effect of total insect abundance on the amount of food delivered to the brood per day could be tested in two ways. The first was to look at the insect sample sizes collected at different levels in the air column by the suction traps, and the second to examine the net samples collected throughout the day. In terms of energy delivered to the nest it was apparent that total insect density had no influence (Figures 3.5.3a, b). Likewise no relationship was found to exist between the numbers of prey items per unit total time delivered to the nest and absolute insect abundance. (Log number insects at; 12.2m, $r = 0.167$, 1.8m, $r = -0.397$, 0.0m, $r = -0.105$, $n = 17$, $P > 0.1$ in all cases. Mean daily net sample number of insects, $r = 0.287$, $n = 15$, $P > 0.1$.)

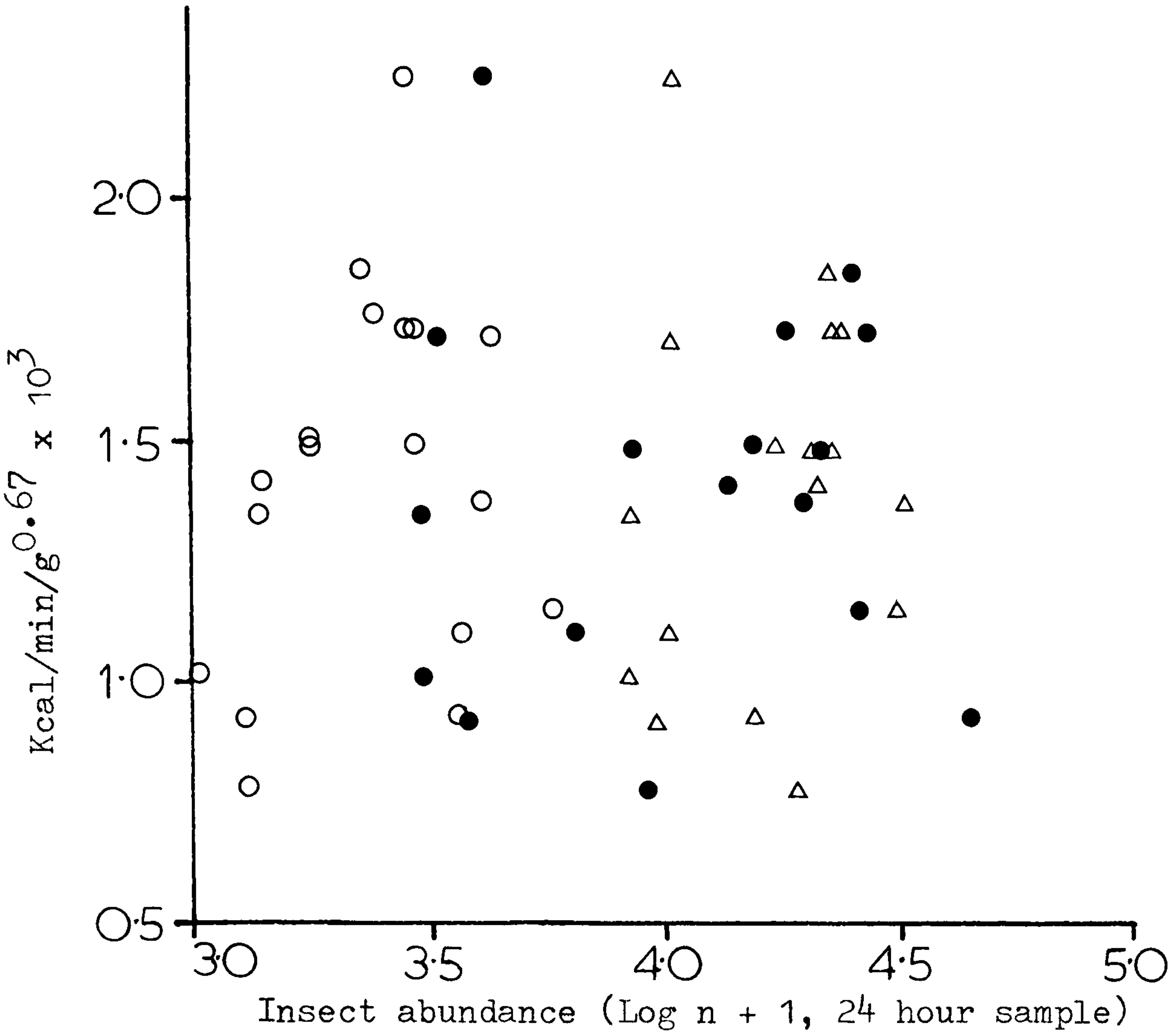


Figure 3.5.3.a. Total aerial insect abundances, measured at different levels in the air-column, do not affect the amounts of food per unit total time delivered to the nest. Open circles, 12.2m, r = 0.272 solid circles, 1.8m, r = 0.178, triangles, ground level, r = 0.217, n = 17, P>0.1 in all cases.

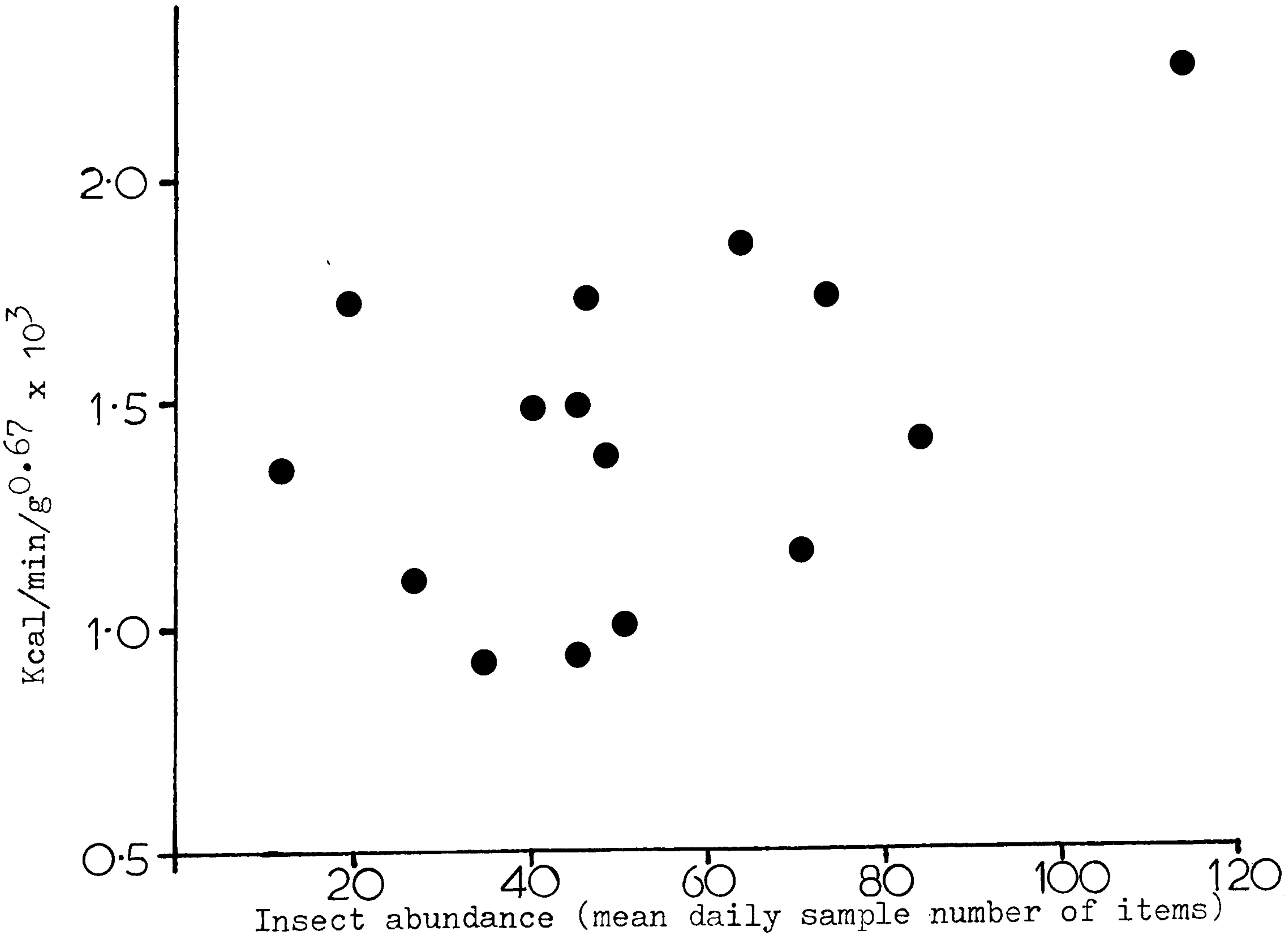


Figure 3.5.3.b. Total aerial insect abundance as measured by the net sampling method does not affect the amount of food delivered to the nest. r = 0.494, n = 15, P>0.05.

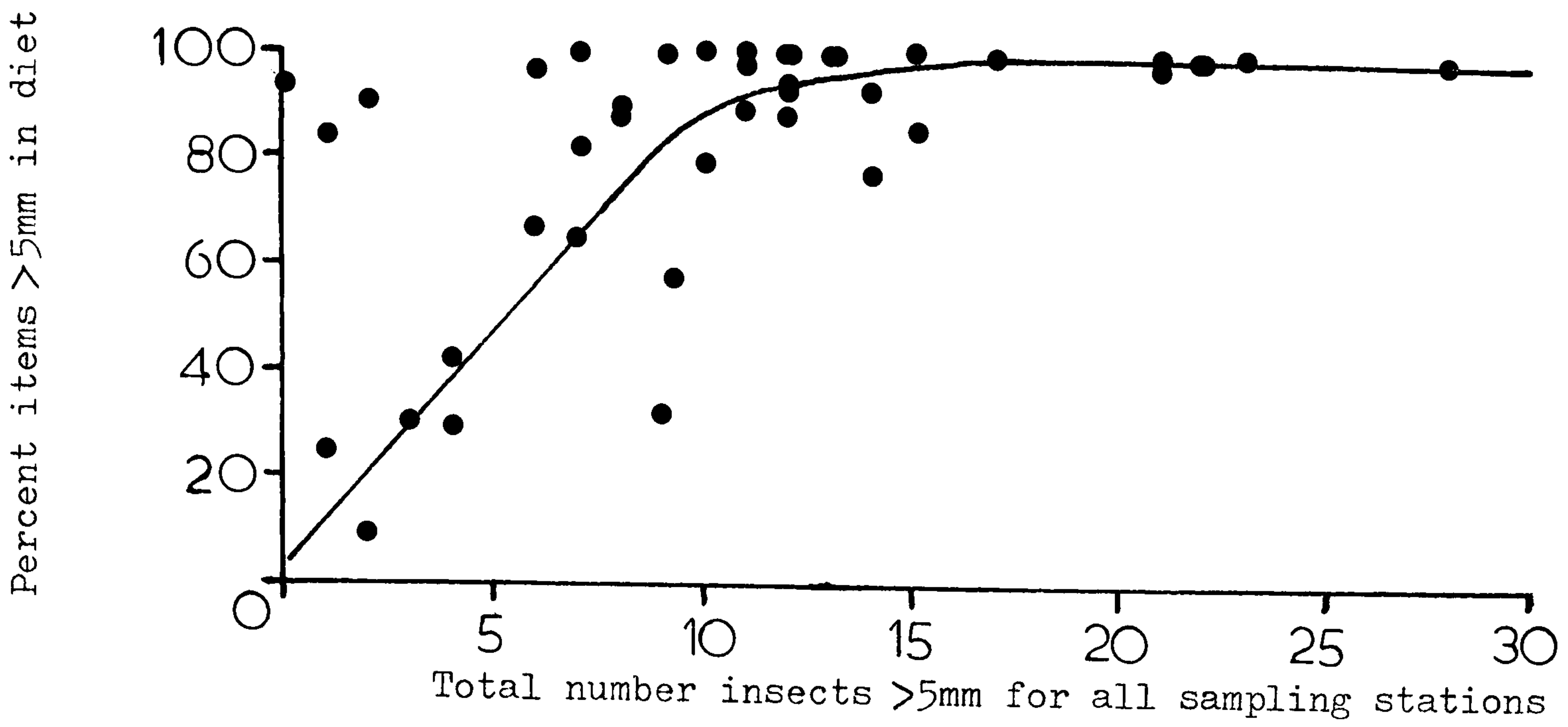


Figure 3.5.4.a. The effect of increasing abundance of large insects on the percentage incorporated into the diet of first broods. Points represent separate sampling periods. Curve fitted by eye. Refer to text for further explanation.

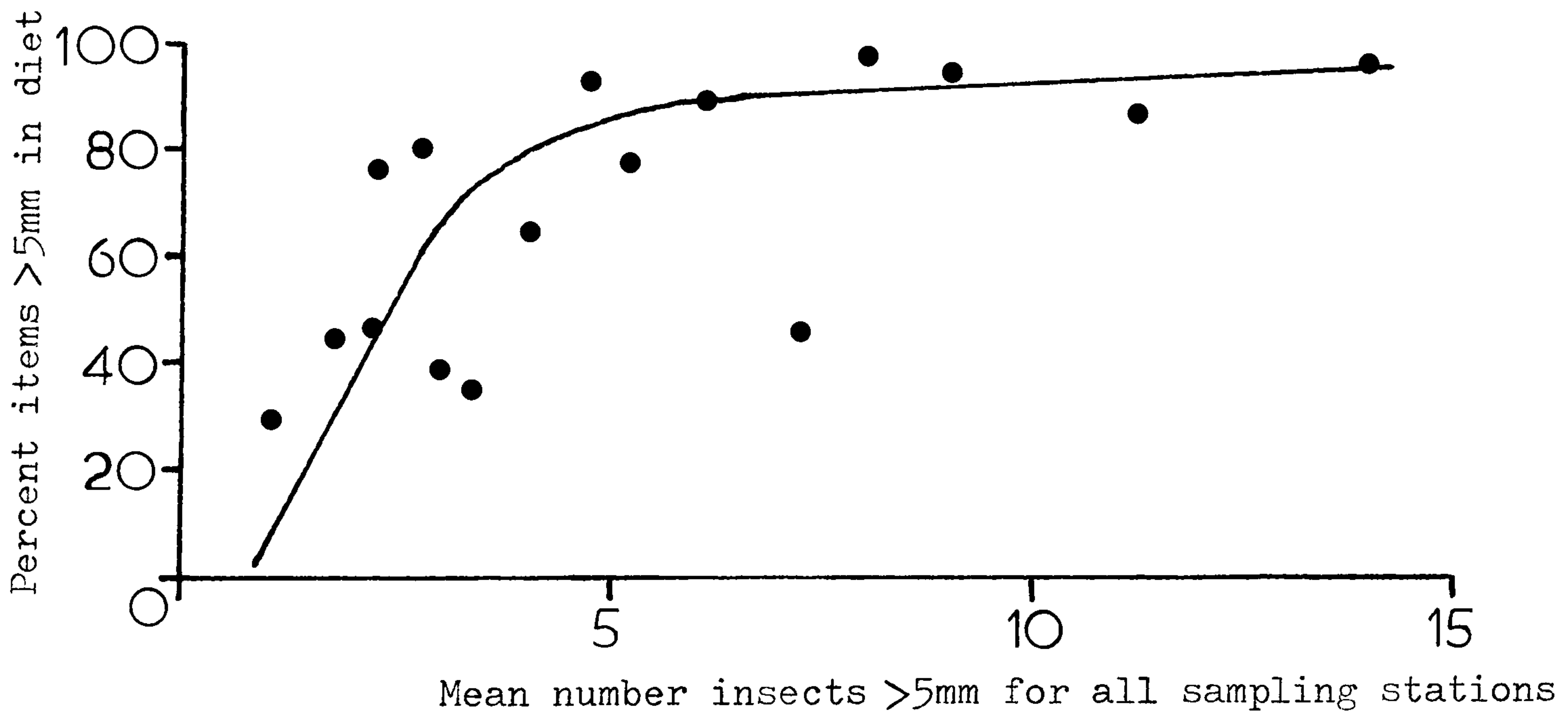


Figure 3.5.4.b. The effect of increasing abundance of large insects on the percentage incorporated into the diet of second broods. Points represent separate sampling periods. Curve fitted by eye.

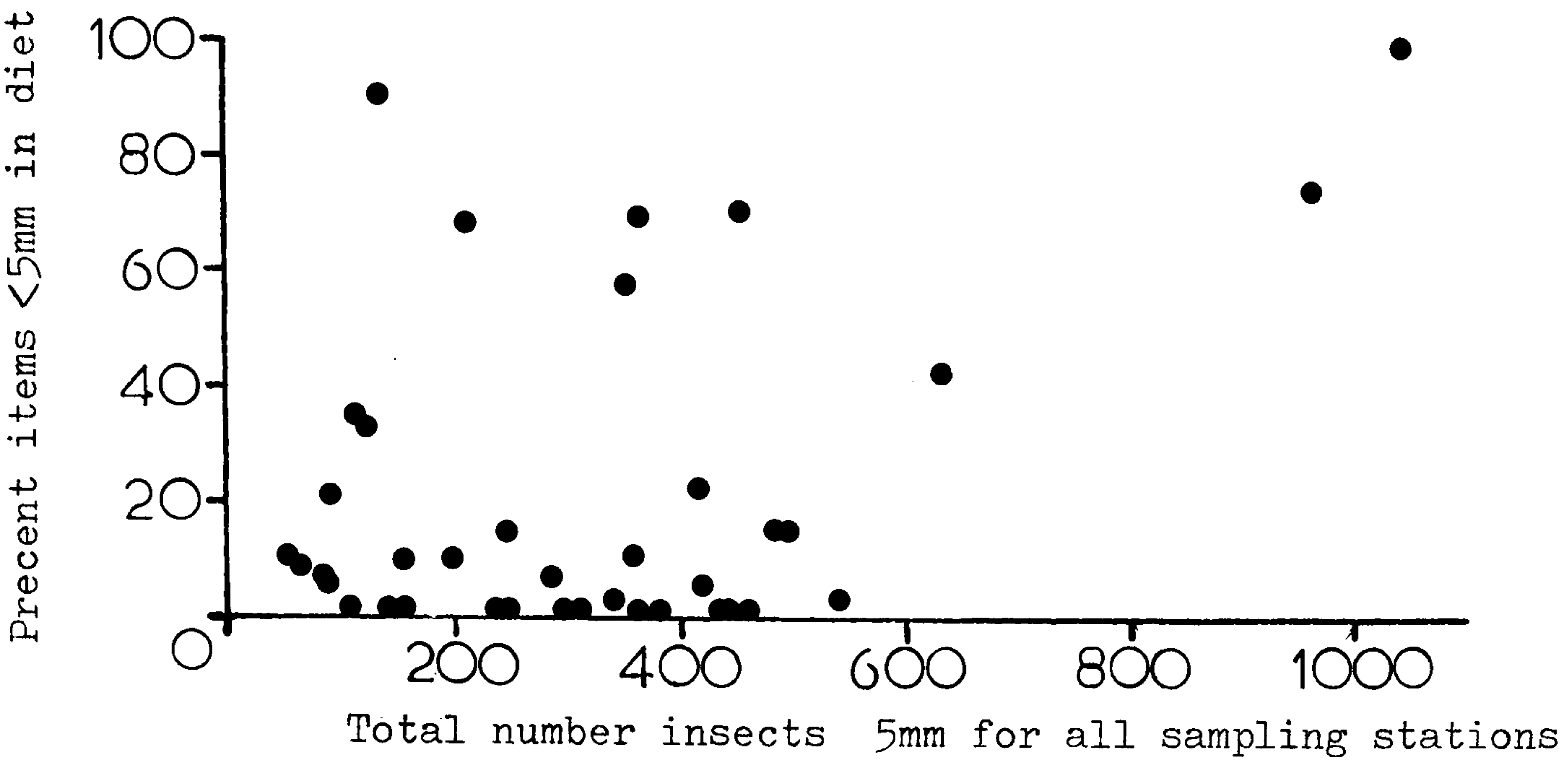


Figure 3.5.5.a. There is no significant linear relationship between the abundance of small aerial insects and the percentage of prey items <5mm in the diet of first broods. r = 0.163, n = 42, P>0.1.

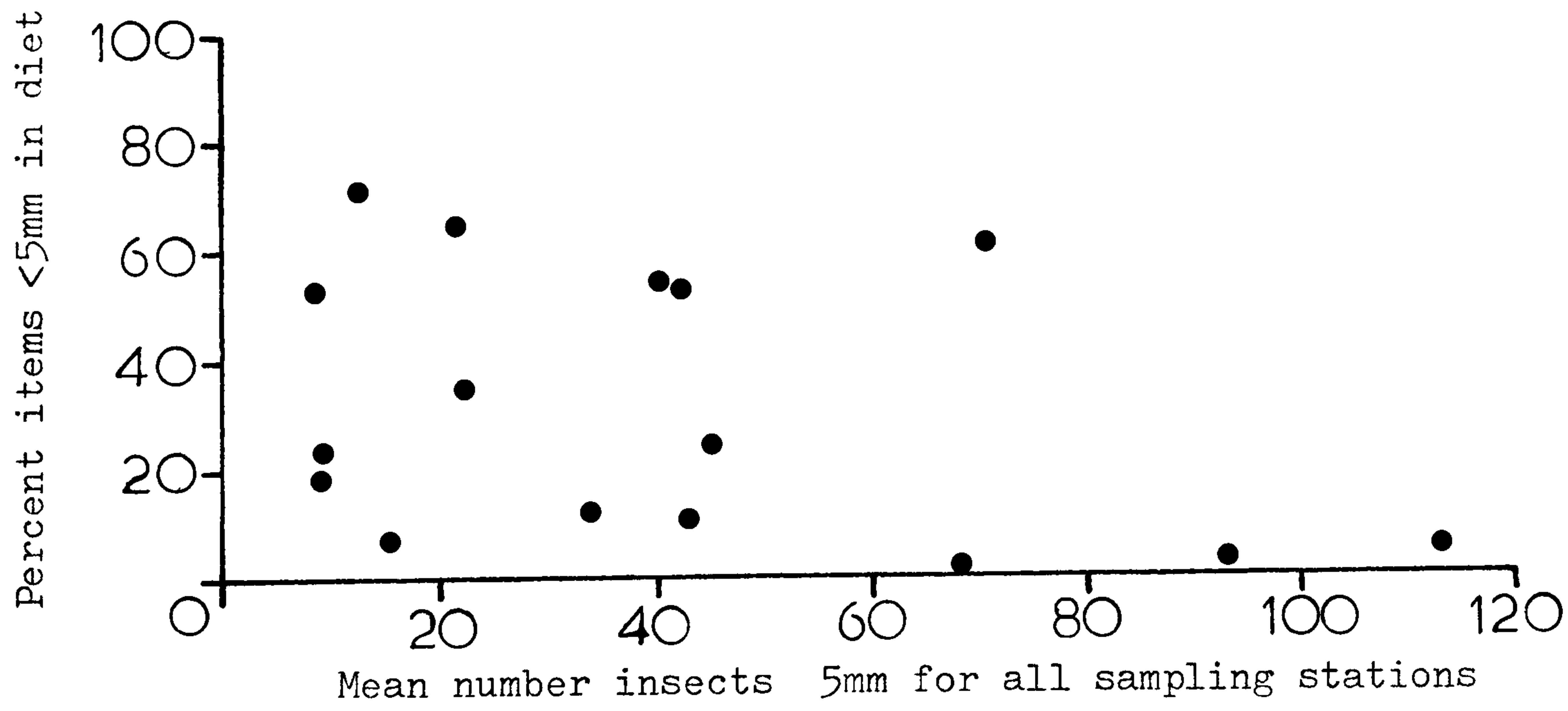


Figure 3.5.5.b. In the diet of second broods fewer prey items <5mm occur when the abundance of small insects is high. r = -0.383, n = 16, P<0.01

It appears that the foraging strategy of the adults, at least under the generally good conditions during the study period, was a response to quality of the prey, and they preferred the larger items. With an increase in abundance of larger insects the adults brought more large prey back to the nest. The incorporation of an increasing proportion of large items into the nestling diet appeared to progress steadily to plateau at the hundred percent level, this being observed for both first and second broods (Figure 3.5.4 a,b). A more gradual rise in the proportion of large prey eaten has been noted for other species, for example the Redshank, Tringa totanus (Goss-Custard 1977) and Spotted Flycatcher (Davies 1977b). The present results accord with the many recent theoretical considerations of foraging efficiency in that the abundance of small insects did not influence their inclusion in the diet of first broods, and a decrease in their proportion of the second brood diet was correlated with an increase in abundance of small insects no doubt as a consequence of the parallel increase in larger insect abundance (Figure 3.5.5 a, b).

The three points in the top left corner of Figure 3.5.4a were due to under-representation of larger taxa in the net samples for the three sampling periods. These occurred on separate days, the particular taxonomic groups being Cordilurinae, Muscidae, Syrphidae and large Acalypterate Schizophora, all of which would have been quite mobile in the favourable weather conditions prevailing on these days.

Diurnal and seasonal effects

The number of feeding visits for the 90 minute periods determined from the automatic nest recording experiments showed some variation throughout the day, which was itself superimposed upon a seasonal difference (Figure 3.5.6). It is apparent that for both first and

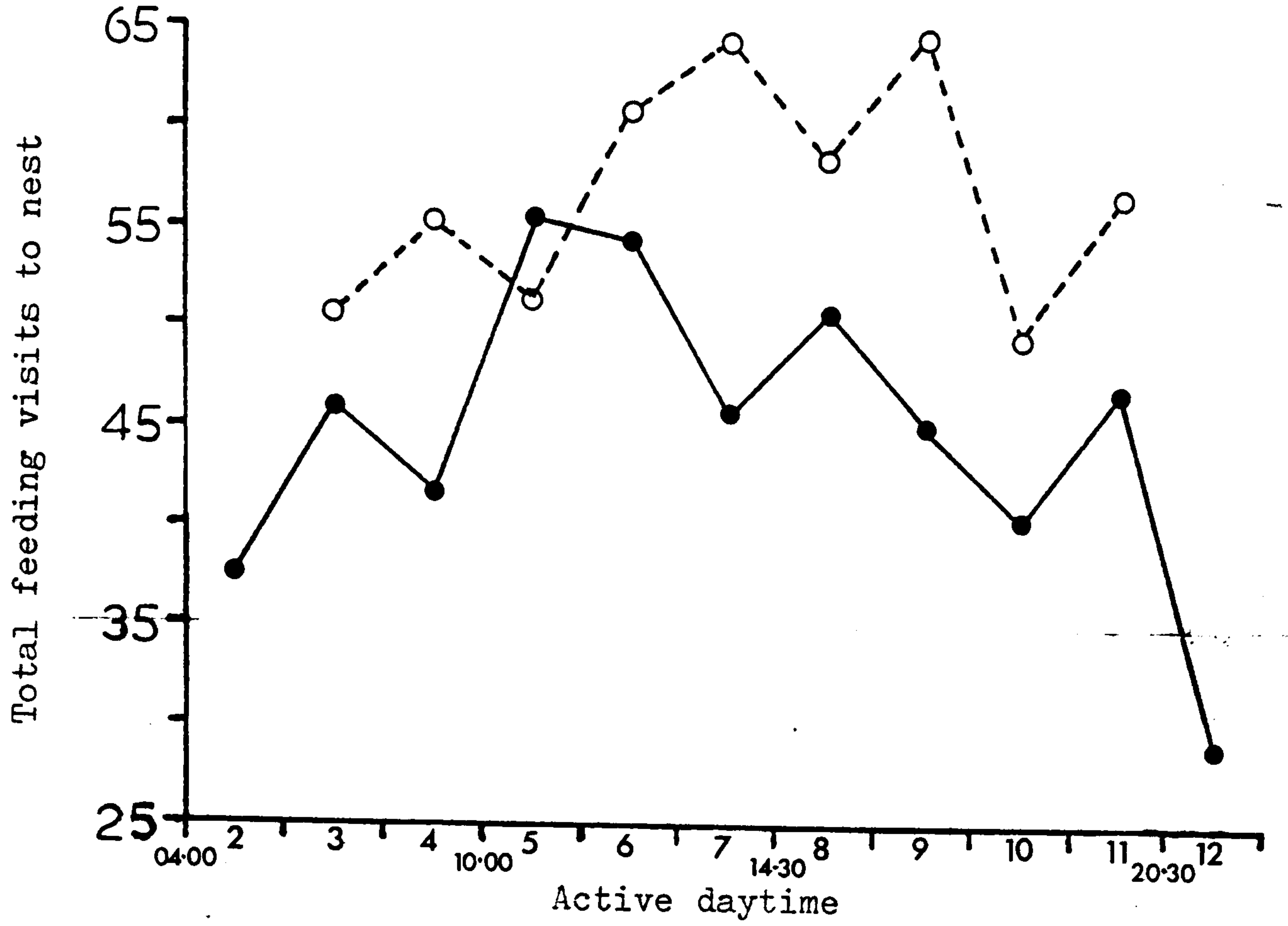


Figure 3.5.6. Diurnal variation in feeding visits to the nest from tagging experiments. Solid circles = first broods (five nestlings), open circles = second broods (four nestlings)

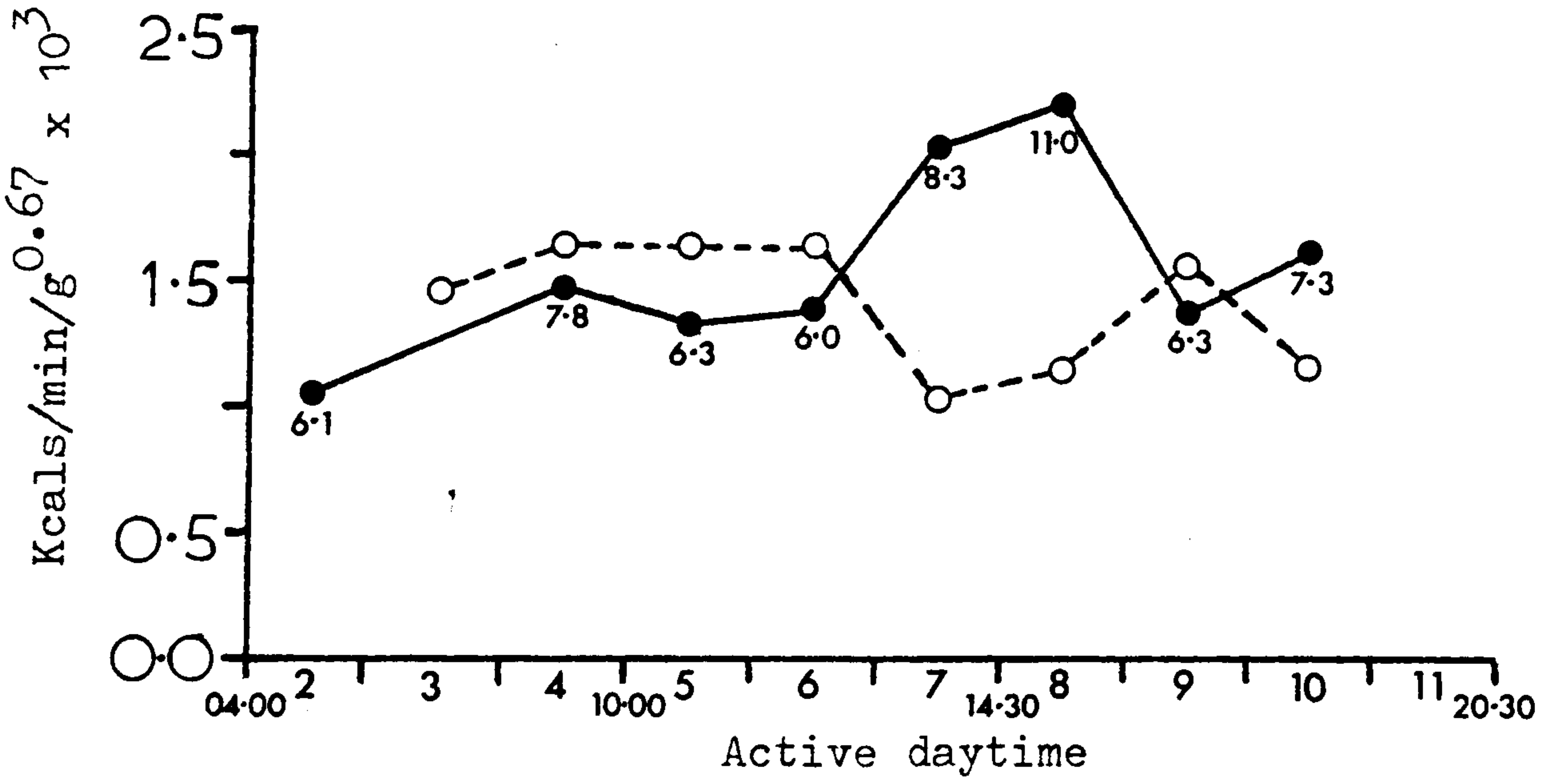


Figure 3.5.7. Diurnal variation in food delivery to the nest in first broods (solid circles) and second broods (open circles) of all sizes. Figures refer to the mean number of boluses delivered to first broods in those time periods.

second broods the number of visits made during the early part of the day and, to a lesser extent, in the evening were fewer than for the remainder of the day. However, the rise in number of visits seemed to occur earlier with first broods and did not peak at the time of maximum daily air temperature, as did the second brood visits. It will be noted that for all time periods but one the numbers of visits made to second broods exceeded those of first broods. Over the whole day the increase of feeding visits from first to second broods was significant and apparently made up almost entirely by the male bird (Table 3.5.2, t = 6.35, n = 80, P < 0.001), the slight increase for females being insignificant (t = 0.71, n = 80, P > 0.1). A similar increase in energy expenditure from feeding first to second broods has been noted for male, rather than female, House Martins (Hails 1977). The effect of raising the number of nestlings in both normal first and second broods was to increase the number of visits to the nest in each case, significantly in the former. Again this was achieved by an increase in male feeding visits (Table 3.5.2, t = 3.92, n = 60, P < 0.001), although the increase in female second brood feeding was near significance (t = 1.93, n = 46, P < 0.1).

TABLE 3.5.2

Variation in the number of feeding visits made to different sized broods

Brood description	No. of nestlings	Mean no. visits/90 minutes ± S.D.				
		Male	n	Female	n	Both
Normal firsts	5	18.4 ± 7.5	48	27.4 ± 10.0	48	45.8 ± 13.9
Normal seconds	4	28.7 ± 6.6	33	29.0 ± 10.0	33	57.7 ± 11.9
Enlarged firsts	7	26.6 ± 8.1	21	26.6 ± 7.6	21	53.2 ± 13.8
Enlarged seconds	6	34.7 ± 19.7	14	36.8 ± 13.6	14	71.5 ± 18.9

With these first to second brood feeding increases evident, it may be expected that the amount of food being delivered would show a corresponding increase. In fact, on a whole day basis the amounts of food per unit total time delivered to first and second broods were very similar, (first broods, 24.5 ± 20.0 kcals/min/$g^{0.67}$ × 10^3, second broods, 31.9 ± 21.7 kcals/min/$g^{0.67}$ × 10^3, $t = 0.55$, $n = 80$, $P > 0.1$). However, the patterns of food delivery throughout the day determined from the choker experiments (Figure 3.5.7) differ from what may have been expected from the previous feeding visit data (Figure 3.5.6, Appendix II). The peak of food delivery to first broods, in disturbed broods, occurred later than the feeding visit peak in Figure 3.5.6, a possible explanation being that bolus size increased in the mid-afternoon period. But, even though some variability in bolus size is apparent, it is the higher bolus numbers for the mid-afternoon period that account for this peak (see Figure 3.5.7). Although direct evidence is lacking, the early afternoon dip in food delivery noted for second broods may have resulted in part from fewer feeding visits by the adults. It is uncertain exactly why these patterns should differ from the feeding visit patterns determined from tagging experiments. The mid-afternoon divergence in amount of food delivered to first and second broods was related to the size and number of items captured per unit total time. Thus, more items were delivered in the morning and evening, but these were smaller than those fewer items caught during the middle of the day (Figures 3.5.8 and 3.5.9). For first broods it is possible that the mid-afternoon decline in prey size resulted from favoured insect prey being much more active at that time of day, since larger items have been shown to be as abundant then as at other times. The absence of a marked mid-afternoon increase in capture of larger items for second broods was the other contributing factor to the observed trough in overall food delivery. The mean

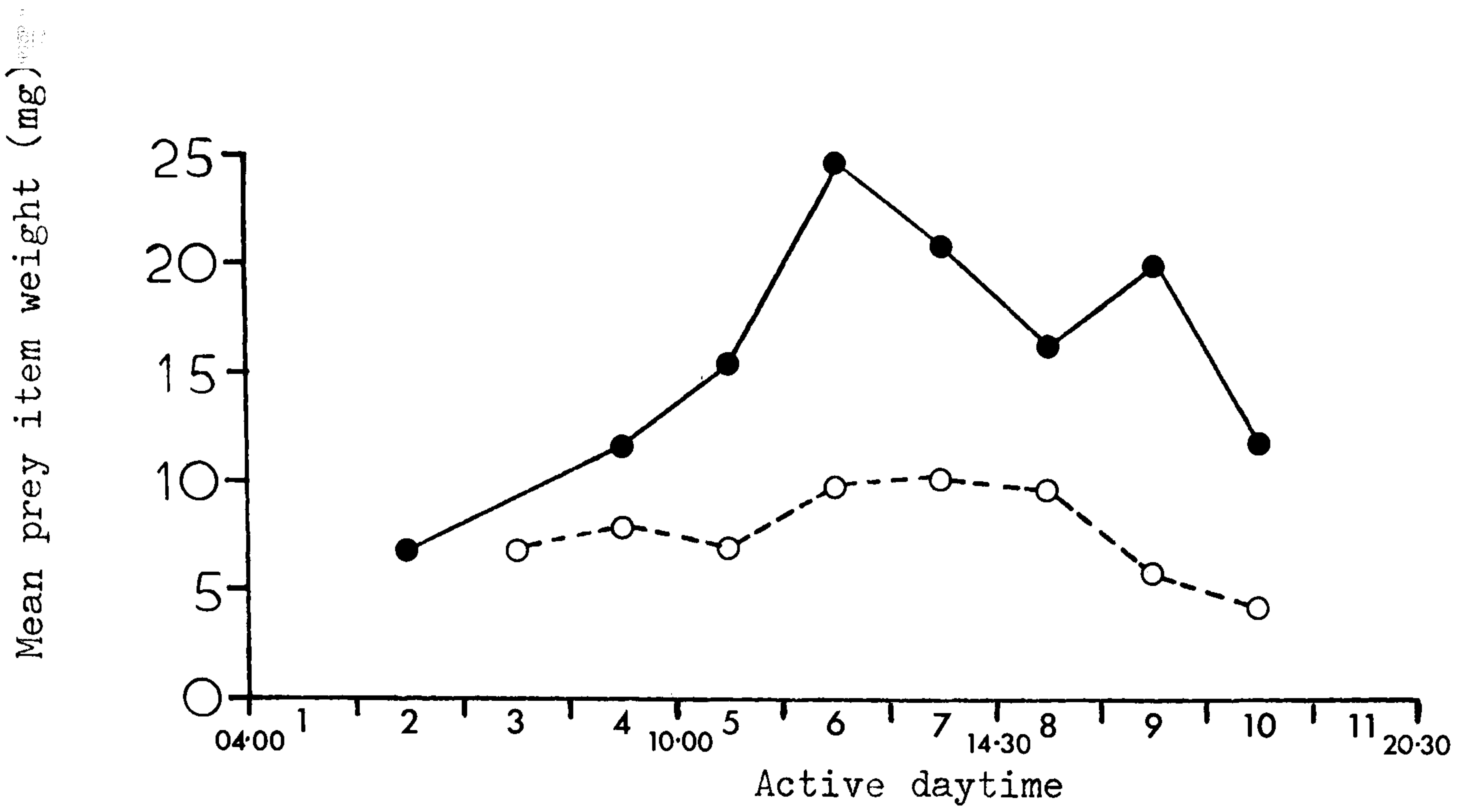


Figure 3.5.8. Diurnal variation in the size of prey items fed to first broods (solid circles) and second broods (open circles).

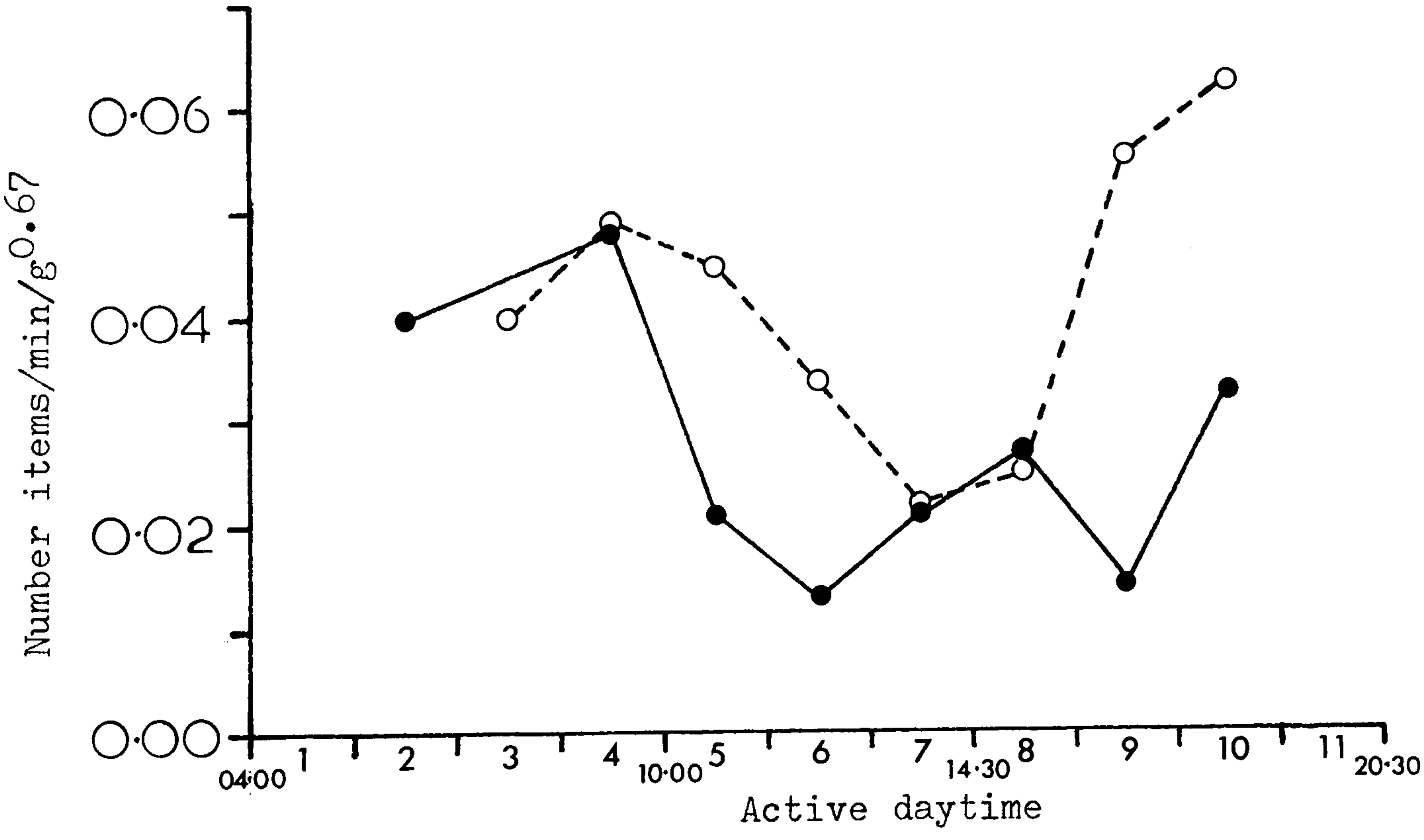


Figure 3.5.9. Diurnal variation in the number of prey items per unit total time delivered to first broods (solid circles) and second broods (open circles).

dry weight of prey items caught for first broods (16.1 ± 10.7 mg) was significantly higher than that for seconds (8.2 ± 4.0 mg, $t = 3.83$, $n = 62$, $P < 0.001$). This was unexpected since a greater abundance of larger items was apparently available during the times second broods were being fed (Figures 3.4.2 and 3.4.3). However, the adults feeding second broods delivered more items per unit total time than those feeding first broods (first broods, 0.027 ± 0.033 items/min/$g^{0.67}$, second broods, 0.040 ± 0.025 items/min/$g^{0.67}$, $t = 2.01$, $P < 0.05$), which implies a partial compensation for smaller prey. Nevertheless, the real rates of capture and delivery of prey items will involve only the time spent feeding nestlings, and therefore it is necessary to separate the total foraging excursion time from that spent on all other activities (the two combine as total time).

3.6 The energy expended

Before implementation of the automatic nest-visit recording experiment, preliminary observations of adult swallows feeding nestlings had established that both sexes tended to feed in bouts interspersed with longer periods away from the nest for activities such as self-feeding and preening. Within the feeding bouts the duration of individual foraging excursions was never less than thirty seconds and rarely more than six minutes. In the following analysis of the chart records therefore, only times within these limits were taken as foraging excursions to feed nestlings and any interval greater than six minutes was alloted to "other activity time".

The feeding excursion times for both sexes throughout the day were very similar (Table 3.6.1) and a plot of the mean excursion times for the sexes combined shows little variation, with the longest being confined to the first three or four hours

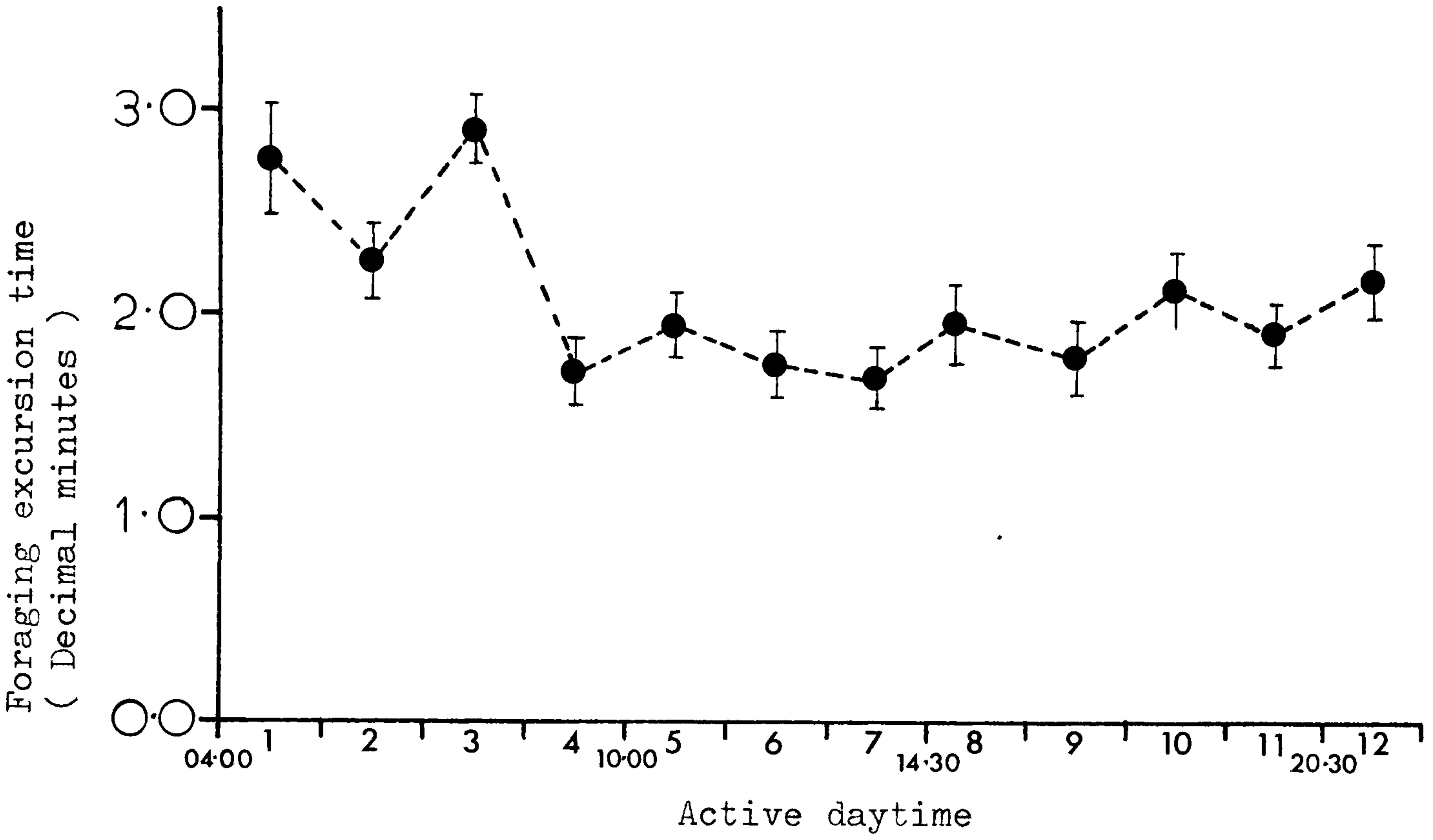


Figure 3.6.1. Diurnal variation in the mean foraging excursion times (± 1 S.E. for adult Swallows feeding first broods of five nestlings.

TABLE 3.6.1

The mean foraging excursion times for adult Swallows feeding first brood nestlings

Number in brood	Mean excursion time (decimal minutes)		n	t	P
	Male	Female			
5	2.16 ± 0.74	1.87 ± 0.31	44	1.69	> 0.1
7	2.23 ± 0.39	2.03 ± 0.39	44	1.55	> 0.1

of the morning (Figure 3.6.1). The overall mean foraging excursion time for adults feeding normal first broods (five nestlings) was 2.02 decimal minutes, (which for an average Swallow weight of 20.42g gives a mean foraging excursion energy cost of 0.045 kcals), and the mean value of 2.13 for feeding broods raised to seven nestlings was not significantly higher ($t = 0.896$, $n = 44$, $P > 0.1$). Since bolus size for different sized first broods remains constant and they are collected in the same period of time, it appears that increased food delivery to larger broods is indeed a function of the number of visits. And a greater number of visits therefore means a reduction in the time the male, and possibly female, have to devote to other activities. If this includes feeding themselves then a weight loss may occur in those parent birds with large broods. A realistic viewpoint is that the parent birds will or can sacrifice only so much of their other activity time and further investment in the brood is constrained by the necessity to self feed and the accompanying conflict of time allocation.

No data are available on foraging excursion times for adults feeding second broods and so it is a matter of speculation as to the probable situation. It seems unlikely that the excursion times would be longer, given the greater number of visits per unit time, as this would represent a serious, if not impossible, incursion into other activity time. Assuming the excursion times were the same as for first broods then again with a greater number of visits the adults would be investing more time in the brood. Given that the adults deliver more prey items per unit total time to second broods, the situation where foraging excursion times are equal to first broods means that the actual catching rate within each excursion could remain the same. But since it has been shown that an equal amount (same number kcals) of food is delivered per unit total time, then both the size of each bolus and the mean size of prey items contributing to it would be smaller. A seasonal decline was found for the size (dry weight) of boluses brought to the nest by adult Sand Martins (Chapter 4) and the same decline may occur with Swallows.

Shorter excursion times for feeding second broods, together with the greater number of visits, could result in the same overall time investment as for first broods. In this case however the catching rate would show an increase, although the bolus size would still remain smaller than for first broods. Certainly the results of flight speed trials show the adult birds feeding second broods to be flying faster than the theoretical most economical cruising speed of 8.61 m/s (Table 3.6.2), but this may also occur with first broods.

TABLE 3.6.2

Flight speeds of adult Swallows whilst feeding second broods

Distance m.	Time s.	Velocity m/s
350	25.5	13.73
300	30.0	10.00
300	28.0	10.71
500	49.0	10.20
550	55.0	10.00
400	37.0	10.81
	Mean	10.91

The catching rate of Swallows may also conform to a classic functional response curve (Holling 1959a, b). Hence, at a certain density of prey, an upper limit of the catching rate is reached and prey densities above this level evoke no increase in consumption. Therefore the higher densities of larger prey found to be available at the time of second brood feeding may in fact have been unexploitable.

The final outcome of the same amounts of food per unit total time being delivered to first and second broods is that the latter received less on a whole-day basis because of the fewer daylight hours in which to forage.

3.7 Factors influencing choice of feeding patch

Observations of the feeding adults showed them to have preferences for particular sectors or patches within the area around the nest-site. Why they should forage in some patches and ignore others seemd to result from two factors. Patches chosen whilst feeding first broods were found to have larger prey than those which were passed over (Table 3.7.1). Only in 7% of the samples were insects

TABLE 3.7.1

Factors influencing choice of feeding patch; differences between stations

	Chosen Stations	Rejected Stations	t	n	P
Mean insect dry weight (mg) during first-brood feeding	1.01 ± 0.57	0.34 ± 0.18	7.26	84	< 0.001
Mean insect dry weight (mg) during second-brood feeding	1.15 ± 0.64	1.08 ± 0.61	0.33	32	> 0.1
Distance (m) to feeding patch where mean insect size at rejected stations greater than at chosen stations. (Second broods).	205.5 ± 86.7	330 ± 137.4	2.42	20	< 0.05

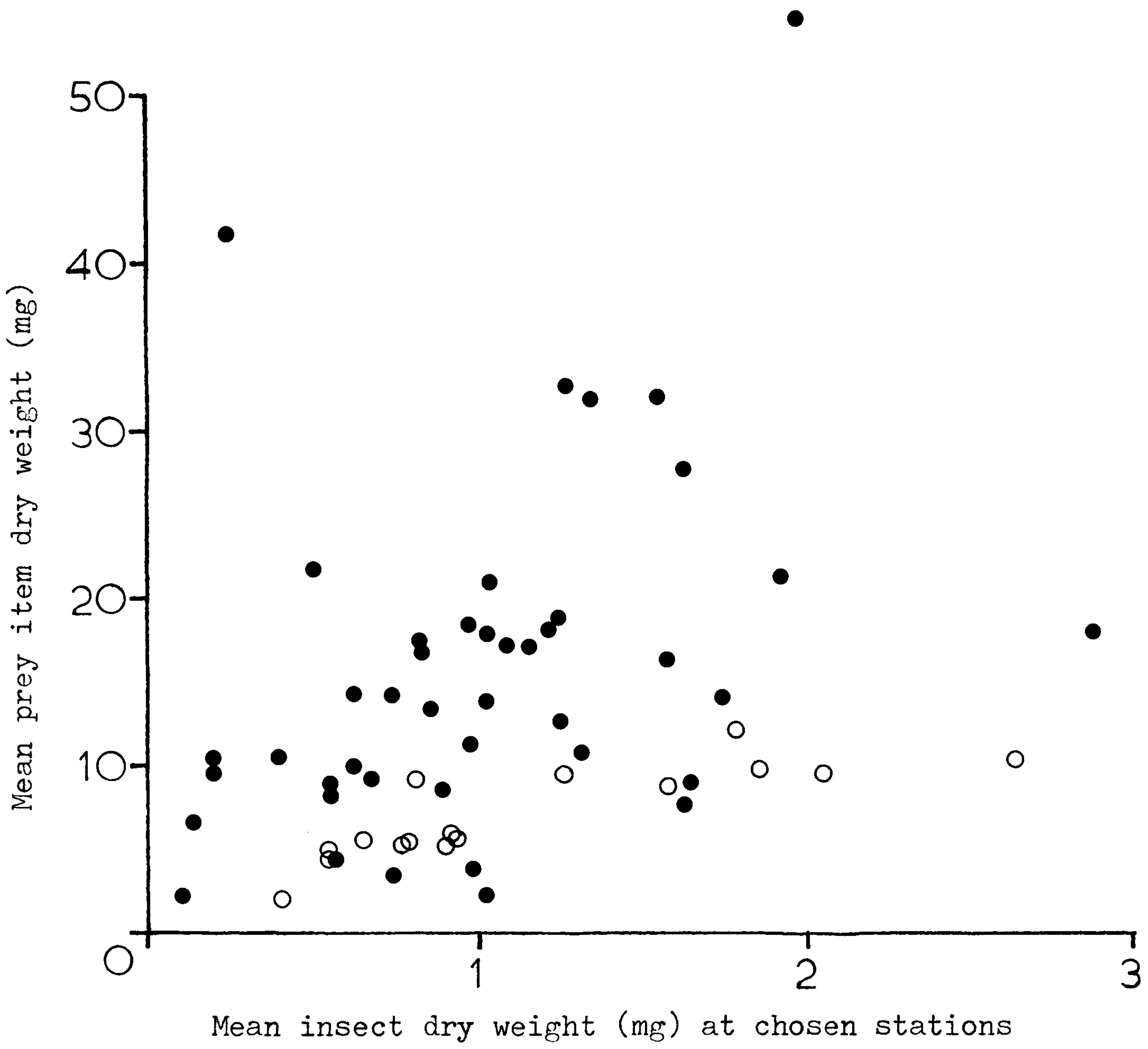


Figure 3.7.1. The relationship between the size of prey items brought back to the nest and the size of insect prey netted at the stations where the adults were feeding. r = 0.301, n = 58, P<0.02, solid circles = first broods, open circles = second broods. Points represent separate sampling periods.

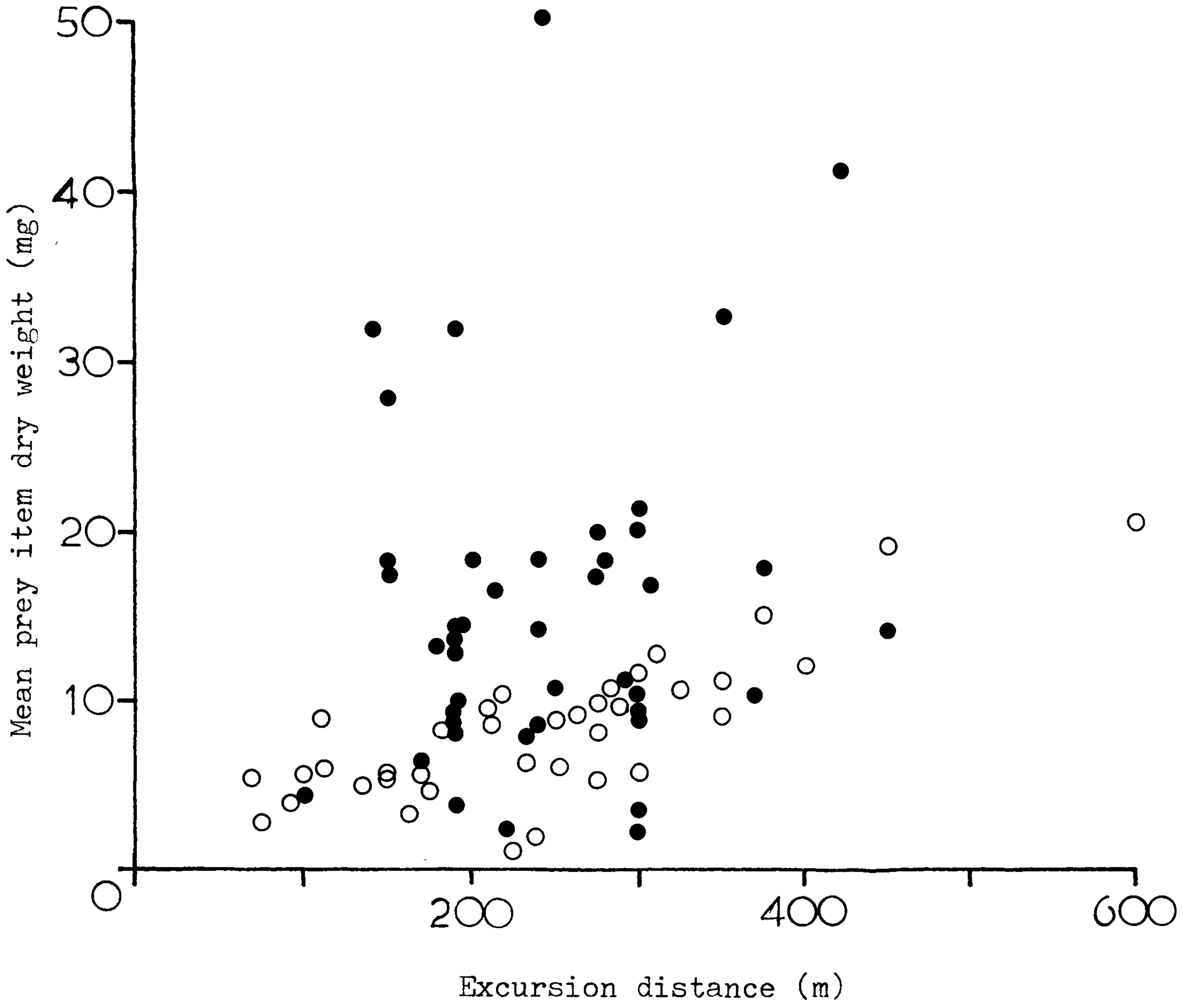


Figure 3.7.2. The relationship between the size of prey items brought back to the nest and the distance the adults went to catch them. r = 0.308, n = 80, P<0.01. Solid circles = first broods, open circles = second broods. Points represent separate sampling periods.

larger at the rejected stations, and even then this was probably because the largest insects at the chosen stations could be caught by the Swallows but not by the sampling net. However, during second brood feeding, the patches in which feeding occurred had insects which were not significantly larger than those in the patches which were ignored. This being the case, on what basis did the Swallows choose the particular patches in which they were observed to be feeding? A comparison of the mean distance travelled to the patches chosen and the distance required to reach the others provided a possible explanation. It was found that the rejected patches would have always required the birds to travel further than they actually did (Table 3.7.1). Hence it appears that, for adults feeding second broods, the cost of going further was greater than the reward, in terms of larger insects being available. It seems likely that travelling further would increase the foraging excursion time and, as stated previously, the adults cannot invest more time in this way. That the adults feeding second broods probably do not invest more time is shown by the fact that they travelled no further than those feeding first broods (first broods distance, 258.4 ± 76.5m, second broods, 239.1 ± 111.8m, $t = 0.81$, $n = 64$, $P > 0.1$). To go beyond these limits may be sub-optimal in terms of distance and/or time. Up to these limits the mean size of prey items brought back to both first and second broods was a function of the mean insect size in the patches where the adults were foraging (Figure 3.7.1) and the distances to those patches (Figure 3.7.2), although no direct correlation between available insect size and distance was apparent ($r = 0.074$, $n = 58$, $P > 0.1$).

Given the similar insect sizes available at the chosen stations, (mean insect dry weight first broods, 1.01 ± 0.57 mg, second broods

1.15 ± 0.64 mg, $t = 0.79$, $n = 58$, $P > 0.1$) and same distance to the patch, it is evident that adults feeding second broods brought back smaller items than first-brood adults. Possible compensation by taking more prey items for the same distance travelled was not observed ($r = 0.082$, $n = 72$, $P > 0.1$).

The distance travelled to a feeding patch did not appear to vary with the brood size ($r = -0.069$, $n = 42$, $P > 0.1$) or with time of day ($r = 0.023$, $n = 81$, $P > 0.1$)

3.8 Foraging efficiency

The processes of obtaining food, by search, pursuit and capture, and its ingestion and digestion, all require energy. For an animal to survive therefore the ratio:

$$\frac{\text{Food energy assimilated}}{\text{Energy expended during its collection}}$$

must be equal to one, and should be much greater for the net surplus of energy will be required to power the other essential processes of the body.

The fore-going sections have dealt with how adult Swallows feeding nestlings set about collecting food, the amount of food they actually harvested and the energy they expended whilst collecting this food. Ideally the net energy intake of the two adults and the brood they are feeding should be determined but there are several factors militating against this. The extent of self-feeding and the rate of food intake of the adults whilst doing so are unknown, and the assimilation efficiencies of both adults and nestlings have not been determined for this species. However, since parent birds devote most of their daylight hours to feeding the nestlings, the maximisation of the net energy gain to the brood must be assumed to be of paramount importance. It is not realistic to expect adult Swallows to ingest prey items during foraging excursions to feed nestlings because they collect a large food-ball, (cf single identifiable items of Great Tits, *Parus major*, (Royama 1970) and Starlings, *Sturna vulgaris*, (Tinbergen 1976, K. Westerturp, pers. comm.)), and the assimilation efficiency of nestlings is here assumed to be 100%. The resulting equation is simplified from Lawton (1973):

$$\text{Foraging Efficiency (F.E.)} = \frac{\text{Food energy (kcals) delivered to the brood}}{\text{Energy (kcals) expended during its collection}}$$

With the objective of the adults being to maximise the above ratio it is of value to determine the factors causing greatest variation in foraging efficiency, and to see if the point of maximal efficiency corresponds to observed feeding behaviour. Given that bolus weights and foraging excursion times are not known for second broods, only foraging efficiencies for first broods are presented here.

Foraging efficiency was found to vary between 5.39 and 22.14, with a mean of 10.24. These values are comparable with those of a North American finch, the Dickcissel, *Spiza americana* at 12.8 and three species of tropical hummingbird at 3.8 to 22.2, although another hummingbird, *Eugenes fulgenes*, had values from 7.0 up to 70.0 (Lawton 1973, Table II). Therefore Swallows feeding nestlings exhibit foraging efficiencies which may be regarded as normal, although it would be of interest to determine the ratio for self-feeding adults to see if the mean was different.

3.8.1 Factors influencing foraging efficiency

(a) Brood size

It was found that foraging efficiency did not increase with a corresponding increase in size of the brood ($r = 0.031$, $n = 42$, $P > 0.1$). The three highest efficiencies were related to broods mid-way along the size co-ordinate (Figure 3.8.1). However, a larger sample is required for a full analysis of brood size effects.

(b) Time of day

No clear relationship of foraging efficiency to particular times of day was discovered apart from the early morning where all values except one were low (Figure 3.8.2). These lower values might be expected given that foraging excursion times have been shown to be longer at this stage of the day.

Since it has been previously demonstrated for first broods that the size of prey and amount of food brought to the nest relate to foraging at certain (chosen) stations (patches), variation in foraging efficiency will probably be associated with characteristics of the prey at these stations. However, sample correlates were performed for total insect abundance, abundance of large insects (> 5 mm), and the mean insect weight at all stations, but these proved to be insignificant ($P > 0.1$).

For chosen stations the following results emerged:

(c) Total insect abundance

The absolute abundance of insects at the chosen stations was not correlated with foraging efficiency ($r = 0.197$, $n = 42$, $P > 0.1$) and no peak in the distribution was noted.

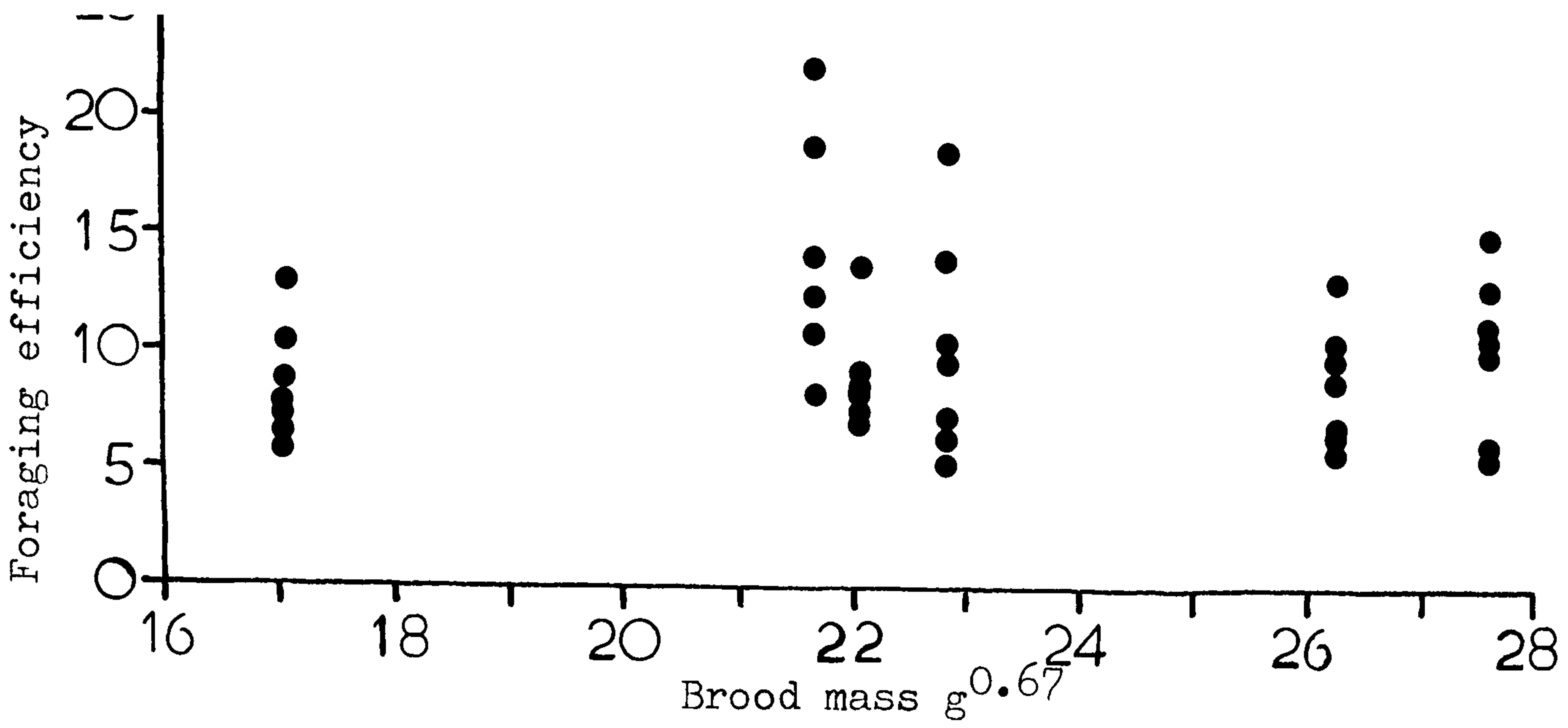


Figure 3.8.1. The effect of brood size on foraging efficiency.

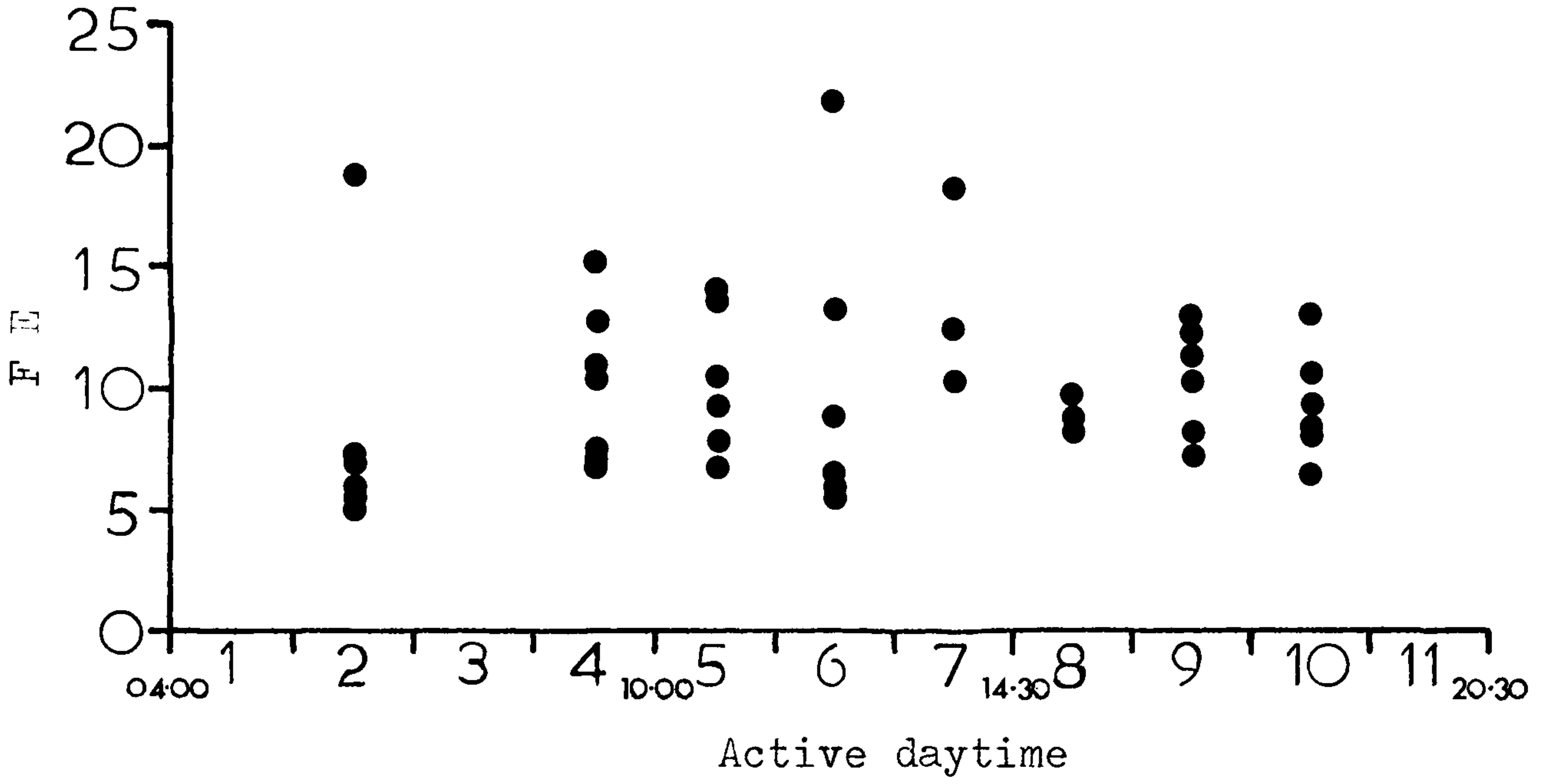


Figure 3.8.2. Diurnal variation in foraging efficiency.

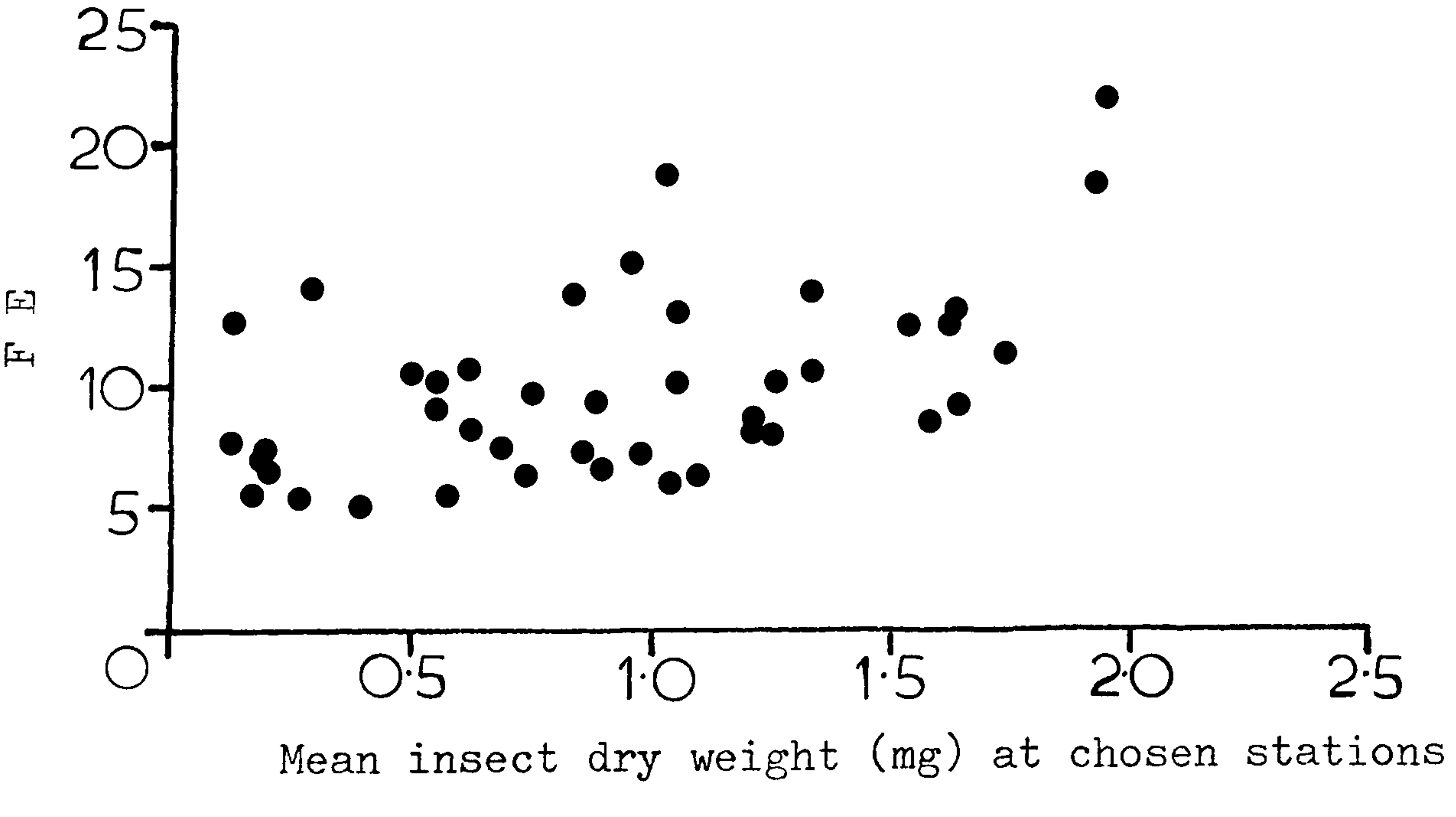


Figure 3.8.3. The relationship of foraging efficiency to the average insect weight in the patches where foraging occurred.

$r = 0.516$, $n = 42$, $P<0.001$

(d) Abundance of large insects, > 5mm length

The correlation of foraging efficiency with the size of large insects at the chosen stations was not significant ($r = 0.280$, $P > 0.05$). The effect of considerable differences in weight of prey types having the same length can be obscured in this form of analysis and a direct measure of weight may be more appropriate.

(e) Mean insect weight

Foraging efficiency was found to be positively correlated with mean insect dry weight (mg) at the chosen stations (Figure 3.8.3). This finding is supported by the evidence that larger prey items are caught where the mean insect weight is higher (Figure 3.7.1). However, these relationships do not give any idea as to how large potential prey items can be until they become difficult to pursue and/or handle, thereby increasing the time spent foraging and possibly causing a drop in the foraging efficiency ratio.

Since Swallows take prey items which on average are flying faster than those taken by the other aerial feeders, it may not be possible to determine the effects of prey mobility on the feeding efficiency of this species in isolation. Indeed, a correlation of foraging efficiency against the mean flight speed (Vmr) of the prey was not significant ($r = 0.142$, $P > 0.1$), and no peak and fall-off in the distribution of points was observed.

3.8.2 Prey type

It was found that 82.8% of the prey items brought to first broods were larger than 5 mm body length (71.5% for second broods). Of these, 85.7% were attributable to six taxonomic sub-groups of the order Diptera (Table 3.8.1). Within the available Acalypterate

TABLE 3.8.1

The proportional contribution of different prey types to the nestling Swallow diet compared to their representation in the environment

Taxon	Percent available	Percent diet
Tipulidae	5.59	1.52
Tabanidae	0.40	4.60
Empididae	3.96	6.59
Syrphidae	11.58	23.27
Acalypterates	23.84	28.15
Muscidae	4.93	15.40
Cordilurinae	19.57	7.73
Others	32.13	12.74

Schizophora and other taxa, most of the individuals occupied the smallest size class. However, the majority of Acalyperates that contributed to the greatest proportion of the diet were larger (Figure 3.8.4a). Whilst the same was true for the other taxa, overall these groups were far less important in the diet and, together with the Acalypterates, no fast flying insect types were involved. A slightly larger proportion of Empididae were taken as prey than were generally available and these were barely different in size range ($\chi^2 = 8.44$, $P > 0.05$), this family not notably consisting of fast-flying types. More Tipulids were available than Empidids but were not selected to the same extent. They are included in this presentation because those comprising the prey were on average much larger than those available. This shows that the adult Swallows are capable of taking very large prey items. Possibly a greater proportion of Tipulids would be represented in the diet if the mean size available was larger.

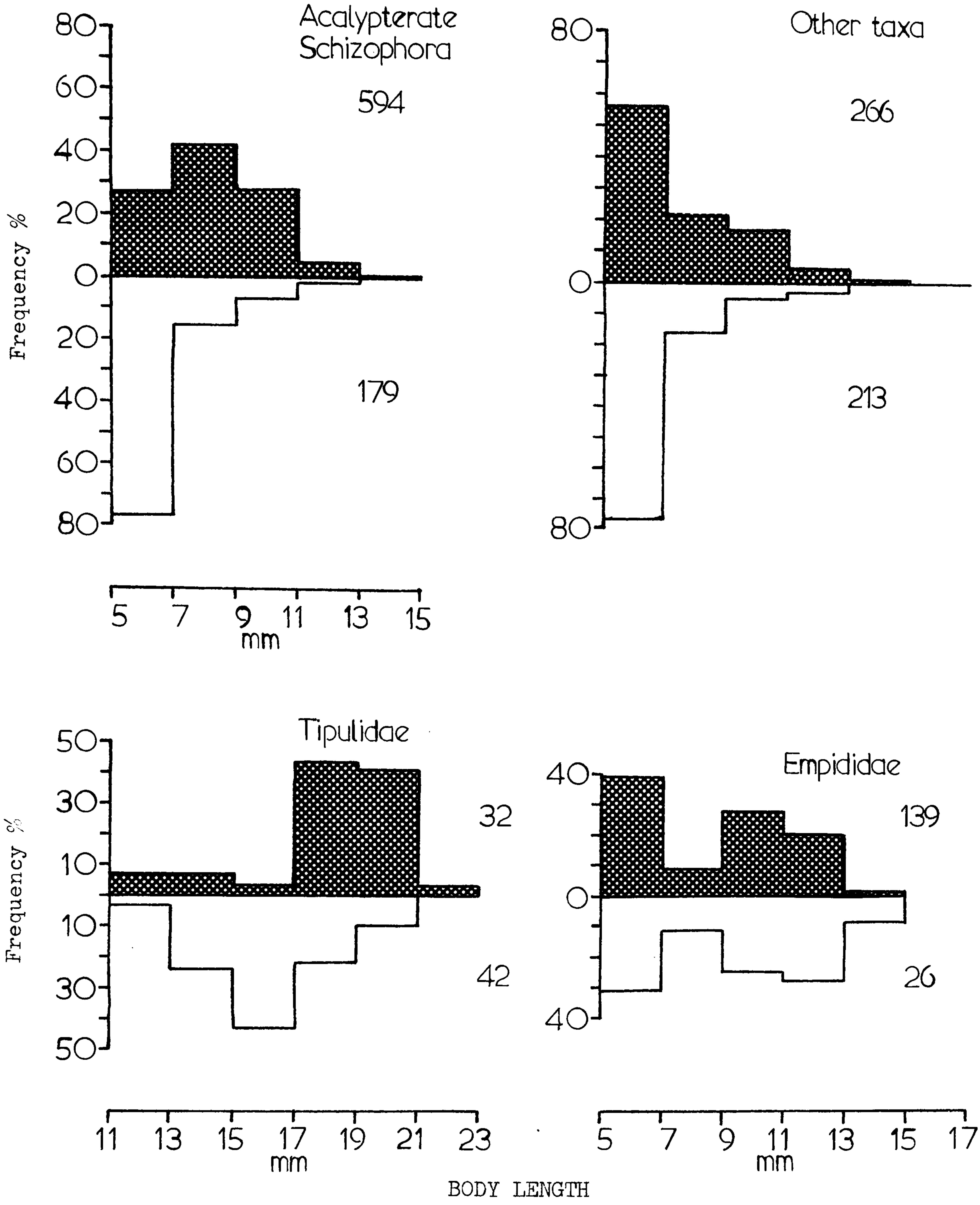


Figure 3.8.4.a. The sizes of major prey types >5mm fed to nestling Swallows compared to the sizes available. The shaded distributions represent diet. Sample sizes are shown.

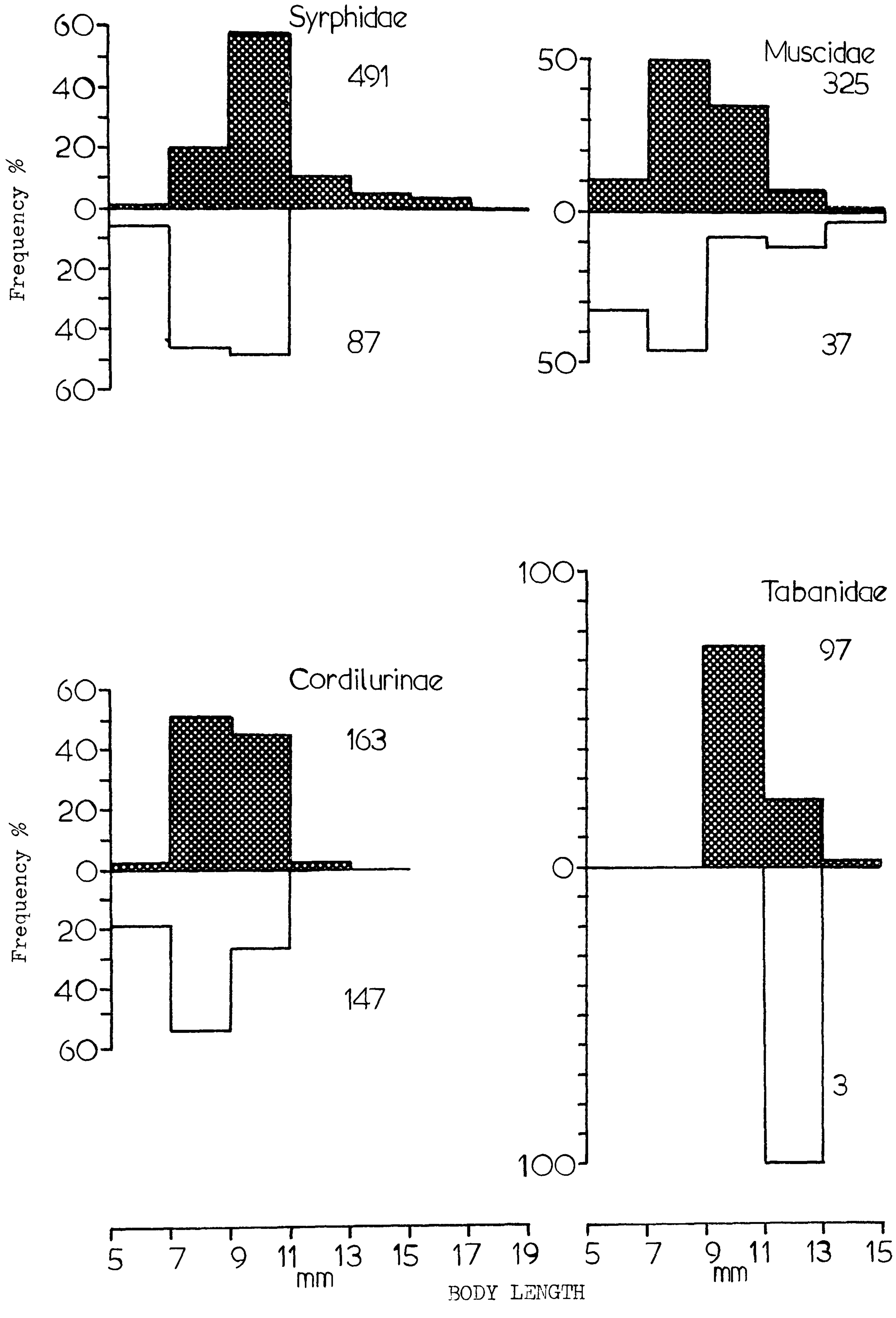

Syrphidae
491
87
Muscidae
325
37
Cordilurinae
163
147
Tabanidae
97
3
Frequency %
Frequency %
60
40
20
0
20
40
60
50
0
50
100
0
100
5
7
9
11
13
15
17
19
mm
5
7
9
11
13
15
mm
BODY LENGTH

Figure 3.4.8.b.

Although the net could adequately sample large slow-flying prey such as Tipulids, the largest size classes of the fast-flying taxa were probably under-represented. Therefore with the Syrphidae and Muscidae being heavily selected for (Table 3.8.1), it is probable that the peak size classes in the diet (Figure 3.8.4b) were optimal in that smaller items involve an unnecessarily high catching rate, and larger items require an energetically costly pursuit. Syrphids are likely to be easier to catch than Muscids due to their characteristic hovering. The fast flying Tabanids were larger than the peak sizes of Syrphids and Muscids, although the very few sampled by the net were larger still than the most frequent size in the prey. This is further indication that prey mobility rather than prey size is the constraint to selection of larger items and the birds were in fact selecting the optimal sizes of these fast flying taxa with respect to mobility.

Dung-flies (Cordilurinae) were the second commonest prey type available to the feeding Swallows, but they formed only a small proportion of the diet. Since they are slower moving than either Syrphids or Muscids they would have been more available to the net, but equally more available to the Swallows on this basis, and therefore Cordilurinids must be ranked lower in preference for other reasons.

The mode for Tipulids in the diet peaked at a relatively much larger size class than the modal peak for those available, as compared to the distance between diet and availability modes for faster flying types. Hence, if the sampling net was more efficient, the resulting shifts in modal peaks of fast flying types to larger size classes would emphasise the importance of mobility in selection of prey.

3.9 Experiment to increase "other activity time".

This short experiment was designed to artificially increase the amount of time a pair of Swallows devoted to activities other than feeding the brood, and to note any compensatory behaviour. The method was simply to place a predator (a stuffed Tawny Owl, *Strix aluco*) at the entrance to the nesting shed for 30 minute periods every 90 minutes throughout the day (6th July 1976). No visits were made to the nest (containing five nestlings) during each 30 minute period and the sum of these periods constituted the extra other activity time. Subsequent feeding visits to the nest were automatically recorded. The day's production of faeces was collected, together with faeces from a control brood of the same size, similar age, and situated at a nearby farm.

3.9.1 The effect on prey selection

Little difference was observed in the types of prey taken by the experimental and control Swallows (Table 3.9.1) and the size distribu-

TABLE 3.9.1

Prey types brought to nestlings where an artificial predator has been positioned compared to those returned to an unobstructed nest

	Percent in diet with predator	Percent in diet with control
Anisopodidae	5.59	4.75
Empididae	4.04	5.70
Syrphidae	15.22	19.30
Acalypterate Schizophora	33.54	31.65
Muscidae	8.07	8.86
Cordilurinae	8.70	13.61
Total	74.53	83.87

tions of prey were very similar (mean body length (mm) of prey for experimental Swallows; 9.49 ± 2.47, for control Swallows, 9.44 ± 2.71, $t = 0.242$, $n = 630$, $P > 0.1$). It may be concluded that the time taken up by the predator was not compensated for by the Swallows selecting different sizes or types of prey.

3.9.2 The effect on foraging excursion time

The mean time taken to complete an excursion to collect food for the nestlings by both sexes was 1.78 ± 0.25 decimal minutes. This was not significantly lower than the mean time for both sexes feeding broods of five nestlings in a normal situation (2.02 ± 0.17 dec. min., $t = 1.47$, $n = 33$, $P > 0.1$). Hence, it appears that the adults do not shorten the foraging excursion time (by not going so far or speeding up) to compensate for possible encroachment of enforced "other activity" time.

3.9.3 The effect on the number of feeding visits

The number of feeding visits per hour made to the experimental nest was 20.96 ± 7.27. This was a significant reduction on the number of visits per hour made to normal first broods of five nestlings (30.22 ± 8.92, $t = 3.51$, $n = 58$, $P < 0.01$). Rather than making up for lost time by increasing the feeding rate, the adults were so adversely affected as to make fewer visits. Given that they had similar excursion times and took essentially the same prey as in a normal situation, the brood would ultimately have received less food at the end of the day. An increase in feeding rate the following day is possible but this was not tested.

The implication for the experiments with chokers is that the presence of the experimenter would probably reduce the number of feeding visits; this effect was in fact observed. It is assumed that this feeding rate reduction was uniform throughout the day. The fore-going discussions, particularly of foraging efficiency, are not altered, because the prey selected and the foraging excursion times remain unchanged.

CHAPTER 4

FORAGING AND COLONIALITY IN SAND MARTINS

4. FORAGING AND COLONIALITY IN SAND MARTINS

If animals are going to live in colonies or groups they will maintain these units only if the fitnesses of individuals within colonies are higher than the fitnesses of non-colonial conspecifics. It is instructive to identify the selective factors responsible for the evolution and present day maintenance of the colonial habit.

According to Alexander (1971, 1974) there may only be three evolutionary reasons for coloniality; (a) the existence of patchy food supplies means that individuals may otherwise locate food too infrequently, or relatively large single prey may require group attacks, (b) a lowering of predation may result from aggressive group defence or the opportunity may arise for individuals to use the group as cover, i.e. the "selfish herd" effect (Hamilton 1971) or (c) there may be extreme localisation of some resource, such as suitable breeding sites for some marine birds and mammals. Only in the first two cases do grouped individuals gain because of the presence of others (Alexander 1974) and, in previous studies of Sand Martins, these two cases have separately been cited as of major importance in the evolution of their coloniality. Hence, Emlen (1971) and Emlen and Demong (1974, 1975) have suggested that social facilitation of foraging as a response to localised aggregations of the aerial insect prey constitutes a principal advantage of coloniality, and that differential predation has a relatively minor effect. Conversely, Hoogland and Sherman (1976), in a thorough study of advantages and disadvantages of coloniality in Sand Martins, concluded that decreased predation was the major selective factor in the evolution of colonial breeding and that social facilitation of feeding did not occur. Opposing interpretations of the likely causes of coloniality exist for a number of other species, for example with the studies of Ward (1965), Zahavi (1971) and Ward and Zahavi (1973) (mainly on the Black faced Dioch, *Quelea quelea* and Pied/ White Wagtail), compared to contrary conclusions reached by Gadgil (1972). Social foraging has been observed in colonial species such as Great Blue Herons *Ardea herodias* (Krebs 1974), White Pelicans *Pelecanus onocrotalus* (Behle 1944), Cliff Swallows *Petrochelidon pyrrhonota* (Emlen 1952), Brewers Blackbirds, *Euphagus cyanocephalus* (Horn 1968) and Tricoloured Blackbirds *Agelaius tricolor* (Orians 1961). These interpretations of social foraging are well balanced by the number of studies where groups of birds have been shown to vigorously mob and deter predators, for instance in Black-headed Gulls *Larus ridibundus* (Kruuk 1964), Franklin's Gulls *L. pipixcan* (Burger 1974), Brewers Blackbards (Horn 1968), Barn Swallows (Smith and Graves 1973, Snapp 1973, this study), House Martins (Lind 1962) and Rough-winged Swallows *Stelgidopteryx ruficollis* (Lunk 1962).

Whatever the interpretation of coloniality however, the aspect of how evolution of the colonial habit may have affected the time budgets of individuals rearing offspring within a colony has been neglected. The present study investigates this aspect of time allocation to various activities, and how foraging in a colonial situation is affected.

4.1 Description of the colony

The colony chosen for study was situated in a clean sand bank at a quarry site. It contained about 200 active nests at the peak of the breeding season in July. The layout was typical and the approximate dimensions of the colony are shown in Figure 4.1.1, together with the positions of what were considered "edge" and "centre" nests or burrows. The study was performed throughout the breeding season of 1976.

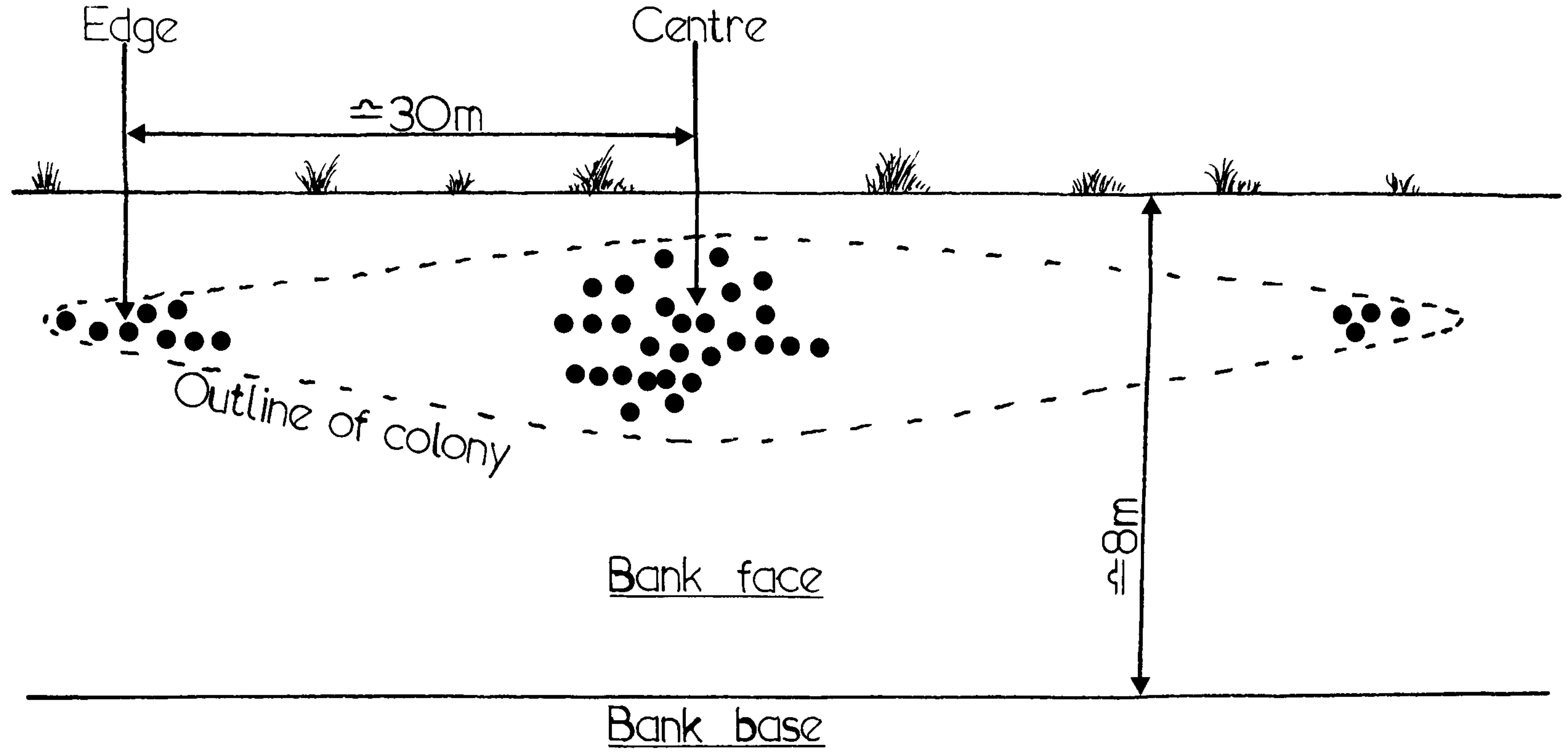


Figure 4.1.1. Diagrammatic representation of the Sand Martin colony with positions of edge and centre nests indicated.

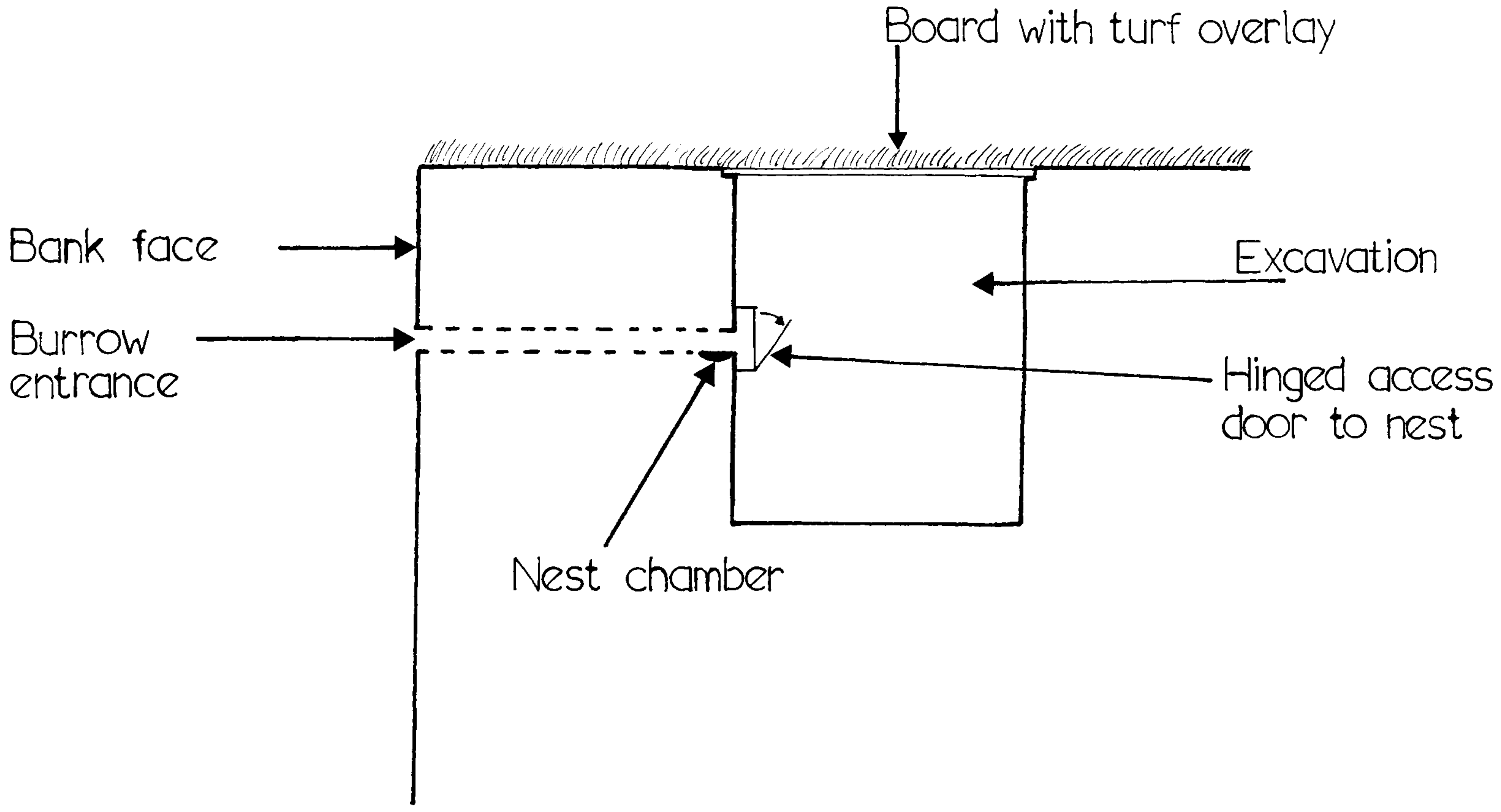


Figure 4.2.1. Diagrammatic representation of the method of access to the experimental broods.

The position and growth, but not necessarily the ultimate size of a colony can vary with the presence of burrows from the previous year. It is often the case that the previous year's burrows will have been obliterated, particularly at quarry sites, and the Sand Martins will then colonise a new face. If old burrows are in existence then they will often be ignored and a new colony will be started elsewhere as there is usually ample space and the nest-holes are invariably closely grouped; even so the new colony may be placed immediately adjacent to the old grouping. In other instances the old burrows may be used again by some birds with the remainder excavating new holes in the same general area. The colony in the present study formed initially from a nucleus of old burrows. The clumped distribution of burrows within large sand banks and the scarcity of single burrows indicates that coloniality in this species has not evolved as a response to shortage of suitable breeding sites. Compact grouping of nests in spacious banks has been reported as typical in other studies of this species (Stoner 1936, Petersen 1955, Hoogland and Sherman 1976). If colonies result only from nest site shortage then, to offset potential increased intraspecific sharing of other resources above that of single nesters, minimisation of nearest-neighbour breeding synchrony should be expected. However, Hoogland and Sherman (1976) found synchronization to be frequently in operation in large colonies, this being further evidence against habitat shortage.

METHODS

4.2 Food brought to the nest

Food brought to the nest could vary in a number of ways as a result of position in the colony and stage of the breeding season. The potentially most important variables were identified as:-

(a) the amount of food energy per unit total time delivered to the brood,

(b) the number of feeds contributing to the energy delivered,

(c) the size (dry weight) of the boluses brought to the nest,

(d) the average size (dry weight) of prey items within each bolus,

(e) the average number of prey items comprising a bolus,

(f) the number of different prey types and the proportionate contribution of each type to the diet.

Food was collected by using the choker method and was subsequently analysed as before (Chapter 3). The time intervals for food collection throughout each experimental day were again fixed at 90 minutes with six such periods each day (excepting 4th June where there were five). Collection was simultaneous for an edge nest and a centre nest. From previous observations of colony activity three stages of the breeding season were defined and food collection was carried out on two days at each stage (Table 4.2.1). The early and late season food was collected from one brood at each of the centre and edge locations, but two broods (one for each day) were used at each location in mid-season. All nestlings were between 12 and 14 days old.

Access to the nests was from a hole behind the bank face. A complete experimental nest chamber consisted of half a metal tin staked over the exposed natural chamber and with the lid acting as a hinged door (Figure 4.2.1) and insulated against draughts with foam-rubber. Although unlikely, possible feeding of nestling at one location, whilst

TABLE 4.2.1

Definition of the breeding season stages and statistics of the experimental broods

Breeding Season Stage	Food Collection Dates	Number of nestlings		Brood size (mass g.$^{0\cdot67}$	
		Centre	Edge	Centre	Edge
Early	4th June	5	5	18.41	18.19
Early first broods	5th June	5	5	19.19*	18.95*
Mid	2nd July	4	4	15.35	16.17
First broods and early second broods	6th July	4	4	16.96	16.71
Late	20th August	4	4	15.97	15.86
Late second broods	21st August	4	4	16.63*	16.53*

* To eliminate possible effects on weight from artificial feeding from the first day, these weights were determined by adding the expected daily weight increases from the standard growth curve.

collection of boluses and substitute feeding of nestlings was performed at the other was prevented by temporarily blocking the burrows.

Distance to the foraging site could not be measured since feeding adults were invariably out of sight of the colony. For this reason net sampling of aerial insects could not be carried out, and data from the insect suction traps were considered inappropriate for a study of a single colony of Sand Martins restricted to one locality, as opposed to a number over a wide area.

4.3 Attendance at the nest

Attendance of a pair of birds at the burrow may be expected to vary from causes additional to that of change in feeding frequency. These can be classified as disadvantages of coloniality and entail for example one or both of a pair allocating time to defend the nest site, nest-materials and the mate. It may be expected that vigilance at the nesting burrow will vary with positioning in the colony and with stage in the breeding season.

To test this, a comparison was made between the feeding visits to the nest and the total visits observed. The numbers of feeding visits in each 90 minutes were equal to the numbers of meals delivered to each brood in that time. Total visits to the nests were monitored during each 90 minute period by observing the birds entering the marked experimental burrows and not just perching at the entrance. The occupying adults were not colour marked and it was assumed that a bird actually entering the burrow was the tenant. This may have led to a slight under-estimation of total visits if the tenant merely perched at the burrow entrance. Since an edge burrow and centre burrow could not be observed simultaneously, they were observed alternately every ten minutes. This resulted in a 40 minute record of nest visits for each location which was then extrapolated to visits over the 90 minute period, assuming no major alteration of attendance rate.

4.4 The effect of predators

If coloniality in Sand Martins is maintained as a complete or partial response to decreased predation it may be supposed that the fitness of individuals will be elevated most at the sites of greatest nest concentration (as well as at the largest colonies). In terms of time allocation to the various nesting activities it may be expected that birds in the centre of the colony would be more effective at minimising the time devoted to deterring predators than those nesting at the periphery.

To test this hypothesis an artificial predator (stuffed Tawny Owl) was positioned at the colony on top of the bank mid-way between the marked nests containing young at both centre and edge locations. A mobbing response was elicited from all the birds immediately the predator was positioned and continued for five minutes until the predator was made to "disappear" by toppling it into a hole with a pull-cord. With the disappearance of the predator, the interval to when the first adult birds alighted at and entered the centre and edge burrows was timed. Following these timings the birds were given a 30 minute break before the predator was again positioned for another five minutes. All replicates were collected on the 23rd July 1976, with five at each of the morning, mid-day and evening periods.

4.5 Food brought to the nest and the allocation of time for feeding nestlings

The data here depend on a few sample nests and hence their interpretation depends critically on how far they are representative of other nests in that location or season. The calculated statistical significance levels should be evaluated in the light of this assumption.

The results of the food collection experiments clearly show differences in energy brought to a standard brood size between centre and edge nests and between seasons (Table 4.5.1, Figure 4.5.1). More food was brought to the centre nest early in the season whilst the reverse was apparent at mid-season. Both differences were significant but that for early season was far more pronounced (Table 4.5.2). No significant difference between the nest locations was noted for the late season.

There was a significant decline in the amount of energy received by centre colony broods at mid and late seasons compared to that received by early centre broods, but no significant difference between broods of the former two seasons was found (Figure 4.5.1a). The decline from the early season was a result of fewer meals being brought to the nest (Figure 4.5.1b, Table 4.5.4), and also a significant drop in the average bolus size (Figure 4.5.1a, Tables 4.5.1 and 4.5.3). This seasonal decrease in bolus size was also pronounced in the food brought to the peripheral colony nests (Figure 4.5.1c). However, only the amount of food delivered to late edge broods was significantly lower than both earlier seasons because of fewer and smaller meals, whilst mid-season food delivery was elevated above that for centre nests at this season due to larger boluses and more feeding visits (Figure 4.5.1b, c, Tables 4.5.1 and 4.5.3). With no significant difference in bolus size of early edge and centre colony birds, the greater amount of food delivered to centre broods was a [illegible] visits.

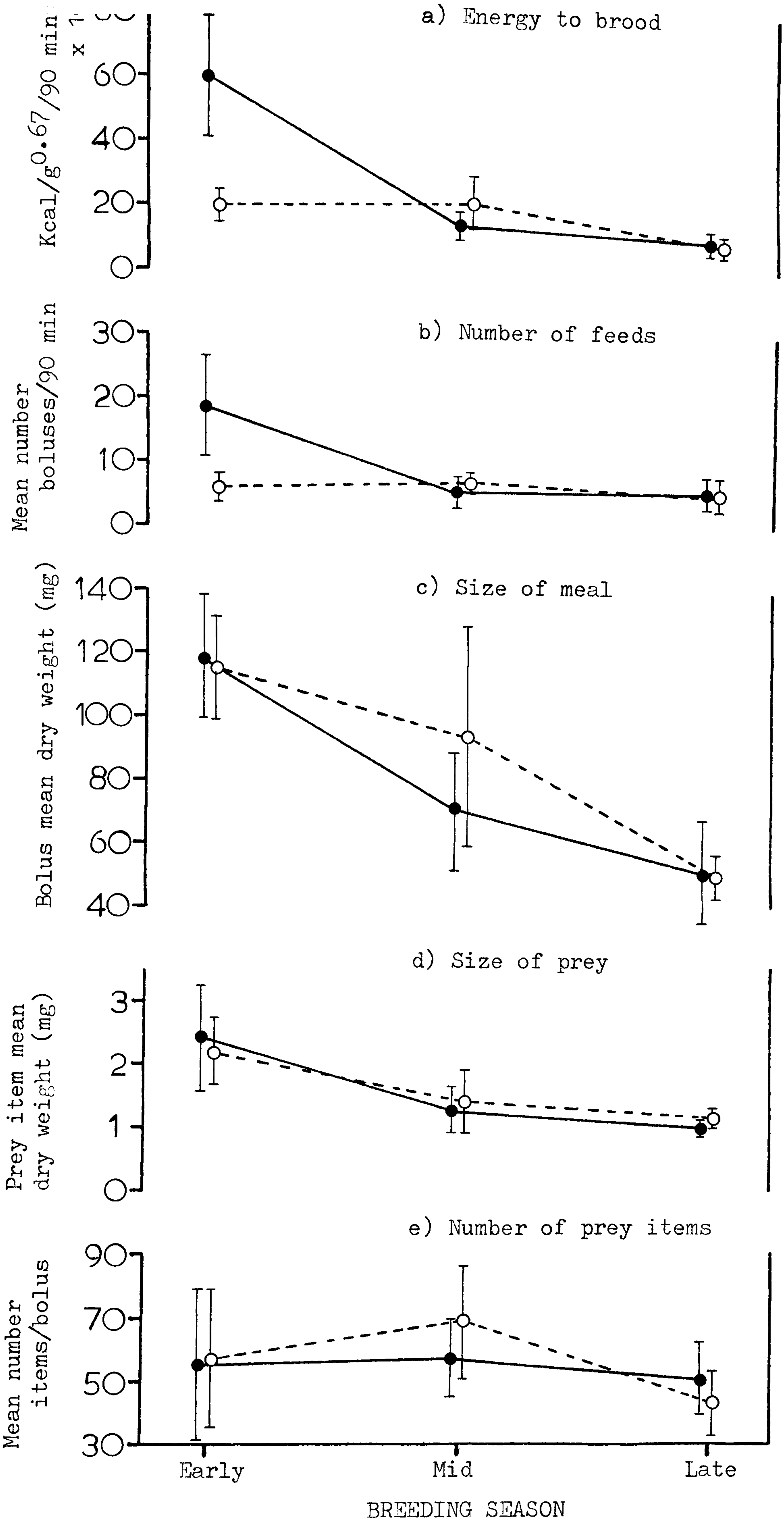


Figure 4.5.1. The components of variation in the amounts of energy delivered to Sand Martin broods at different stages of the breeding season. Solid circles = centre colony nests, open circles = edge colony nests, all ± 1 S.D.

TABLE 4.5.1

Analysis of food brought to the experimental Sand Martin broods (all means ± S.D.)

	Early		Mid		Late	
	Centre	Edge	Centre	Edge	Centre	Edge
$Kcals/g^{0.67}/90$ mins × 10^2	59.75 ± 19.64	18.77 ± 5.55	12.60 ± 5.54	21.78 ± 8.61	9.84 ± 3.37	8.49 ± 3.23
Bolus mean dry weight (mg)	118.20 ± 20.45	115.06 ± 16.67	70.23 ± 18.59	94.29 ± 34.97	51.26 ± 16.46	49.32 ± 7.61
Prey item mean dry weight (mg)	2.41 ± 0.83	2.18 ± 0.54	1.27 ± 0.37	1.41 ± 0.51	1.01 ± 0.11	1.16 ± 0.13
Mean number items per bolus	55.05 ± 23.83	57.09 ± 21.66	57.17 ± 12.11	68.45 ± 17.89	50.06 ± 10.18	42.98 ± 10.28

TABLE 4.5.2

Analysis of variance of energy per unit total time (K cals/$g^{0.67}$/90 mins × 10^2) delivered to the centre and edge broods at the three season stages

	Df	Sum of Squares	Mean Square	F	P
Total	69*	27230.43	394.64		
Blocks	11	1917.04	174.28		
Treatments	5	21671.94	4334.39	31.74	< 0.001
Season	2	9097.04	4548.52	33.31	< 0.001
Location	1	1768.14	1768.14	12.95	< 0.001
Season × Location	2	10806.76	5403.38	39.57	< 0.001
Error	53*	7236.56	136.54		

* n = 72 with two missing plots.

Means Test For all values > L.S.D. = 7.48, $P < 0.05$

Location:

	Centre/edge
Early	40.98
Mid	8.15
Late	0.05

Season:

	Early/Mid	Early/Late	Mid/Late
Centre	47.21	50.54	3.33
Edge	1.92	9.51	11.43

N.B. n = 66, Significances are unchanged by excluding missing plots replicate.

TABLE 4.5.3

Analysis of variance of bolus weights (mean/90 minutes) delivered to the centre and edge broods at the three season stages

	Df	Sum of Squares	Mean Square	F	P
Total	69*	89775.20	1301.09		
Blocks	11	8525.69	775.06		
Treatments	5	67174.93	13434.99	50.59	< 0.001
Season	2	38688.31	19344.16	72.84	< 0.001
Location	1	706.63	706.63	2.66	> 0.05
Season × Location	2	27779.99	13890.00	52.30	< 0.001
Error	53*	14074.58	265.56		

* n = 72 with two missing plots.

Means Test For values > L.S.D. = 13.3, P < 0.05

Location:

	Centre/Edge	
Early	3.14	L.S.D. = 13.9 (11 replicates)
Mid	24.06	
Late	1.94	

Season**

	Mid/Late
Centre	18.97
Edge	44.97

** Early season not compared with others due to unpaired replicates

TABLE 4.5.4

Attendance at the nest. Seasonal and locational variation in the number of feeding visits and total visits to Sand Martin nests

Season	Colony Location	Total visits/ 90 mins. Mean ± S.D.	Feeding visits/ 90 mins Mean ± S.D.	t	P
Early	Centre	21.5 ± 5.7	18.7 ± 7.8	0.97	> 0.1
	Edge	10.4 ± 3.2	6.0 ± 2.2	3.71	< 0.01
Mid	Centre	26.8 ± 11.9	5.5 ± 1.6	6.15	< 0.001
	Edge	12.8 ± 7.2	7.3 ± 1.2	2.62	< 0.05
Late	Centre	6.7 ± 1.7	5.9 ± 1.3	1.20	> 0.1
	Edge	5.4 ± 2.0	5.3 ± 1.9	0.24	> 0.1

TABLE 4.5.5

A centre/edge colony comparison of the time elapsed from when an artificial predator was removed from the colony to the first entrance to the burrow by a parent Sand Martin

		Mean time (decimal mins)	
Time of day B.S.T.	n	Centre	Edge
06.30 to 09.25	5	2.75	4.27
12.05 to 15.10	5	3.72	6.68
18.45 to 21.15	5	2.60	3.84
Total mean ± S.D.		3.02 ± 1.41	4.92 ± 1.85

The smaller boluses brought to nests at both locations in the mid and late seasons had a smaller mean weight of constituent prey items, and there were fewer items in each meal in the late season. The significantly larger boluses brought to mid-season edge broods resulted from a greater number of items, particularly as the mean prey item weight was lower (Figure 4.5.1, Table 4.5.1). The seasonal decline in mean size of prey items parallels the situation found with Swallows (Chapter 3).

The proportion of visits to the nest which were for feeding the young varied with nest site in the colony and with season (Table 4.5.4). In the early season there appeared to be no significant difference in the visits made to the centre nest, but the total visits to the edge nest were significantly greater than the number of feeding visits. Likewise at mid-season total visits to edge nests were greater, but the difference between total visits and feeding visits was far larger for centre nests at this time. At late season no significant difference between feeding and total visits was found for either colony location.

The results of the artificial predator experiment showed the edge nesting pair to be taking consistently longer to return to the burrow than the centre pair (Table 4.5.5, $t = 3.17$, $P < 0.01$). It has been shown that the mobbing response of this species is only elicited from intruders into the colony which are known predators (Hoogland and Sherman 1976) and therefore, since the stuffed owl was mobbed vigorously, it is probable that edge nesting birds would exhibit the same delayed return to the burrows with live predators. Of nine suspected or proven mammalian predators, and fourteen avian predators listed by Mead and Pepler (1975), successful predation on

Sand Martins was confirmed for Tawny Owls. In terms of releasing time for other important activities, such as feeding the brood, it follows that the centre nesting birds will be at a selective advantage. Hoogland and Sherman (1976) found that larger mobs of Sand Martins were more effective in deterring predators and postulated that the larger mobs formed by centre colony nesters resulted in a lower incidence of predation than would occur at the edge.

4.6 Within-colony differences in prey type selection

A comparative analysis of food types brought back to the separate nests showed variation with season and location (Table 4.6.1). There was a marked difference in the prey types contributing to the diets of the late season edge and centre nesters, and the proportion of types common to the two nest positions was low. By comparison, the proportions of prey types common to centre and edge sites earlier in the season were higher, and more of the same taxonomic groups made up the bulk of the diets, particularly at mid-season. This has the implication that either the food sources were more uniform in taxonomic representation earlier in the season, or that the centre and edge birds exploited the same concentrations to a greater extent.

TABLE 4.6.1

Within colony variation in insect prey types (> 2 percent of diet) fed to nestling Sand Martins at different stages of the breeding season

Season:	Early		Mid		Late	
Colony Location:	Centre	Edge	Centre	Edge	Centre	Edge
Prey type						
Ephemeroptera	21.77%	32.17%	39.96%	48.75%	3.55%	32.28%
Plecoptera		2.07				5.76
Aphididae	7.34	8.15	24.87	29.16	39.06	20.52
Psyllidae			3.33	2.15	7.78	
Chironomidae	13.66	9.32	7.81	6.52	11.16	16.99
Simuliidae			5.47	3.17		8.63
Anisopodidae	25.72	10.04			5.54	
Bibionidae	15.91	21.86				
Mycetophilidae						3.18
Brachycera			2.13			
Empididae	3.51					
Acalypterates					2.76	2.19
Chloropidae			2.05			
Opomyzidae			3.44		4.27	
Lonchopteridae					2.58	
TOTALS	87.91%	83.61%	89.56%	89.75%	76.70%	89.55%
n	10,580	3,435	3,866	5,913	3,543	2,750
Total number of prey types	35		29		42	
Proportion common to both locations; percent	62.9		69.0		35.7	

CHAPTER 5

A WIDER VIEW OF AERIAL FEEDING

5. A WIDER VIEW OF AERIAL FEEDING

The major part of this study has centred on the feeding ecology of three hirundines and one swift species in a maritime region of Europe during their breeding season, the north temperate summer. It would be of interest to relate these feeding behaviours to the situation in the Western Palearctic region where there are additional sympatric aerial feeding species, and to see if these patterns are maintained throughout the extensive Palearctic ranges. Of equal importance is an understanding of the significance of the wintering areas in terms of altered food quantity and quality and possible concurrent changes in the exploitation behaviours of these species. With many more indigenous species in the wintering areas, it may be the case that the Palearctic species alter their foraging strategies. Finally, what impact does the winter influx of migrants have on the native populations in Africa?

METHODS

5.1 Data collection in the winter quarters

All D. urbica and A. apus, together with the majority of Palearctic H. rustica and R. riparia, winter in the Ethiopian region, i.e. south of the Sahara (Moreau 1972). For seven weeks from the end of December 1975 to mid-February 1976 (i.e. the Palearctic mid-winter, southern hemisphere summer), data on the feeding ecology of these four species and several indigenous species were collected in Malawi at approximately latitude 14° South.

Observations of air-space utilization were carried out in the same "patch" format as for the Palearctic observations (Chapter 2), but with a few differences. Because it was the local wet season there was some variation in weather conditions and although the restricted number of observations did not allow comparison of their influence on feeding behaviours, wind and temperature variation at least was minimal. Rainfall was largely confined to later in the day and all observations were made before this occurred. The relative scarcity of some of the indigenous species accounts for some small samples and, since observations were necessarily opportunistic, the sample size varies somewhat between species. For two species, *Hirundo fuligula* and *Psalidoprocne pristoptera*, the observations did not include all patch types since they both apparently frequented habitats distant from areas of standing water. Most observations were made at 60-90m above sea level, but some were made at approximately 900m and altitudinal restrictions in distribution meant that the two above-mentioned species were only seen above this level.

Determination of actual food taken was only possible for *H. rustica* principally because it was the only species to habitually perch in large numbers on telephone wires. This habit allowed the collection of faeces from below the wires which was undertaken in several localities at several times throughout January and early February. No attempt was made to relate separate collections to preceding weather conditions because the reliability of the swallows to re-group at the same resting (not roosting) places was doubtful and because there were no notable changes in the weather pattern from day to day. No nests of native breeding species were found and no sampling of the available aerial insects was carried out.

Biometrical measurements of Hirundinidae and Apodidae

The importance of various morphological measurements in relating functional design to ecological segregation has already been demontrated (Chapter 2). To expand these hypotheses and to relate morphological differences to the specific foraging patterns evident in Malawi, detailed measurements of museum skins were performed. These data were used in conjunction with further useful measures from the literature to calculate the characters previously shown to predict most accurately the segregating mechanisms amongst these aerial feeding birds.

To avoid confusion, vernacular names are not used in this chapter and nomenclature follows Gruson (1976) and Voous (1977).

RESULTS

5.2 Some general considerations

Ecological isolation between the four Palearctic species during the breeding season has been shown to be maintained primarily by partitioning of air-space and the size and flight characteristics of the insect prey. The concomitant adaptations of the birds were shown to be flight speed, manoeuvrability based on the elongation of the outer tail-feathers, and bill shape. The relative importance of these characters can be assessed by comparison with more species comprising other aerial feeding communities.

The three main characters have been calculated for swifts and swallows of three zoogeographical areas and are presented together with bill size (Table 5.2.1 and Figure 5.2.1). It is apparent for at least two aerial feeding communities that an increase in flight speed is paralleled by a decrease in manoeuvrability and therefore faster flying predators would not be expected to have larger, more mobile prey items forming a major part of their diets. This premise rests on the experience of diet analysis and observations of the four

TABLE 5.2.1

Speed of flight, manoeuvrability, bill shape and bill length in Hirundinidae and Apodidae.[1]

Region (Breeding)	Flight Speed Vmr (m/s)	Manoeuvrability Index Outer tail/wt.	Functional Bill Shape	Bill Length (mm)
Western Palearctic				
Apus apus	9.66	1.84	2.06	7.16
A. pallidus			2.06	7.13
A. melba	11.55	0.83	2.13	9.95
Riparia riparia	8.29	4.06	2.21	6.80
Hirundo rustica[2]	8.61	4.91	2.34	8.61
H. daurica[3]	9.25[3]	4.22[3]	2.27	7.17
H. rupestris	9.01	2.27	2.28	8.47
Delichon urbica	9.13	3.12	2.07	7.24
Ethiopian				
Apus aequatorialis	11.80	0.97	3.20	10.00
A. barbatus	9.40	1.78		
A. affinis	9.34	1.77	2.38	6.10
A. caffer	8.29	3.42	2.62	6.27
Chaetura boehmi	9.04			
C. ussheri	9.52	0.97		
Cypsiurus parvus	7.29	8.57	2.36	4.50
Riparia paludicola	7.86	4.58	1.62	6.50
R. cincta	9.01	2.57	2.84	9.50
Hirundo aethiopica	7.79	5.80	1.63	7.88
H. angolensis	8.39	3.63	2.08	8.63
H. albigularis[4]	8.47	3.38	1.95	9.50
H. dimidiata	8.00	5.67		7.25
H. atrocaerulea	7.98	11.40[5]		7.25
H. smithii	7.98	6.37	1.85	7.35
H. nigrorufa	7.83			
H. senegalensis	9.72	2.92	2.65	10.70
H. semirufa	9.66	4.84		9.50
H. cucullata	9.30	3.97		8.50
H. abyssinica[6]	8.73	5.53	1.66	6.73
H. griseopyga	7.66	8.04	1.36	5.37
H. spilodera	8.96	2.75		8.75
H. fuligula			2.28	9.08

TABLE 5.2.1 (cont.)

Region (Breeding)	Flight Speed Vmr (m/s)	Manoeuvrability Index Outer tail/wt.	Functional Bill Shape	Bill Length (mm)
Ethiopian (cont.)				
Psalidoprocne pristoptera[7]	7.48	8.25		6.00
P. albiceps	7.82			
Nearctic				
Chaetura pelagica	8.98	1.60	2.64	5.33
Stelgidopterix ruficollis	8.49	3.26	1.61	6.80
Tachycineta bicolor	8.89	2.80	2.28	6.78
T. thalassina			2.22	5.28
Hirundo rustica[8]	8.71			
Progne subis	10.79	1.54	3.21	12.12
Petrochelidon pyrrhonota	9.14	2.45	2.23	7.80

1. For those species for which sufficient data were available to calculate the indexes.

2. Hirundo rustica rustica.

3. H. daurica rufula, calculated from mean of weights of smaller H. d. scullii (Eastern Palearctic) and larger H. d. emini (Southern Africa).

4. H. albigularis albigularis.

5. Based on tail length of males only.

6. H. abyssinica unitatis.

7. P. pristoptera orientalis: P. pristoptera holomelaena has V_{mr} = 7.88, M.I. = 7.16, F.B.S. = 1.40, BL = 5.85.

8. H. rustica erythrogaster.

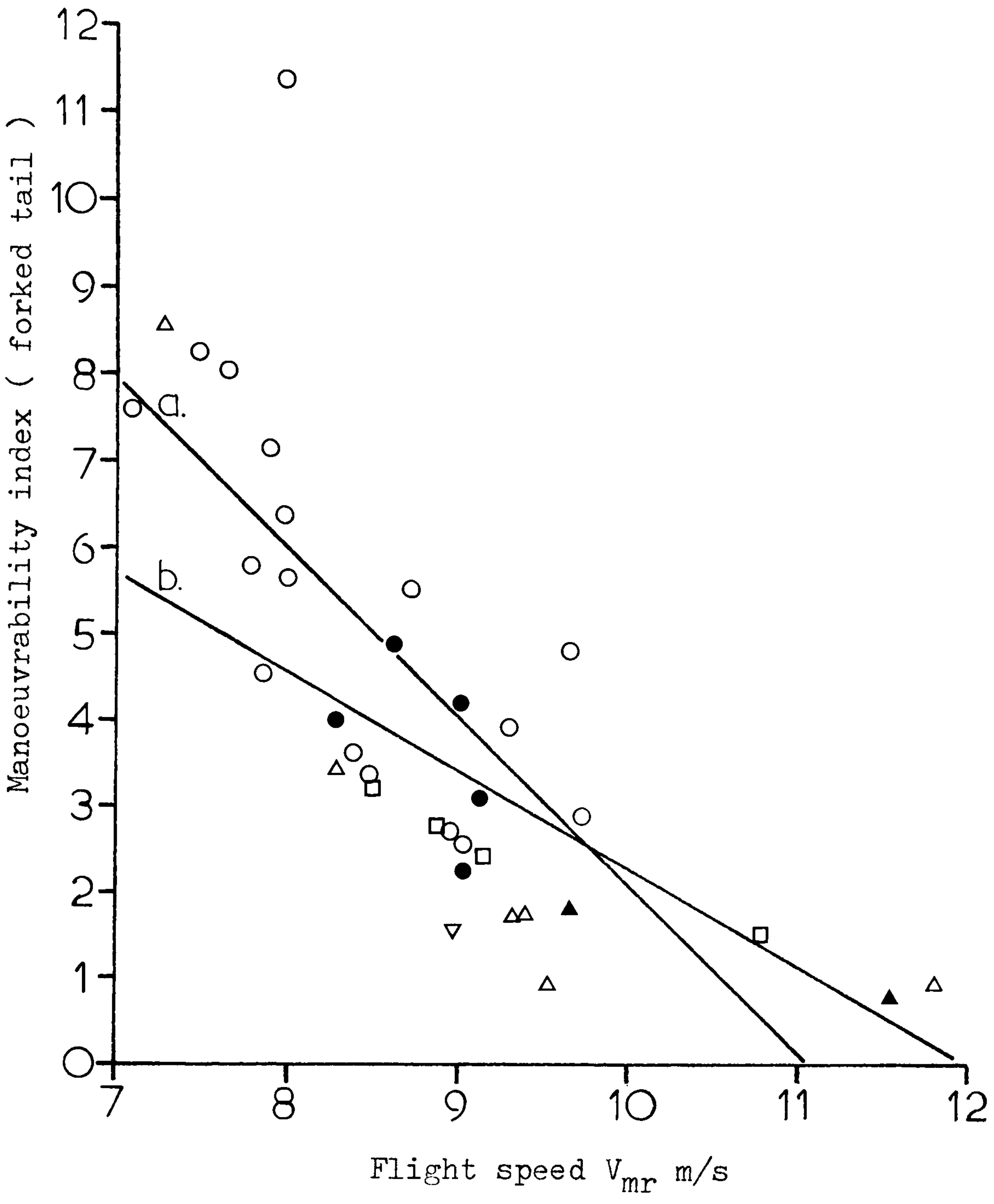


Figure 5.2.1. The relationship between speed of flight and ability to turn in swifts and swallows. ○ = Old World Hirundinidae, △ = Old World Apodidae, □ = Nearctic Hirundinidae, ▽ = Nearctic Apodidae. Infilled symbols refer to Western Palearctic species.

Line a = Ethiopian species, $y = 21.676 - 1.955x$, $r = -0.791$ $P<0.001$.

Line b = Western Palearctic species, $y = 13.486 - 1.117x$, $r = -0.811$, $P<0.02$.

aerial feeding species breeding in Britain, where the two faster-flying, less manoeuvrable species feed at higher levels and do not need to turn quickly for an aerial insect fauna comprised mainly of weakly-flying and passively transported taxa. No significance can be attached to the different slopes because not all the constituent members of each community are plotted. The addition of H. rustica erythrogaster in particular would raise the Nearctic community slope ($y = 7.92 - 0.60x$) and improve the correlation ($r = -0.714$, $P > 0.1$), but exclusion of the very high H. atrocaerulea does not significantly alter the Ethiopian community slope. Even with females included for this species it undoubtedly would still have a high manoeuvrability index. Apus affinis and A. caffer were not included in the Western Palearctic community because they are rare members of it, although they do fit near the slope.

There is the added complication of sub-speciation within the native aerial-feeding community of southern Africa (see Hall and Moreau 1972). H. albigularis for example is represented in Zambia by the smaller race albigularis and the larger ambigua, the former wintering and the latter breeding. Again with H. abyssinica, the larger race ampliformis breeds in Malawi and Zambia whilst the smaller unitatis is found further south. Noticeable differences such as these can alter the flight characters, as exemplified by the difference in the P. pristoptera races (Table 5.2.1), and may lead to shifts in the positions of species in the community, although the extent to which changes for one species dictate changes in others, if any, is not known. As far as this study is concerned, in cases where Ethopian sub-species occur there are in fact only sufficient data to calculate characters for one, and these are accepted as the species character. This is to avoid obscuring the broader relationship of

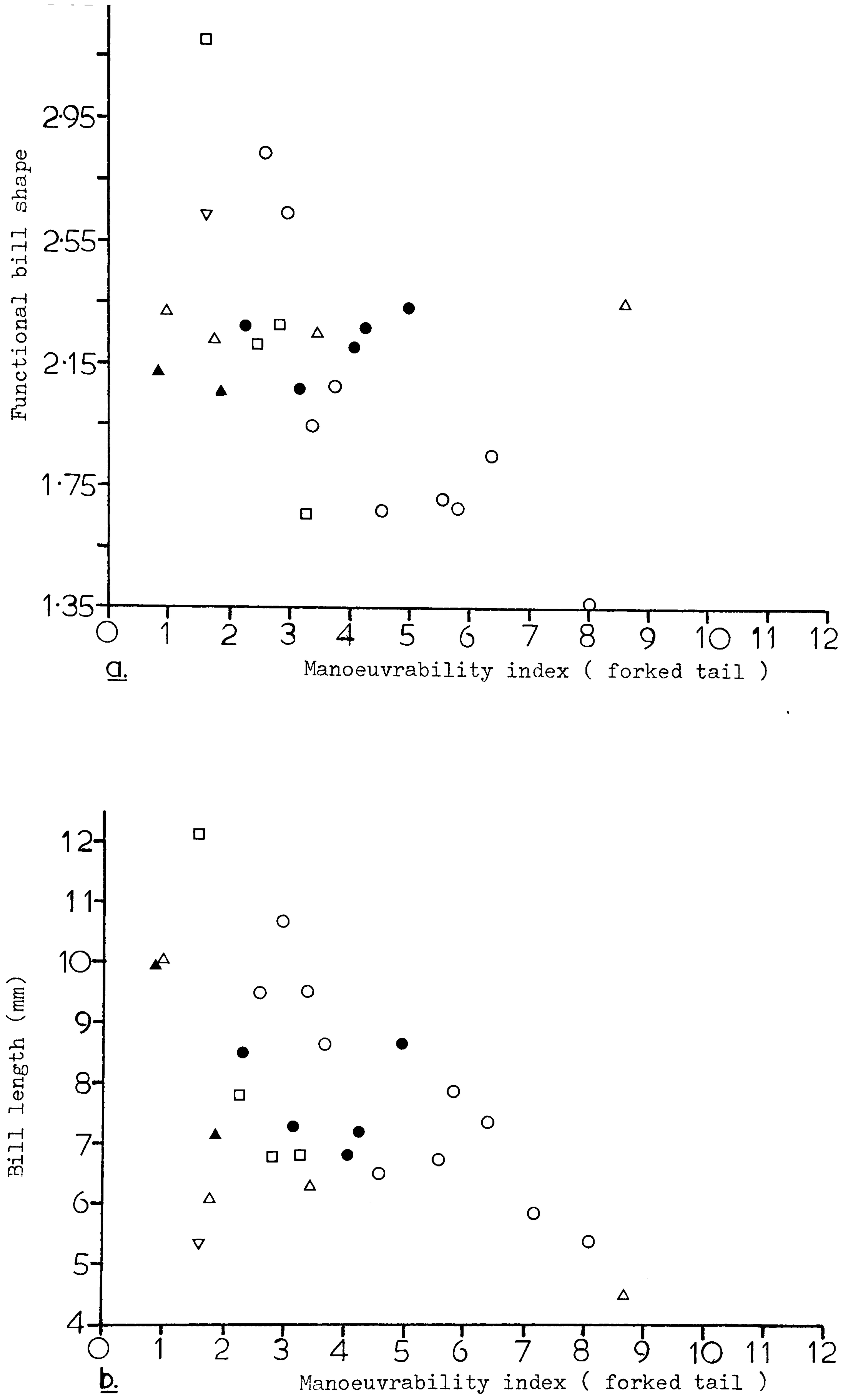


Figure 5.2.2. Bill shape and size in relation to manoeuvrability in swifts and swallows. Symbols as in figure 5.2.1. For bill shape, $r = -0.564$, $n = 25$, $P<0.01$.

the Palearctic species with the Ethiopian breeding community.

If increased manoeuvrability allows more mobile items to be captured, it may be expected that larger items would also be involved and a larger bill shape index would result. Again taking species from the three major regions into account this does not appear to be the case since manoeuvrability indexes are negatively correlated with functional bill shapes (Figure 5.2.2a). Within the scatter of points however the Palearctic pattern (infilled symbols) is largely preserved, but this is hardly satisfactory, particularly as bill length (Figure 5.2.2b) and width measures are equally confusing. There are likely to be significant differences between the aerial-insect faunas of the Ethiopian and the two temperate regions (although suction trap comparisons are lacking), but no differences between the two temperate regions are likely to be marked enough to cause such differences in bill shape, as various sampling investigations have shown (Glick 1939, Freeman 1945, Schoener and Janzen 1968, Johnson 1969). Selection for bill size and shape of course depends not just on what food is available but what part of this resource other members of the particular aerial feeding guild are utilizing. This embraces a large number of other families in the Ethopian region as well as diverse groups at lower latitudes in the Western Palearctic, notably Pratincoles (Glareolidae), and Bee-eaters (Meropidae). In the Nearctic region the large tyrranid flycatcher family may make up for the deficit of these other groups, but different selection pressures may arise from these different communities to account for the observed anomalies in bill shape sequences of hirundines and swifts of the separate regions. If selection is greatest on those characters associated with flight performance then any effect on bill shape adaptation may be relaxed, and therefore not obvious in such an analysis. Improved observations of particular air-space preferences, together with local sampling of aerial insects and detailed diet analysis, may reveal the relative importance of these characters. Further discussion will relate primarily to manoeuvrability and flight speeds.

5.3 The African situation

In the Ethiopian region 32 hirundine species are recorded as breeding and there are an additional five Palearctic breeders wintering, one of which (H. daurica) has a race breeding south of the Sahara. All five western Palearctic swifts winter in this region and three of these have more extensive breeding populations here, together with sixteen other native species (Gruson 1976). Madagascar accounts for two swifts and a swallow from these totals.

Of this collective total, a minimum of nineteen swallow and nine swift species breed in the southern part of Africa and most of these are represented in Zambia and Malawi. It is evident that the Palearctic species are coming to Africa to winter alongside many more potential competitors and the pertinent questions must be, (i) how do they achieve co-existence with these indigenous species and (ii) how do the African species themselves segregate? Moreau (1972) has estimated that each year totals of 90, 220 and 375 million D. urbica, H. rustica and R. riparia respectively migrate from $25 \times 10^6 km^2$ of the Palearctic to winter in no more than $20 \times 10^6 km^2$ of Africa: these totals are conservative and do not account for the vast numbers of A. apus. Not only do all these birds have to co-exist with the native species, they do so at the time when several in southern Africa are breeding (Figure 5.3.1; compiled from dates in McLachlan and Liversidge 1957, Mackworth-Praed and Grant 1963,

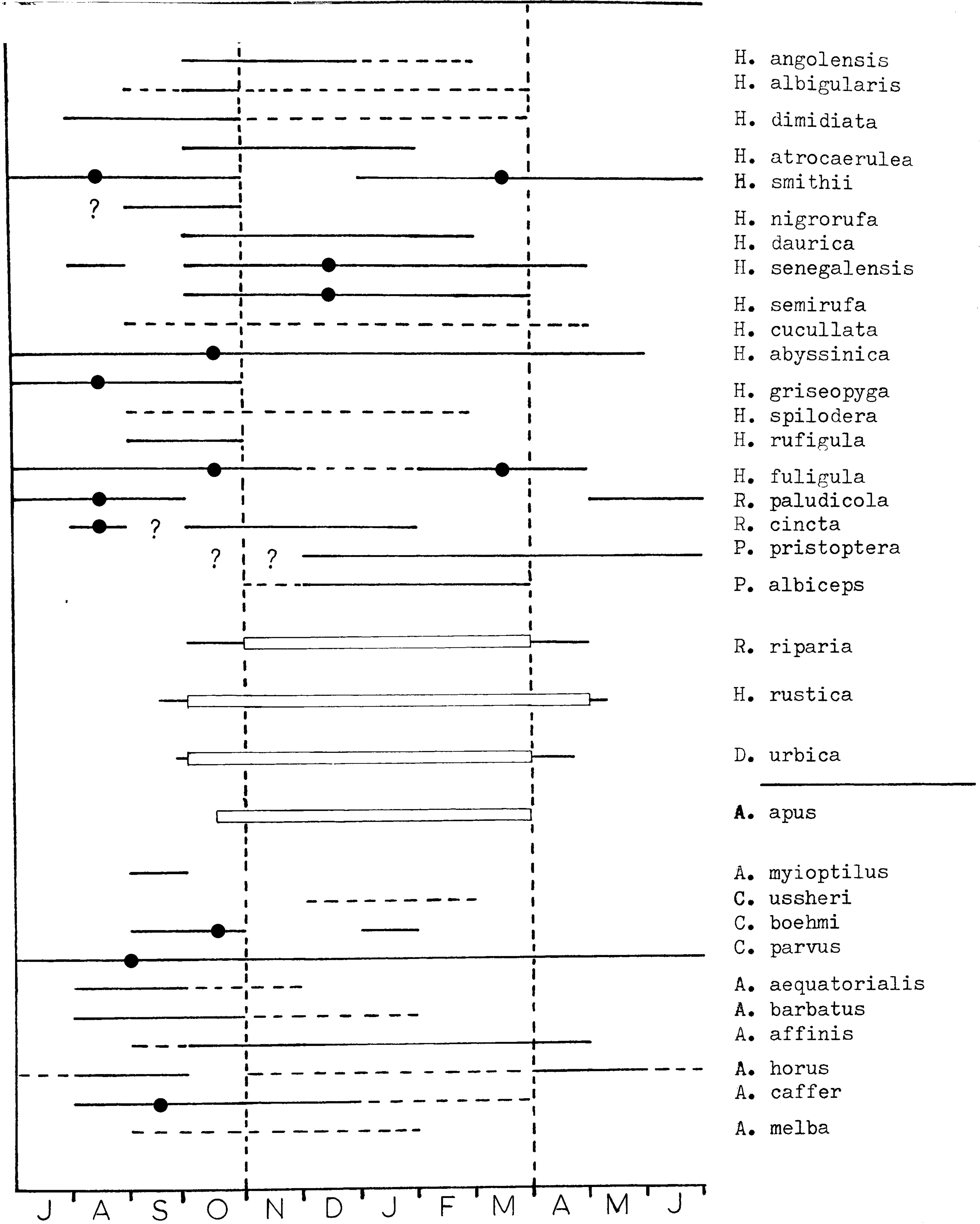


Figure 5.3.1. Months in which southern African Hirundinidae and Apodidae are recorded as breeding or probably breed. Solid lines refer to Malawi and Zambia, broken lines to elsewhere in southern Africa. Circles refer to apparent peaks in breeding cycles in Zambia. Blocks are months in which the Palearctic species are regularly recorded, with the ranges also shown. The vertical dashed lines denote the Palearctic species "winter".

Benson 1953, Benson et al 1971) and therefore increasing the demand on aerial insect food.

Spatial segregation

(a) The effects of altitude (above mean sea level)

In Britain and over most of the Palearctic breeding ranges differences in altitude are not so great as to materially affect the proportionate species composition of the aerial feeding community with respect to breeding density. At very high altitudes the major four species will have a lowered nesting density although *D. urbica* and *A. apus*, having greater foraging ranges, can nest higher in natural cliff sites, alongside *A. melba*, particularly in the south of their ranges, e.g. the Pyrenees. However, homogeneity of the habitat is preserved over much of the altitudinal range and the aerial insect faunal pattern parallels this uniformity apart from local fluctuations. Only *R. riparia* may be excluded from high rocky areas (but is still recorded as using available earth-banks, however small).

In tropical and sub-tropical Africa vegetation types across the range of altitudes in areas where Palearctic species are wintering show marked change compared to the uniformity over a similar range in the temperate region. Few comparative data on the African aerial insect fauna are available with respect to variation in density and quality throughout the air-column, between habitats, and therefore at different altitudes. In the Neo-tropical region sampling within vegetatively different habitats in the dry season has shown differences in insect density and diversity (Janzen and Schoener 1968), although the sampling procedure was not for aerial insects. Hespenheide (1975) demonstrated differences in quality of aerial insects between habitats and more particularly between wet and dry seasons, also in the Neotropical region. In East Africa the populations of aerial insects in a savannah habitat have been shown to peak just after the onset of rains, and to be at a low level in the dry season (Sinclair 1978); occasional rain-storms at the end of the long dry season were also shown to be accompanied by flushes of insects.

The main four Palearctic species have been recorded throughout the altitudinal range in southern Africa, but most winter at mid to low altitudes, particularly *R. riparia* which tends to be found in association with standing water. Hence, they may experience altitudinal differences in insect food and also come into feeding contact with most indigenous species, even though these may be confined to certain altitudinal ranges. In Malawi and Zambia *H. rustica* is commoner at lower altitudes (Benson 1953, Benson et al 1971) and any potential competitive effects on the breeding species should be more distinct here than at higher levels. Of the indigenous Hirundinidae there appears to be considerable altitudinal segregation and amongst the more closely related forms there is apparently much geographical interspecific replacement (Benson et al 1971). The Apodidae also exhibit altitudinal separation but these are fewer species, the segregation is less marked and, by nature of their greater foraging ranges, this will probably be further reduced. Of the species studies in Malawi only *H. fuligula* and *P. pristoptera* were restricted to high altitudes. The remaining eleven species were found at lower altitudes and were all recorded feeding in the same areas.

(b) Segregation by nest-sites

In the Palearctic region ecological isolation of the four major species by nest-site choice is largely inoperative (cf Lack 1971). Historically, nest-site preference may have been important in delimiting geographical range, but the reliance on man-made structures for nesting sites (including quarries by *R. riparia*) has ensured the breakdown of this isolating mechanism (since there are few places where modern man has not built). Of the other Western Palearctic species breeding in the south, most use natural sites (rock faces or cliff sites) and some segregation may result, although they will still come into contact with the other four species.

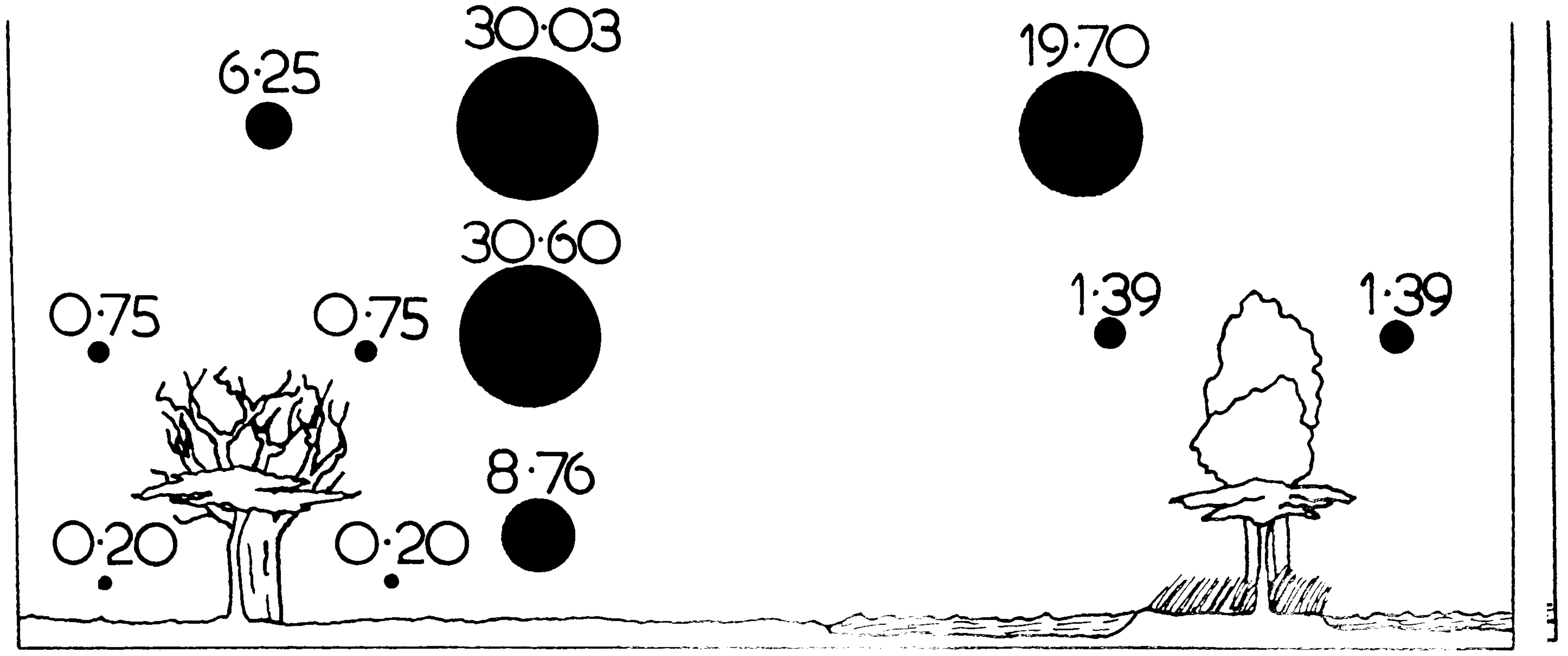
Nest site preferences of the hirundine species breeding in Zambia have been considered important in determining distribution and avoidance of competition (Benson et al 1971, R.J. Dowsett pers. comm.). Certainly throughout southern Africa as a whole man-made structures are few compared to the Palearctic region and, although several swift and swallow species are increasingly using these as nesting sites, the majority remain in natural situations. For some species, nest site preferences will not be independent of altitude, for example swifts using rock-faces which occur mainly in highland areas in Zambia and Malawi, and *Cypsiurus parvis* nesting in palms, both native and introduced species, confined to lower altitudes. Again the effect of restriction to a particular habitat because of nest site preference will be less important for swifts due to their greater foraging ranges and higher feeding stations.

Nesting site limitation will not operate during non-breeding when wandering and subsequent species mixing will take place. Furthermore, there are areas where diversity of potential nest sites over short distances will ensure that several species are found feeding in the same air-space. The effect of increasing use of artificial nest-sites on the inter-mixing and population densities of the native species are as yet undetermined. In the present study seven indigenous species found at lower altitudes were all feeding alongside each other, and some evidence of current breeding, e.g. song, nest-site prospecting, courtship flights, was apparent although no nests were found.

(c) Differences in feeding station

For the four Palearctic species observed at all altitudes the resulting air-space utilization patterns (Figure 5.3.2a, b) were similar to those displayed during the breeding season in Britain (refer to Figure 2.8.11a, b). Slight differences at individual levels were apparent, but the essential height segregation was maintained or indeed enhanced. Out of these four H. rustica again dominated the lowest patches with more noted over water, R. riparia concentrated in open areas mainly at mid-height and very few A. apus and no D. urbica were recorded low down. The lack of association with vegetation may in part be attributable to those fewer observations but probably reflects the absence of wind and low temperature effects in reducing insect density in the open areas and concentrating them near shelter-belts. The high-feeding A. apus and D. urbica confirm other observations of the habits of these two species in Africa, particularly with respect to the scarcity of sightings of the latter (summarised in Moreau 1972). Apparently D. urbica is as nomadic and high-feeding as A. apus and other swifts whilst wintering in Africa, and is confined much more to these upper levels than in the breeding area where attachment to nest sites will constrain this behaviour. The increase in high level feeding, both for the above

SWIFT



HOUSE MARTIN

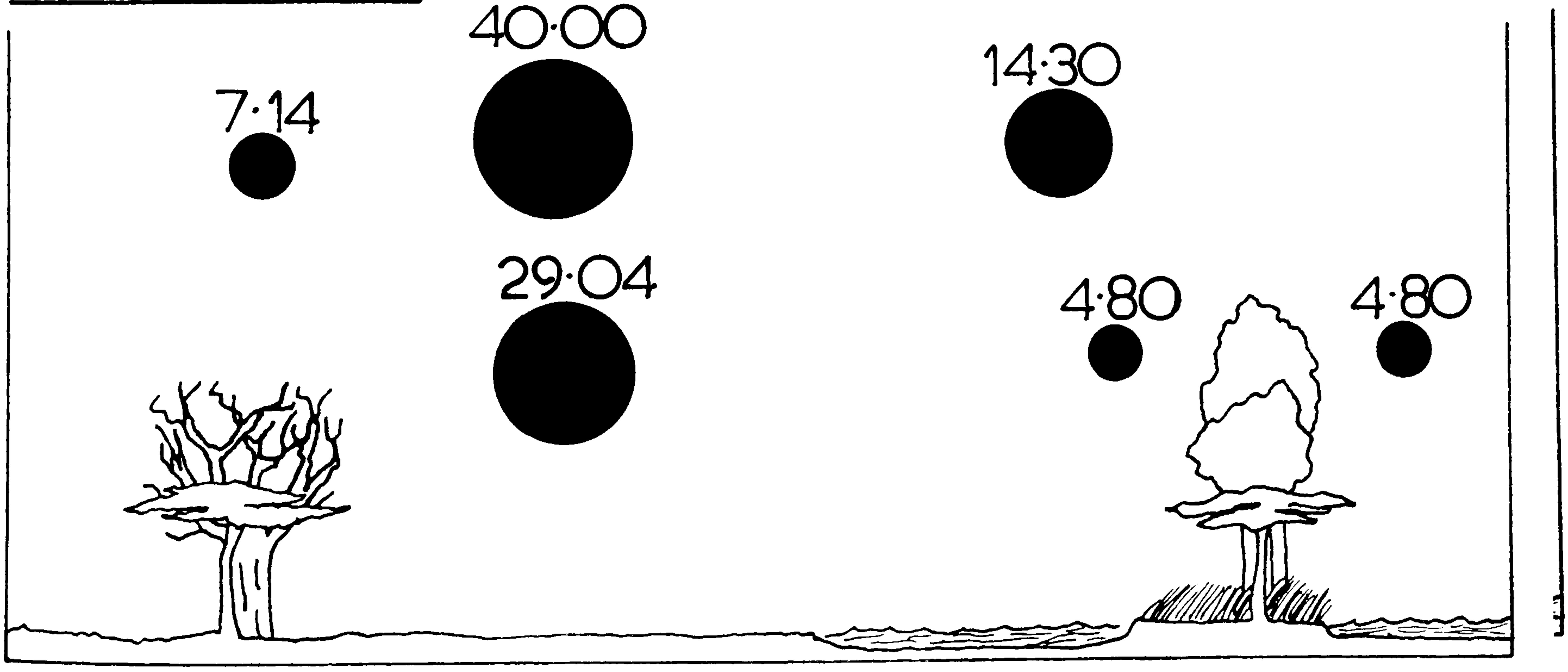


Figure 5.3.2.a. Feeding stations of the Palearctic species in all weather conditions combined during January and February 1976 in Malawi.

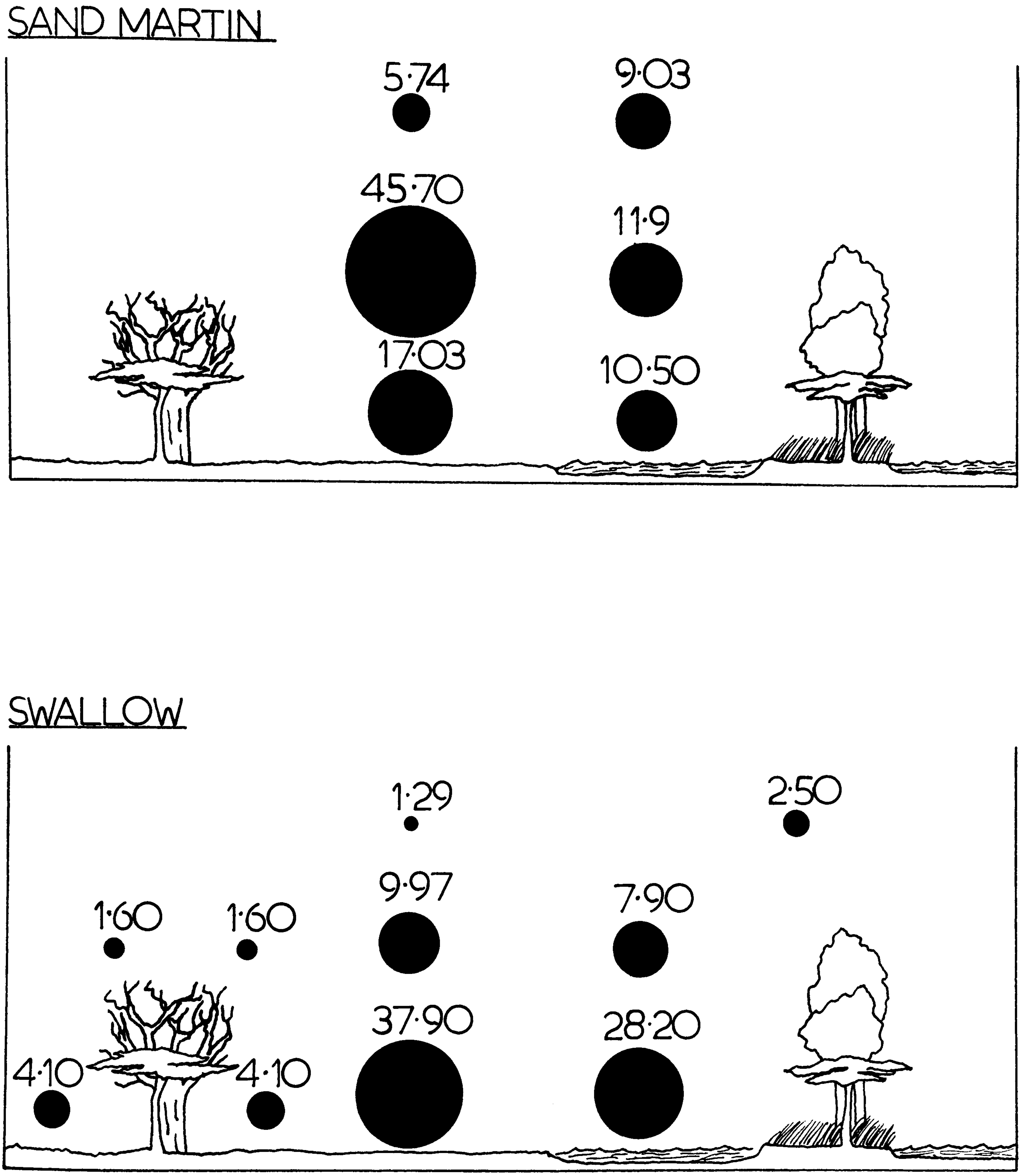

SAND MARTIN
5·74
9·03
45·70
11·9
17·03
10·50
SWALLOW
1·29
2·50
9·97
7·90
1·60
1·60
37·90
28·20
4·10
4·10

Figure 5.3.2.b.

Palearctic species and some native species, increases the chance of missing very high birds. This will affect calculation of overlap values which accordingly must be regarded as likely maxima. Including height observations of all species, the mid and low level mean heights remained little changed at 12.7m and 2.9m respectively (12.5m and 2.2m in the Palearctic), but the high level mean was increased to 76.2m (from 43.4m). Despite this difference, all four species were maintaining those foraging strategies adopted for co-existence within the breeding area and the impression of *D. urbica* as an energy-minimising, aerial plankton feeder (cf Griffiths 1975) is reinforced.

The air-space distributions of the seven native co-existing species (Figure 5.3.3a, b) showed them to be segregating in air-space utilization. Thus there were the two swifts, *A. caffer* and *C. parvus* feeding alongside *H. senegalensis*, although the former appeared to concentrate high over water and was not associated with vegetation as were the other two. Although some *Riparia paludicola* were feeding high, this species concentrated at a mid level over open ground and water, with more at lower levels than noted for *R. riparia*. Sharing the air-space over open water with *R. paludicola* were *H. smithii*, *H. griseopyga* and *H. abyssinica*, the former two being noted in literature as always associated with water. Two thirds of *H. smithii* were observed feeding in this situation, and a greater proportion of this small species occurred at low levels than for all other aerial feeders except *H. rustica*. *H. griseopyga* and *H. abyssinica* were apparently equally represented at mid and low levels but more observations for the latter species are needed. It is notable that five of the native species were feeding in association with vegetation, whilst this was infrequent for the Palearctic species. In summary, the native species where they occurred together were obviously adopting

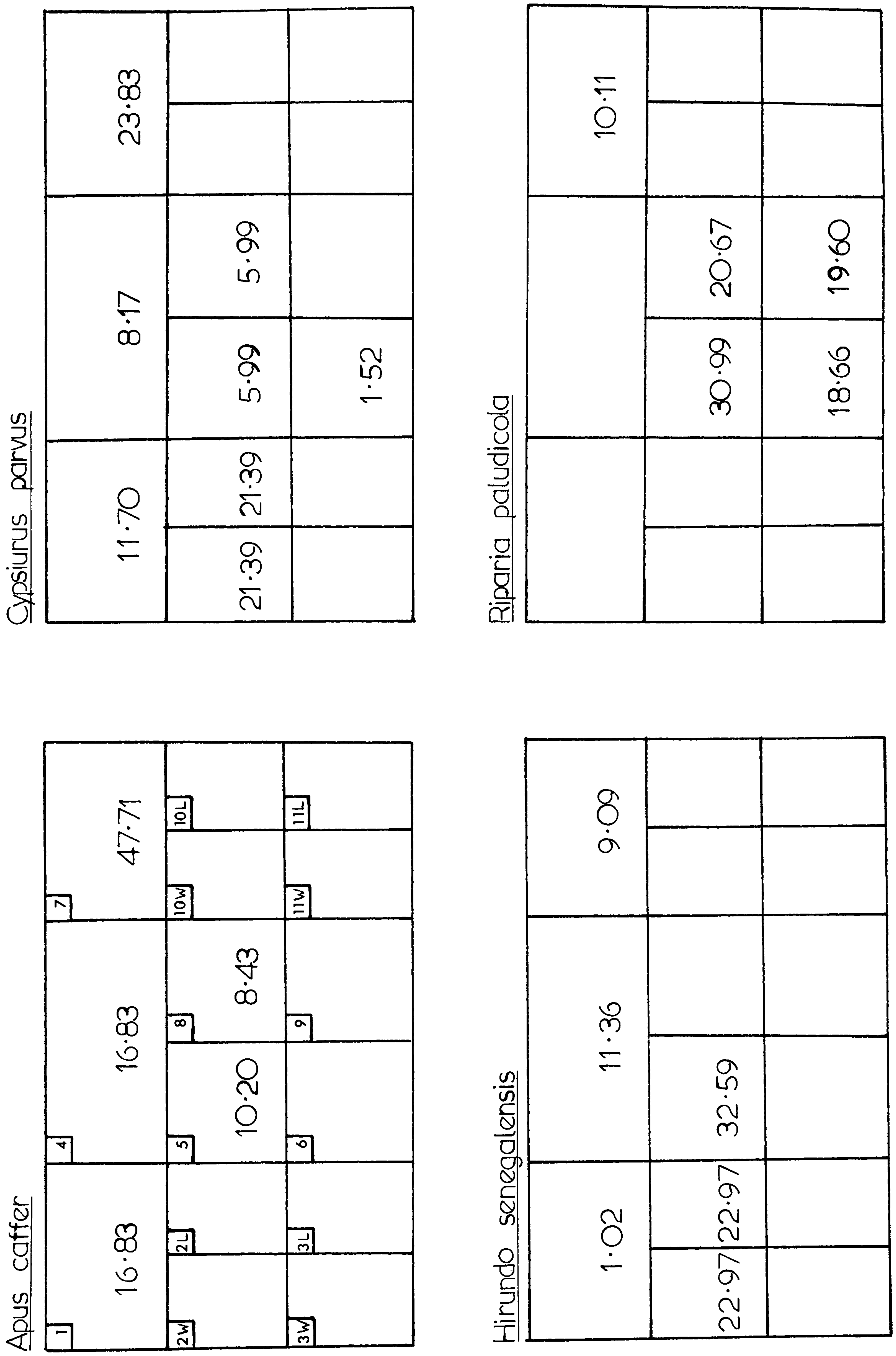


Figure 5.3.3.a. Feeding stations of native African aerial feeding species in all weather conditions combined in Malawi, January and February 1976. These species are not geographically isolated.

Hirundo griseopyga

<table>
<tr><td colspan="2"></td><td colspan="2"></td><td colspan="2"></td></tr>
<tr><td>3·13</td><td>3·13</td><td>25·00</td><td>18·75</td><td></td><td></td></tr>
<tr><td>6·25</td><td>6·25</td><td>18·75</td><td>18·75</td><td></td><td></td></tr>
</table>

Hirundo abyssinica

<table>
<tr><td colspan="2"></td><td colspan="2"></td><td colspan="2"></td></tr>
<tr><td></td><td></td><td>25·00</td><td>25·00</td><td></td><td></td></tr>
<tr><td></td><td></td><td></td><td>16·67</td><td>16·67</td><td>16·67</td></tr>
</table>

Hirundo smithii

<table>
<tr><td colspan="2"></td><td colspan="2"></td><td colspan="2"></td></tr>
<tr><td></td><td></td><td></td><td>38·33</td><td></td><td></td></tr>
<tr><td>14·58</td><td>14·58</td><td>4·17</td><td>28·33</td><td></td><td></td></tr>
</table>

Figure 5.3.3.b.

Psalidoprocne pristoptera

33·33	33·33				
16·67	16·67				

Hirundo fuligula

20·85	20·85				
29·15	29·15				

Figure 5.3.4. Feeding stations of two native African species that are geographically isolated (altitudinally) from the other species studied in Malawi. Observations were again in all conditions in January and February 1976

different feeding stations, and it is suggested these are mechanisms evolved to allow co-existence within the same areas. From the aspect of competition with the Palearctic species, A. apus and D. urbica will apparently come into contact with A. caffer, C. parvus, presumably other swifts, and H. senegalensis to some extent. R. riparia and R. paludicola have distinctly similar spatial distributions and the respective diets would repay investigation. H. rustica would appear to share more of its air-space with other species particularly over water, although it dominates the low open ground. Again, analysis of diets and feeding proximities to vegetation could be rewarding.

For the two hirundine species found at higher altitudes, the few observations indicate a preference for feeding close by vegetation and quite low. These results accord well with published information on the habits of P. pristoptera, but fewer details are available for H. fuligula (Figure 5.3.4).

In addition to patch categorisation of the air-space, the actual mean feeding heights of the species were examined (Table 5.3.1, Figure 5.3.5). At a high level A. caffer was apparently the highest feeding species, although this may in part be because it was breeding in the area and therefore with fewer non-visible birds than nomadic A. apus and D. urbica. C. parvus and H. senegalensis were considerably higher than R. riparia and R. paludicola, which themselves ranged higher than the other species, between which less obvious differences were noted. It is evident that the mean heights of H. fuligula and P. pristoptera would not fit into a height sequence if they too were co-existing in the same area. A notable difference in the height distributions of the Palearctic species was that A. apus and D. urbica

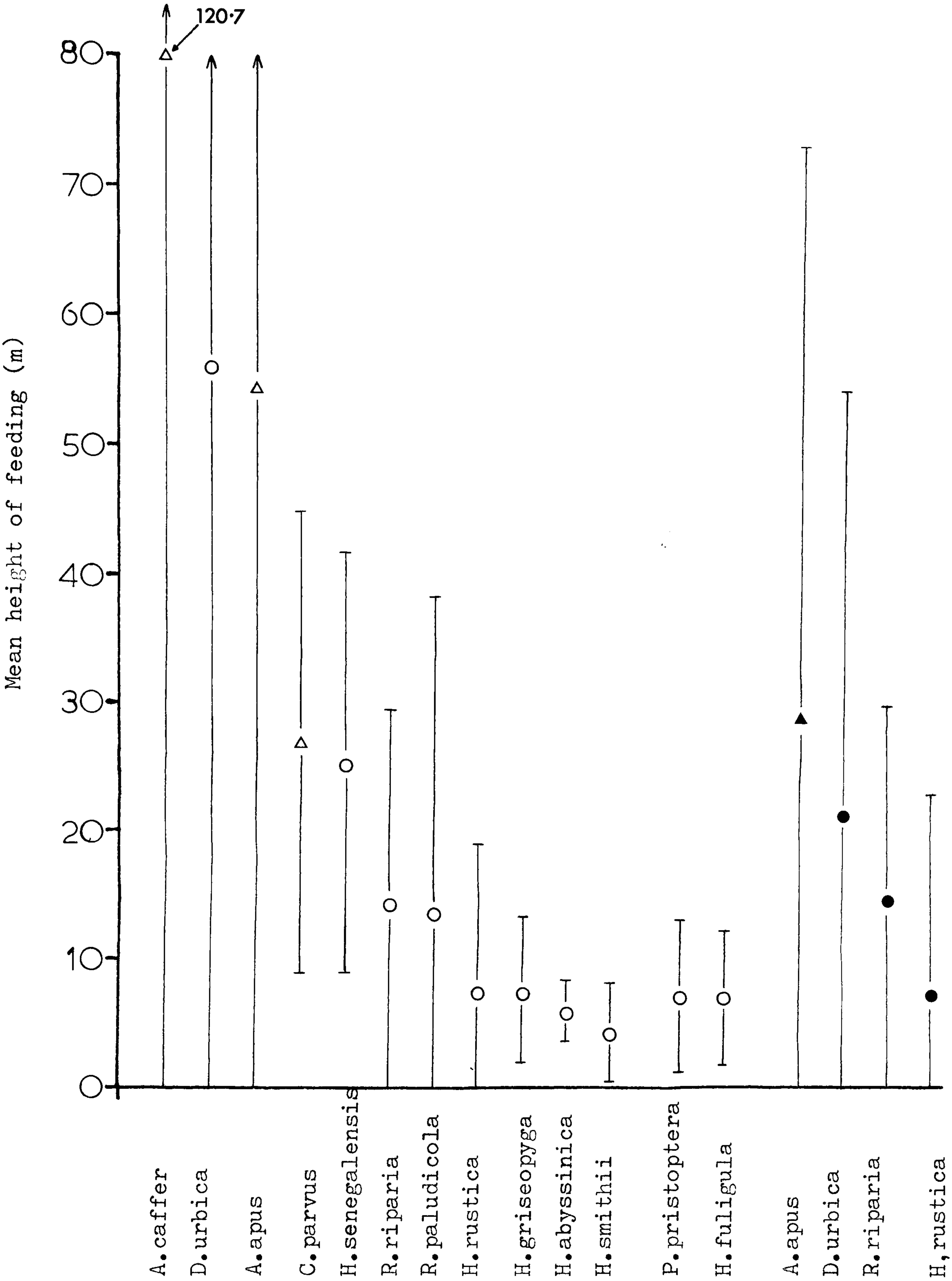


Figure 5.3.5. Comparison of mean heights above ground level (± 1 S.D.) of Hirundinidae and Apodidae feeding in southern Africa (open symbols) and Britain (solid symbols).

TABLE 5.3.1

Mean heights of feeding and air-space niche breadths of Hirundinidae and Apodidae in Africa

	Height (m)	S.D.	Number of observations	Niche breadth B
Apus apus	54.7	75.9	46	4.261
A. caffer	120.7	139.1	11	3.314
Cypsiurus parvus	27.0	18.0	13	5.680
Riparia riparia	14.5	15.1	31	3.537
R. paludicola	13.8	24.8	37	4.500
Hirundo rustica	7.6	11.3	95	3.994
H. senegalensis	25.4	16.4	24	4.292
H. smithii	4.4	3.9	13	3.684
H. abyssinica	5.9	2.0	5	4.799
H. griseopyga	7.6	5.7	19	5.626
H. fuligula	7.1	5.3	8	3.893
Delichon urbica	56.2	104.8	11	3.645
Psalidoprocne pristoptera	7.2	6.1	5	3.601

both ranged much higher, but R. riparia and H. rustica remained virtually unchanged.

Since the ability to turn has been shown to diminish with increase in flight speed, and that A. apus and D. urbica fly faster and higher, it may be expected that an inverse relationship should exist between mean height of feeding and manoeuvrability. This indeed was apparent for the aerial-feeders in Malawi, although the Apodidae were too few for a separate analysis (Figure 5.3.6). A significant inverse relationship was maintained with inclusion of the Apodidae ($\mathrm{Log}_{10}y = 1.8497 - 0.1211x$, $r = 0.600$, $P < 0.05$), but untransformed values suggested separate curves for the two families. For swallows at least, it is suggested that increased manoeuvrability is an advantage at lower levels, and the best strategy for poor manoeuvrability is to feed high.

It is evident that the air-space niche breadth values (Table 5.3.1) were all low compared to those determined for the Palearctic species in Britain (Table 2.8.17). These Palearctic species feeding in Africa appear to spread over fewer patches, and the native species similarly show this further concentration into particular sectors of the air-space. Niche breadth scores may be slightly increased for some species with more observations. Since broadening of air-space niche breadths have been shown to accompany lowered insect densities in association with poor weather conditions, it may be inferred from the narrow niche breadths in Malawi that aerial insect availability is high, at least during the wet season.

In relating niche breadths to overlap between species pairs (Table 5.3.2) it was apparent that the values for Palearctic hirundines

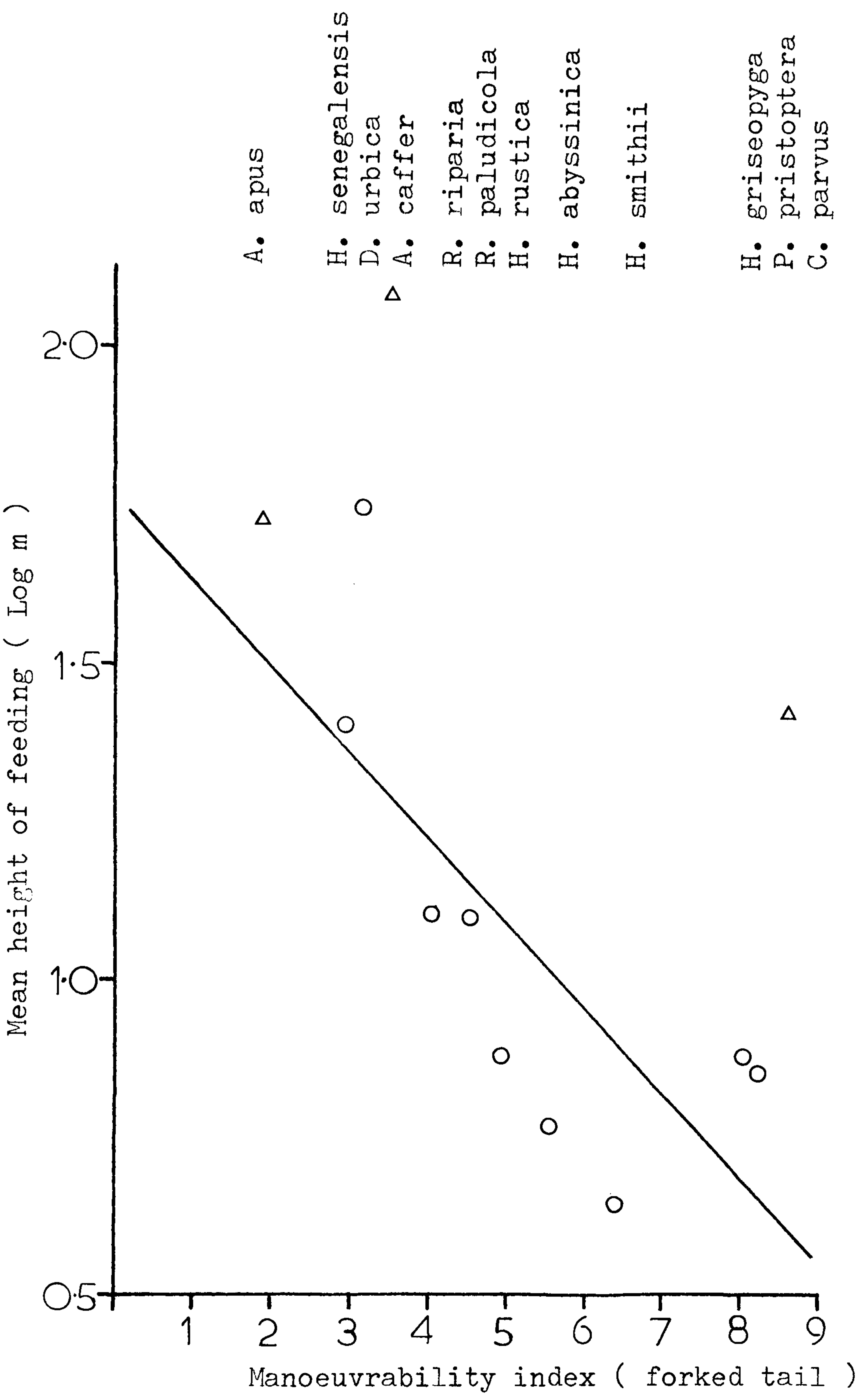


Figure 5.3.6. Mean height of feeding in relation to turning ability for Hirundinidae (Log y = 1.7694 - 0.1348x, r = -0.748, P<0.02) and Apodidae in southern Africa.

TABLE 5.3.2

Aerial feeders in Malawi: pairwise overlaps in air-space

	SWA	SM	HM	SW1	PS	WRS	MS	ERS	GRS	LSS	WTS	ASM	RM
H.r. SWA		0.47	0.29	0.30	0.14	0.11	0.18	0.09	0.80	0.40	0.53	0.75	0.12
R.r. SM			0.62	0.74	0.28	0.38	0.65	0.00	0.83	0.67	0.30	0.91	0.00
D.u. HM				0.95	0.41	0.62	0.61	0.00	0.32	0.30	0.00	0.42	0.00
A.a SW1					0.50	0.69	0.67	0.02	0.45	0.35	0.02	0.57	0.02
C.p. PS						0.66	0.73		0.24	0.11	0.11	0.29	
A.c WRS							0.36		0.17	0.18	0.23	0.37	
H.se MS									0.47	0.37	0.00	0.48	
P.p. ERS													0.88
H.g. GRS										0.73	0.67	0.94	
H.a. LSS											0.60	0.75	
H.sm.WTS												0.58	
R.p. ASM													
	Hirundo rustica	Riparia riparia	Delichon urbica	Apus apus	Cypsiurus parvus	A. caffer	H. senegalensis	Psalidoprocne pristoptera	H. griseopyga	H. abyssinica	H. smithii	R. paludicola	H. fuligula

were considerably less than those experienced in the breeding season (see Table 2.8.23), particularly between *R. riparia* and *D. urbica*. In contrast the overlaps between these species and *A. apus* showed increases, not unexpected for *D. urbica* but rather a function of avoidance of areas near vegetation for the other two, and spuriously increased given the height increase of *A. apus*. Overlaps between the Palearctic and native species were more varied and all low for *H. rustica* apart from with *H. griseopyga*, *R. paludicola* and *H. smithii*, the former two interestingly enough not breeding within the "winter" of *H. rustica*. High overlaps with these non-breeders were more accentuated for *R. riparia*, although high values were also recorded for *H. senegalensis* and *H. abyssinica*. As expected, *D. urbica* and *A. apus* overlapped more with the swifts and *H. senegalensis*. For the native species the highest overlap again was between the non-breeding *H. griseopyga* and *R. paludicola*, and these two showed notably high overlaps with *H. abyssinica* and *H. smithii*. High overlap occurred between *C. parvus* and *H. senegalensis*. Finally, the two high altitude species themselves overlapped considerably but showed little or no overlap with the four Palearctics.

The important points to emerge from this overlap matrix are that low values predominate, but where they are high, particularly with regard to the Palearctic/Ethiopian associations, the native species apparently do not have their main breeding season coincidental with the presence of Palearctic species. This suggests that the aerial insect supply may be inadequate for sustaining the wintering migrant populations whilst allowing all the indigenous species to breed at the same time.

(d) Temporal segregation

No daily peaks in feeding activity were noted although diurnal variation was not studied specifically. H. rustica was observed to spend much time resting and preening on telegraph wires.

5.4 The food of the Swallow, *Hirundo rustica* in Africa

Taxonomic components of the prey

There have been various anecdotal references to the types of food taken by the Swallow in its wintering quarters (e.g. Broekhuysen 1952, Brooke 1956), but no systematic sampling of the diet has been carried out.

Of those taxonomic groups identified in this study (14.8% were unidentifiable) almost 50% were Hymenoptera (Table 5.4.1), with a minimum composition of 19.4% flying ants. Coleoptera were the next most important group and the remaining 14.7% were accounted for by four further orders. Compared to the 82.4% contribution of Diptera to the diet in the Palearctic (Table 2.8.14) the 7.6% taken in Africa represents a drastic reduction and reflects the increased preference and/or increased availability of Hymenoptera and Coleoptera. These prey proportions taken in Africa are very similar to the composition of the diets of the swifts and swallow studied by Hespenheide (1975) in Central America where he found Hymenoptera predominating (59-81%), fewer Coleoptera (18.5%), and very few Diptera (3.4%). These proportions were in contrast to the relative abundances of available taxa where Diptera were commonest (52-75%) followed by Hymenoptera (15%) and Coleoptera (10%). Hespenheides explanations for the discrepancy were avoidance of more mobile, energy expensive Diptera and selective feeding on local aggregations of swarming Hymenoptera.

TABLE 5.4.1

Frequency occurrence of different prey taxa in the diet of *H. rustica* in Africa

Trichoptera	0.50		
Orthoptera	0.33		
Isoptera	0.17		
Heteroptera	1.96		
Homoptera	2.35		
Aphidoidea	1.76		
Diptera*	3.72		
Schizophora	1.57		
Nematocera	0.98	Total Diptera	7.64
Culicidae	1.37		
Hymenoptera*	20.35		
Symphyta	0.59		
Ichneumonoidea	2.15		
Chalcidoidea	1.57	Total Hymenoptera	48.34
Proctotrupoidea	0.48		
Sphecoidea	3.33		
Formicoidea	19.37		
Coleoptera*	30.14		
Curculionidae	6.65	Total Coleoptera	36.79

* Unspecified taxa

In Africa there has been much mention of the abundance of swarming ants and termites. Certainly for the latter group, Sinclair (1978) showed them to be the most abundant in light trap catches during the wet seasons.

Moreau (1939) recorded *H. smithii* as bringing termites to the nest during heavy rain when other insects were less available, and limited faeces analysis showed Hymenoptera, including Formicoidea, to predominate in the diet of nestling *P. pristoptera holomelaena* (Moreau 1940) together with some Coleoptera. *A. caffer* apparently brings predominantly Hymenoptera to the nest, including ants and parasitic groups, with fewer Coleoptera, Hemiptera and a small termite species (Moreau 1942). All prey items identified in the faeces of this species were minute as may have been predicted from its air-space distribution. It appears therefore that the increase of Hymenoptera in the diet of *H. rustica* may just reflect increased availability and not avoidance of more mobile Diptera.

The mean mobility of prey taken is certainly reduced from the value found in the Palearctic, and presumably is a function of increased selection for the slower Hymenoptera and Coleoptera (Table 5.4.2). In addition the niche breadth (B) along this dimension is

TABLE 5.4.2

A comparison of the size and mobility of prey taken by *H. rustica* in the Palearctic and Ethiopian regions

	Britain			Malawi		
	Mean	S.D.	B	Mean	S.D.	B
Size $\text{Log}_{10}\text{mm}^2$	1.764	0.335		1.795*	0.337*	
Mobility Vmr Log m/s	0.648		2.998	0.588		1.965

* Normally distributed: skewness = 0.19, kurtosis = -0.86

$P < 0.01$ for both, n = 600

reduced from that in the Palearctic. Selection of larger Hymenoptera may be the primary cause of the observed increase in mean prey size in Africa from that in the Palearctic. There was no change in the magnitude of the prey size niche breadth ($F = 1.01$, $P < 0.001$) although this may have been expected to expand in a wet season with an assumed increase in food availability. Given the number of species utilizing the limited food size spectrum, the maintainance of a niche breadth comparable in size to that sustained in the Palearctic implies considerably increased overlaps along this axis and probably compensation by segregation in other dimensions. This is supported by the observed increases in air-space separation.

CHAPTER 6

DISCUSSION

6. DISCUSSION

6.1 Predation strategies and ecological isolation in aerial feeding birds during the Palearctic breeding season

It is apparent from the results in Chapter 2 that ecological isolation is maintained within the aerial feeding bird guild at the time of breeding in temperate latitudes. The evidence suggests that segregation is effected principally by partitioning the air-space and by specialization on certain characteristics of the insect food, primarily the size and mobility of prey. These aspects of ecological isolation may be dealt with separately.

Components of prey preference and associated feeding adaptations

(a) The effect of prey size

A complication in assessing the effect of size upon preference for certain prey types is that all four predators take an average size greater than that available to them. This parallels the findings of other comparative studies (Gibb and Betts 1963, Root 1967, Hespenheide 1971, 1975) and means that, since the birds are selecting within the long-tail of the available distribution (for all three levels, Figure 2.8.1b), one insect type will not be much more or less abundant than another relative to changes throughout the complete distribution. It is likely however that the Swift and House Martin, by taking smaller average prey sizes, will be subject to greater proportional changes in different types than either the Sand Martin or the Swallow. Bryant (1973) demonstrated that for the House Martin prey size accounted for 66% of the selection of different prey types from those insects flying. The present data for the other three aerial feeders does not stand up to such rigorous examination because certain assumptions concerning change in feeding station (the House

Martin is the most generalized in feeding station) and the flight behaviour of local populations cannot be made. It is the contention of this study that prey size plays an important role in the selection of prey types by all four aerial feeding birds. If an available insect prey type is within the profitable (higher net energy gains) size range available to a particular predator, given its morphological adaptations, then the proportion of this prey type in the diet may reflect selection by size. For example, at one end of the scale the Swallow selects Tipulids when their availability compared to other groups is low (even though this taxon does increase in abundance nearer the ground), whilst at the other extreme the Swift incorporates high proportions of Aphids and Psyllids into its diet in contrast to their availability (again though proportionately they increase higher up).

The relative scarcity of larger insects available (Gibb and Betts 1963, Root 1967, Schoener and Janzen 1968, this study) may have some bearing on the distributions of prey sizes selected by the predators. Hespenheide (1971) has indicated the generality of log-normality of prey distributions, and an explanation advanced is that by constant sampling of a spectrum of food sizes adaptation by a predator to rapid short-term fluctuations in food availability could be enhanced. Krebs et al (1977) using Great Tits Parus major in laboratory experiments demonstrated that the change from no selection, i.e. the intake of items as they are encountered regardless of profitability (energy gain in their experiments), to selection of profitable (larger) items was not a one-step process but a gradual incorporation of these more profitable items into the diet. These results were interpreted as sampling by the birds investing time, and hence energy, in estimating encounter rates and profitabilities of different prey types. In the present study, if the birds were sampling in a similar fashion, together with the comparatively large excess of smaller items available, then the observed slightly positive skews of their prey size distributions may not be unexpected.

Skewed distributions could also result if increases in niche breadth were expansions towards the smaller end of the prey size axis. It was demonstrated for the Swallow and Sand Martin that prey size niche breadths expanded on good days with an increase in insect abundance. Expansion towards the smaller size classes could occur if the density of larger items was relatively stable under a wide range of environmental conditions and comparatively large increases in the abundance of smaller types occurred on good days.

In relating prey size to predator body size the differences found between the aerial feeding community in the present study and that in North America (Hespenheide 1971) may not be surprising considering the different species involved. An exhaustive comparison would necessarily include the southern European species, and the different positioning of the European H. rustica rustica and the smaller H. r. erythrogaster within the predator size sequence may be of importance. Other co-existing species differing mainly in body size have displayed differences related to differences in prey size distribution, for example in hawks (Storer 1966) and terns (Ashmole and Ashmole 1967, but see Ashmole 1968). Similarly, Schoener (1968) found the increase in log prey weight with increase in log predator weight of a wide taxonomic variety of raptorial birds to be highly significant.

Several studies have correlated prey size differences with differences in dimensions of feeding apparatus when body size was not similarly related. Pianka (1969) for instance showed that head length of Ctenotus lizards in Western Australia was positively correlated with prey size. Hutchinson's (1959) analysis of ratios of trophic appendages was subsequently extended by others to provide a useful insight into the broad relationships between groups of birds with different feeding ecology and of different areas (Klopfer and MacArthur 1961, Schoener 1965). The importance of other dimensions besides length was emphasised by Ashmole (1968) where he demonstrated how the cross-sectional area of the bill relative to its length (and hence strength) in tropical terns was a far more useful indicator of maximum prey size taken than the measure of bill length alone. It is apparent that the mean prey size taken by aerial feeding birds can be more accurately predicted from a similar structural formulation. That the structure of the jaw muscles of Swallows enables them to exert more force than those of Swifts has been demonstrated by Morioka (1974). It is clear from his study that the Swift jaw muscle structure favours rapid opening and closing at the expense of force, and it is certainly this species that selects the smallest, soft-bodied insects. The stronger jaw muscles of Swallows are a result of their relationship to other passeriform birds, and the involvement of the bill in nest-building activities (digging in sand, carrying mud) may have in part restrained their specialisation with regard to handling of prey.

(b) The mobility of available prey

It has been shown how the different body plans of similar sized members of distinct taxa confer different flight abilities on them. These mobility differences are reflected in the prey types selected, so that the Swallow for example selects proportionately more fast flying Syrphid and Muscid Diptera than are available relative to all insect types in the preferred feeding areas. For all species, the selection of Brachyceran and Cyclorrhaphan Diptera grades from the Swallow selecting the more mobile end of the range to the Swift taking less of these groups and concentrating on the least mobile. These slower flying individuals are in the same size range as Aphids available at the same time, but it is apparent that the Swift selects a larger proportion of the more passively dispersed Aphids than expected from the similar proportions of the two groups available higher in the air-column. The effect of prey mobility over and above that of prey size is difficult to assess from examination of the relative size and mobility overlaps in the diets of the predators. Chapter 2 presents some ambiguity, with a close relationship between the two prey characteristics when all four species are included, but no significant correlation between them when Swallow and Sand Martin are examined throughout the whole breeding season.

For these two species the differences in mean mobility of prey selected on good days serve to amplify a difference in foraging strategy. On bad days when insect abundance is low, Sand Martins cannot pursue a swarm feeding strategy, smaller prey types in the diet are scarce and larger, weak flying taxa are selected. Conversely, on good days Sand Martins can switch to swarm feeding, but also have more mobile types available and this choice is reflected in the wide prey size and mobility niche breadths for this species. Swallows do not respond to increased abundance of small insects to the same extent, being adapted for selection of fast flying insect types and exhibiting a correspondingly narrower mobility niche breadth.

The finding that those morphological features concerned with flight performance best showed adaptation to ecological niche within the aerial feeding bird guild accords with other studies relating morphology, behaviour and adaptation. Newton (1967) emphasised the importance of behaviour in determining morphological adaptation within a group of closely related finches, and Gaston (1974) attributed variation in morphology within the genus *Phylloscopus* to differences in feeding strategy and associated niche preference. Similarly, Partridge (1976) related morphological differences between *Parus* species to variations in foraging habitat structure. Variation in energy expenditure relative to wing-disc loading in hummingbirds has been shown to be an adaptation for differing foraging strategy with differing structural characteristics of the habitat (Feinsinger and Chaplin 1975). Caccamise (1974) has also shown how variation in wing morphology is related to different foraging techniques in aerial-feeding nighthawks.

Although the Swift has a twisting humerus which is of use in turning (Savile 1950), this species and the House Martin are primarily adapted for increased gliding, to reduce energy expenditure (Pennycuick 1969, 1972, Hails 1977), and for faster flight. These adaptations enable them to cover greater distances at their higher feeding stations where insect abundance is often lower and the encounter rate of prey is proportionately reduced.

(c) The abundance of available prey

On good days, with high aerial insect abundance, the niche breadths of the Swallow and Sand Martin expanded to include more mobile prey types and, at least for the latter species, to include larger proportions of smaller prey items. These increased niche breadths could have merely reflected the selection of a greater range of sizes and mobilities of prey within the same taxonomic groups as taken on bad days. However, it is implicit in the divergence of the prey size and mobility niches of the Sand Martin that the diet would include a greater variety of insect taxa. An additional analysis showed the range of taxonomic groups in the diets (the index B) of Swallow and Sand Martin to expand when aerial insect abundance was high, but relatively little of the variance was explained in the absence of the effects of insect size and mobility ($r^2 \times 100 = 25.7\%$ for Swallow, 31.5% for Sand Martin). It is therefore concluded that any effect of absolute insect abundance on prey selection would be secondary to the influence of prey quality agreeing with Bryant (1973) who found that only eight percent of the variation in prey type selection by the House Martin could be accounted for by the isolated effect of absolute insect abundance.

(d) The conspicuousness of available prey

For birds foraging in the air, the need to rank prey items included in the diet on the basis of crypsis in the foraging habitat does not assume the same importance as in other studies (e.g. Royama 1970). Dark-bodied insects may be more conspicuous than light bodied forms (Lewis and Taylor 1965) and hence would be preferentially selected, assuming other attributes to be constant. However, size is likely to contribute more to the conspicuousness of a prey item and the possibility of passive size selection arises whereby larger items are sighted more readily, and consequently taken with greater frequency. This is more of a possibility for the Swift and the House Martin since these two species are less likely to feed in vegetation-enclosed areas than either the Sand Martin or Swallow. Near to vegetation brightly coloured prey items could be at a disadvantage but their frequency of occurrence could not be assessed from faecal samples; it is worth noting that bright colours often involve warning patterns. How crypsis might influence prey selection by the Swift during crepuscular feeding is not known.

(e) Prey selection in relation to unpalatibility

Insect types may be avoided because they are distasteful or possess a potentially injurious method of defence. Davies (1977a) reported an avoidance of Sepsidae (Diptera) by foraging wagtails because they resembled ants and emitted a noxious exudate, but it is evident in this study that aerial feeding birds are not similarly affected and indeed selected for this family (this does not discount the possibility of different species being involved). The obvious avoidance of a group well represented in the available samples can be shown for the social Hymenoptera and attributed to the danger of being stung. There are records of bees and wasps being taken (Lacey 1910, Grant 1945, Stemmler-Morath 1932) but these are few and mainly involve non-stinging drones which demonstrates the remarkable visual acuity of aerial feeding birds. Drone bees fly late in the summer, on few occasions, and apparently fly fast when they do so; they were not taken by any birds during the course of this study. Selection of excellent mimics amongst the Syrphidae however, confirmed the birds excellent discriminatory powers. By contrast a species of swift in the Phillippines is a specialist on honey-bees (Morse & Liago 1968, in Hespenheide 1975).

(f) The flight periodicity of available prey

None of the three hirundines are nocturnal or crepuscular feeders but Swifts sometimes feed in very low light intensities, and there are records of this species flying at night, although there is no proof of feeding whilst doing so. Observations of crepuscular feeding Swifts showed them to concentrate in areas near vegetation particularly in association with water, (any high-flying birds would not have been easily seen however) and one bird caught had a food ball composed entirely of Neuroptera and Trichoptera. Lewis and Taylor (1965), in a comprehensive study of insect flight periodicity, show Psychodids, Cecidomyiids, Chironomids, Neuroptera and Trichoptera to have many representative sub-taxa peaking in flight activity at dusk. This would account in part for the large numbers of the former three groups being represented in the suction trap samples relative to occurrence in the diets of the birds. The Swifts apparently selected proportionately more Neuroptera and Trichoptera relative to their availability in the suction trap samples, and virtually ignored the more abundant taxa. However, size and conspicuousness of larger items may not be the causes of this observed difference, since Tipulids flying at dusk were not selected to the same extent.

Distribution of the food supply, feeding station and niche dynamics

The above characteristics of the insect prey involve spatial and temporal variations which, together with the effects of environmental conditions on insect distribution, have been shown to influence feeding station of the predators. Hence, the extent to which each species will seek out prey aggregations will depend upon location and the quality of constituent food items. For example, Sand Martins feeding low over open ground were observed to adopt a higher feeding station when swarming insect types were included in the diet. Much less predictable is the exploitation of local concentrations of prey, sometimes to the extent of single-species swarms as with some tropical swifts (Hespenheide 1975), and Lack and Owen (1955) found considerable taxon discrimination by Common Swifts. In the present study the aerial feeders were found to be less discriminatory, but not to the extent that unprofitable items were not rejected, and this aspect of foraging presumably functions together with inclusion or rejection of particular patches of the air-space in which to feed. Certainly, the possibility of niche complementarity in preventing increased overlap between the Swallow and Sand Martin demonstrates the inter-relationship of air-space and prey characteristics. Complementarity in foraging patterns in relation to structural characteristics of the habitat has been demonstrated for three closely related Parids (Hertz, Remsen and Zones 1976), and Ulfstrand (1977) suggested inter-specific niche complementarity as explaining why the Pariform guild niche varied much less throughout the year than the total niche sizes of the constituent species. Similarly, Werner (1977) found two co-existing fish species to be food specialists and habitat generalists, whilst a third species with intermediate characters necessarily had to be a food generalist and habitat specialist. Although active inter-specific niche complementarity could not be demonstrated in the present study, the relative specialisation or generalisation of each species is evident (Table 2.8.18). The Swallow is notable for its smaller total niche size and specialization of feeding on fast-flying insects in the lower air-space for which appropriate adaptations have evolved. These may have limited the extent to which this species can return to a more generalised mode of feeding since it is relatively energetically uneconomical for it to feed on smaller prey types at a higher station.

The determination of niche size by social dominance does not appear to function within the aerial feeding bird guild, but is implicated in the organisation of animal guilds over a wide range of developmental levels (Morse 1974). Feinsinger (1976) demonstrated its operation in a guild of nectarivorous birds and also established that niche overlaps were high during peaks of flowering of the major resource plant. Decrease in overlap with higher food abundance would be expected from theoretical considerations (e.g. Emlen 1966, MacArthur and Pianka 1966), but again Zaret and Rand (1971) showed food overlaps of co-existing tropical fish to be highest in the wet season when food abundance was at a maximum.

In the present study the predator species likewise showed increased overlap in characteristics of the prey during conditions of high food abundance, but were more selective with respect to patches of the air-space and hence simultaneously decreased overlap in this dimension. It appears therefore that portions of the environment which were used more efficiently by competitors (for which the appropriate adaptations have been demonstrated) were avoided (MacArthur and Pianka 1966, MacArthur and Wilson 1967), and in this respect the foraging strategies conform to theoretical expectations.

6.2 Foraging efficiency and short term predation strategy in Swallows *H. rustica*

It is of interest to examine the results of Chapter 3 in terms of whether or not Swallows forage optimally, at least whilst feeding nestlings, and how longer term considerations may influence feeding behaviour.

Optimal foraging?

In a review of optimal foraging theory and tests, Pyke, Pulliam and Charnov (1977) have proposed that an animal might make four decisions: (a) which patch types to visit, (b) how long to stay in each patch, (c) which food types to eat in each patch type, and (d) which foraging path to employ in each patch type. They further point out that these categories have usually been treated separately based on the implicit assumption that the decisions are approximately independent.

In the present study choice of patch type and choice of prey type have been examined with the consideration that they may not be independent. The finding that choice of patch was influenced primarily by the quality of prey types within the patch, at least whilst feeding first broods, indicates how the respective decision rules may be applied simultaneously. The discovery that distance to the patch overrides the effect of prey quality poses a number of questions. Although larger items were brought to first broods the adult birds travelled no further to patches than those feeding seconds. With a similar mean excursion distance for first and second broods it seems likely that the constraint of preferred patches being too distant did not apply earlier in the season. The distance to preferred patches will be largely controlled by environmental factors on a seasonal basis (and, for example, a more extensive station sampling programme would be necessary if the birds travelled much further on particularly bad days), and from this reasoning it might be expected that the foraging efficiency ratio would likewise vary seasonally. This would be the case if increase in the ratio was constrained by distance, as a result of environmental fluctuations, even though the feeding behaviour may have been to maximise foraging efficiency. Although such differences between first and second brood feeding could not be tested, it was found that values of foraging efficiency, whilst feeding the former, were no higher at distances greater than the mean excursion than those at shorter distances (and the highest foraging efficiencies approximated the mean excursion distance).

Hence, although foraging efficiency could increase with an increase in size of insects available, it may only do so if these prey are within an optimal distance.

That Swallows should always attempt to maximise net energy intake by choosing the most profitable patches brings in the aspect of their sampling the environment to gain information relevant to such choices. Optimal foraging models have assumed that a predator's behaviour results from sampling and hence knowing the availability of different prey types or patch types. However, the predicted one-step switch from no-selection to selection of more profitable prey types when they increase above a threshold rate of encounter, or more profitable patches which present higher numbers of preferred prey, has not been observed in a number of laboratory studies. For example Krebs et al (1977) found Great Tits to only gradually increase selection of large mealworm prey as these became more abundant and that they still took small prey even when encounter rates with large prey were very high. These results were interpreted as the birds investing time and energy in sampling alternative prey. Similarly, Smith and Dawkins (1971) and Smith and Sweatman (1974) found that titmice, given a choice of patches with differing food abundances, did not conform to predicted optimal behaviour by allocating all time to foraging in those patches with highestfood abundance, but spent progressively less time in progressively worse areas. This was interpreted (Smith and Sweatmen 1974) as a long-term adaptive response to a fluctuating environment, where sampling all areas would be a better strategy than allocating all time to the best patch in the short-term, if the latter strategy ultimately yielded a lower net energy intake when prey distributions altered. Always foraging in the patch with the highest expected reward rate has been termed "immediate maximising" by Krebs, Kacelnik and Taylor (1978) who have pointed out that with this strategy a predator risks choosing to exploit a lower quality patch rather than sampling and then exploiting the most profitable patch. They have shown that captive Great Tits, confronted with two patches of different profitability, first sampled the two patches and then exploited the more profitable patch, and that the relative efforts of exploration and exploitation approximated an optimal solution for maximising the amount of food gained during a feeding period.

The relevance of the above to the present study is that the observed foraging efficiencies may not always be high, or at an expected maximum, if the birds are spending time sampling patches around the nest site during certain foraging excursions. Hence, a low foraging effiency ratio could well represent an investment towards the next high ratio. This assumes that adult Swallows do not carry out all of their sampling during periods of self-feeding, or when they are not feeding nestlings. Any real sampling effect could not be tested in the present study particularly as patches were grouped, and the only relevant comment is that sometimes birds were observed to fly straight to a patch whilst at other times the foraging course meandered. This difference is also pertinent to choice of optimal foraging paths to and within patch types.

Optimal allocation of time to different patches has again been shown in a number of laboratory studies. For instance, Krebs, Ryan and Charnov (1974) showed that Black-capped Chickadees, _Parus atricapillus_, would leave a patch when the rate of food intake dropped to the average for all patch types within that habitat, and that they would leave sooner, i.e. had a shorter 'giving-up time', in better habitats. However, these studies have been concerned with depletion in patches and it may be more usual for no depletion effect to occur in the field situation where Swallows are feeding on aerial insects. This was certainly the case in a study of Spotted Flycatchers (Davies 1977b) where changes in availability of prey depended on whether or not a swarm of flies happened to be within striking distance of a perch. In the present study, assessment of time allocation to different patches would necessarily involve the effects of how quickly a single bolus could be collected.

Theories of optimal prey choice have been formulated by many authors (e.g. Schoener 1971, MacArthur 1972, Werner and Hall 1974, Charnov 1976) all with essentially the same conclusions. The Swallows in the present study conformed to some of these conclusions, the first being that when the abundance of larger, more profitable prey types was low they ate both large and small prey types (but see discussion below). The second conclusion, again agreeing with theoretical predictions, was that with an increase in abundance of larger prey, the Swallows selectively ignored smaller prey types irrespective of their abundance. A further conclusion of optimal diet choice theories is that predators should prefer prey types according to their rank order of profitability (net energy yield per unit handling time). This could not be demonstrated directly for Swallows although increase in net energy yield per foraging excursion was correlated with increase in average size of insect available. Additionally, selection of the most frequent large taxa was in some cases independent of abundance and qualitatively associated with an optimal size and flight ability of the prey type.

Foraging, other activities, and optimal allocation of time

Natural selection will favour those individuals in a population that contribute the most to succeeding generations, and for Swallows this will probably be measured over a lifetime incorporating several breeding seasons. In order to maximise fitness in the long-term, a predator ought in the short term to maximise net rate of energy intake (MacArthur and Pianka 1966, Charnov 1973), and for Swallows in the breeding season this will be because feeding competes for time with other activities such as looking out for predators and territory (nest-site) defence. This being so, it follows that a Swallow should make decisions that result in an optimal allocation of time to the various activities and hence maximise its inclusive fitness in the long term (Katz 1974). Sibly and McFarland (1976) and McFarland (1976) have made recent analyses of optimal switching between major activities, but a comprehensive field analysis remains uncompleted and the present study is no exception. However, the results of this study do point to certain problems of time allocation facing individual Swallows whilst feeding nestlings.

The feeding of nestlings was studied within the period of their peak food demand on the adults. That a lower food demand exists at a young stage of the brood is indicated for two other hirundine species. Walsh (1978) found that smaller meals were brought back to younger nestlings of Purple Martins, Progne subis, and Bryant (1978b) showed that House Martin nestling mortality at an early brood stage was more likely to be attributable to poor egg quality, resulting from scarce food supply during egg formation, than lower food abundance decreasing feeding rate. With a lower food demand on them, should adult Swallows still explore and exploit the food supply in an optimal manner? It can be argued that those that do not would be ultimately selected against if current behaviour affected ability to feed the brood at a later stage. Hence, with a lower nestling food demand, those adults foraging optimally would release the maximum amount of time for other activities, such as brooding and self-feeding to build up reserves, which may be assumed to be investment strategies to minimise the effects of increased energy expenditure at the time of peak demand.

Parental investment

Life-span curtailment is a varying cost of reproduction (Williams 1966) and it is conceivable that a brood requiring an adult to make more foraging trips would increase this risk if the bird was more exposed to predators and simultaneously had less time to look out for them. In the present study male Swallows were found to make more foraging trips to larger first broods, females to larger seconds, which would not only increase risk of predation, but would also increase their overall energy expenditure. Hails (1977) demonstrated a parallel increase in energy expenditure with larger broods for male House Martins. Even though it was shown that the adult Swallows could supply food enough to raise the larger broods, if the extra effort shortened reproductive life-span, then these potentially most productive clutch-sizes might not be optimal (Lack 1954, 1966) and would be favoured by a smaller clutch size which increased reproductive life-span and ultimately the total number of off-spring (Charnov and Krebs 1974). Hails (1977) also found an increase in energy expenditure of male House Martins whilst feeding second broods, and male Swallows in this study do show an increase in number of feeding visits to second broods. Although it was shown that Swallows feeding second broods did not travel further than for first brood feeding, and therefore increased energy expenditure for the male would not be incurred this way, smaller meals would result in lower foraging efficiencies and fewer daylight hours would result in less food per day. However, although fewer off-spring result from second broods it is evidently selectively advantageous to attempt a second brood rather than try for a very large first brood since the mortality risk to the male bird is likely to be increased under those circumstances. Additionally, an evolved system of reciprocal altriusm (Trivers 1971, 1972) in a monogamous breeding situation such as with Swallows may mean that the male will devote only a certain amount of extra effort to feeding larger first broods. Therefore a very large brood may be at a selective disadvantage if the female does not increase feeding visits, and she may not do this having already invested much time and energy in egg-laying and incubation. (N.B. male Swallows do not incubate). Also, it would be disadvantageous for the female to risk increased loss of off-spring through the male himself being at increased risk with a larger number of foraging trips. Hails (1977) in fact found male and female House Martins to invest equal amounts of energy for rearing the mean brood size to independence. Further support for the importance of an increase in male feeding visits to the survival of the brood comes from a study of two natural Swallow broods, each of four nestlings, sited close to each other and of similar age (eight days difference) (Purchon 1947). The first brood successfully fledged and the male had steadily increased his rate of feeding the brood; the second brood perished and the second male had a feeding rate no more than that of the female, which in turn had a similar feeding rate to that of the female feeding the first brood.

6.3 Colonial breeding and predation strategy in Sand Martins *R. riparia*

In Chapter 4 differences in food delivery, nest attendance and predator response were found between centre and edge colony Sand

Martins. These differences may collectively provide an insight into the advantages of maintaining a colonial breeding system, but to gain an understanding it is necessary to interpret them in the context of colony activity and its changes throughout the breeding season. During the early season it has been shown that the sample centre nest received more food simply as a result of more boluses being delivered. The birds from the edge nest made fewer visits and hence were devoting more time to other activities which may have been (a) increased wariness of possible predator attack, (b) the need to return to the colony, but not necessarily the nest, to gauge flight lines of other feeding birds, (c) the need to defend the nest-site from depredations of competing conspecifics; or (d) they may have been younger, less experienced birds. The respective foraging excursion times for centre and edge birds feeding nestlings were not determined but it is possible that the edge birds at this season were not able to locate concentrations of food as quickly as centre nesters. If this was due entirely to the fewer birds at edge sites providing fewer guidelines to good feeding areas then this would support the suggestion that a major advantage of coloniality in this species results from social facilitation of foraging (Emlen 1971, Emlen and Demong 1974, 1975). Maintenance of such social facilitation would require a reciprocal system of food-finding signals (Trivers 1971), the existence of which has not been proven for this species. Therefore the possibility remains that selection will be for the capacity to parasitise the food-finding abilities of other individuals, which will themselves attempt to minimise advertising their own foraging success. However, selection for food-finding parasitism may also be expected to be less effective in edge birds if their locating of food concentrations is slower. Neither of the above need be direct determinants of selection for coloniality if their effectiveness depends upon continuing experience of other feeding birds, because other activities to which the birds are committed may effectively limit the time available to gain this experience. Therefore early edge birds may have suffered less exposure to other feeding birds as a combined result of increased predator wariness and intraspecific nest defence. It is certainly the case that the edge area of the colony would still have been the most competitive at this stage with respect to an increase in physical interference, e.g. stealing nest materials and fighting for mates, associated with later colonists.

Extending this possibility to the mid-season situation the smaller amount of food delivered to centre nests may be evidence that any benefit, i.e. gain in feeding time, which resulted from decreased predation was outweighed by competition from conspecifics. This is supported by the observed dramatic elevation of total visits over feeding visits for centre nesters, and suggests that increased conspecific activity, mostly related to the start of second broods, has deleterious consequences in this part of the colony at this season. Further support comes from a study of colonial House Martins where the mean weight of broods fledging in the median breeding week was lower than mean fledging brood weights in weeks before and after the median (Bryant 1978b). Assuming these edge and centre birds did not differ in rate of catching prey, the observation that the former caught more per foraging excursion implies that centre birds were not prepared to spend as long away from the nest as were edge birds. If their respective foraging excursions were of equal duration then the centre nesters may have taken longer to locate food sources, and again this could have resulted from less exposure to other feeding birds due to committment to the nest-site.

The most straightforward interpretation of these observations therefore, is that coloniality in Sand Martins has evolved to minimise predation and thereby save time which can then be devoted to food finding. A secondary consequence of this is that the birds have begun to use or help each other in finding food but this requires continuing experience of other feeding birds. This experience may be limited by the time involved in performing other activities, mostly associated with competition from conspecifics, and the limitation will vary with locality and season. Furthermore selection will apparently be for early nesting with the fitnesses of centre nesting individuals being higher than all others. These are the birds which benefit most from decreased predation, bringing back more food to the larger broods characteristic of early nesters (Stoner 1936, Petersen 1955) and hence increasing survival chances of the off-spring (Perrins 1970). Nestlings of these earlier nesters will emerge when many adults are near the colony and group defence, together with selfish herd effects will result in greater protection.

With reference to a peak number of birds, including the first fledged juveniles, being at the colony in mid-season, increased attraction of predators may have resulted (Tinbergen 1952, Kruuk 1964, pers. obs.), and those adults feeding young at this stage may have had to invest more time in mitigating its effects. However, if many more "pairs of eyes" and increased mobbing nullified this effect then the observed extra visits to the nests at this time were probably a response to increased conspecific activity. Noting that mid-season is the stage of late first-broods, the observed poorer foraging success may have been related to younger, less experienced adults. The smaller bolus sizes of the mid-season birds could reflect inexperience, but both edge and centre were collecting smaller items than early nesters, and both known experienced and suspected inexperienced Swallows brought smaller items to their second broods. The decline in mean size of prey items could be associated with an increase in preferred smaller, swarming insect types at mid-season, as suggested previously (Chapter 2). However, as shown for Swallows (Chapter 3) birds feeding later in the season may not be prepared to travel far enough to collect sufficient larger items.

With very few breeding pairs remaining through until the late season, the positioning of any particular occupied burrow as edge or centre is spurious since fragmentation of the colony makes them in effect all edge nests. Therefore it is expected that conspecific interference would be at a minimum, but an increased incidence of predation might result, although there is no evidence to support the latter inference. Therefore, since no significant increases in total visits above feeding visits were noted, the potential importance of indirect limitation of foraging success by conspecifics is underlined. Certainly, the few feeds comprised of smaller and fewer prey items suggest that preferred insects were difficult to locate at this late stage when numbers of other feeding birds would be minimal. If the late breeding birds gain less experience of foraging conspecifics, in terms of being able to locate food concentrations quickly, they will probably need to range over larger areas and are less likely to simultaneously feed in the same patches as are earlier nesters. Hence, the taxonomic identities of prey in the diets of edge and centre birds nesting late are likely to be less alike than for earlier edge and centre nesters which may exploit the same insect swarms. Indeed, prey type differences between late edge and centre birds were found to be greater than for earlier nesters (Table 4.6.1).

In this context, although selection is apparently for early nesting in the colony centre, those birds attempting to nest too early will likewise encounter too few birds, and the unpredictable food supply will limit the ability of females to build up adequate reserves for egg-laying. This interpretation depends on the representativeness of this small sample and must be regarded as tentative.

6.4 Predation strategies and ecological isolation in aerial feeding birds in the African tropics

Central to this discussion of foraging strategies of wintering migrants, in the presence of resident members of the same guild in Africa, is food abundance variation in relation to season. This relationship has been investigated in a number of studies of tropical ecosystems, particularly that of Sinclair (1978) who has shown marked peaks in nocturnal aerial insect abundance coinciding with wet seasons in East Africa. Karr (1976b) has demonstrated notable peaks of insect and fruit eating birds in resident communities in central America coinciding with the wet season. Fogden (1972), in a forest in Sarawak, found that insect abundances were lowest in the period before the monsoon season and that open spaces above vegetation exhibited greater variation. Similarly higher variations in insect abundance in and above the canopy have been reported by Smythe (1974), the peak in biomass occurring in the early rainy season. This peak was 6-8 times higher than the dry season biomass and mainly involved the 5-15mm size class which is that most heavily exploited by insectivorous birds. Janzen and Schoener (1968) found dryer habitats in Costa Rica to have lower insect densities in the dry season, although some other habitats had higher abundances (Janzen 1973). Zaret and Rand (1971) found food abundance in a tropical freshwater ecosystem to be higher in the wet season and likewise Hespenheide (1975) reported increased aerial insect abundance in the wet season in Central America.

The evidence therefore supports an increased food abundance during tropical wet seasons, and the observation that many migrants move from south of the equator in Africa to a position further north just before the local rains (March/April) lends further support to this (Moreau 1972). The timing of the wet season is undoubtedly important in the wintering ecology of the Palearctic species. In the pre-wet season period (Jan/Feb) in Malaysia, C. J. Hails (pers. comm.) has found aerial insect abundances (from suction traps sampling a similar insect size range to that sampled in Britain - see Chapter 2) to be of a similar level to those of the temperate summer plateau. Comparative mean figures of samples at 1.8m height are 3.45 (Log_{10} n + 1) in Malaysia and 3.69 to 3.86 from May to August in Britain. Large populations of H. rustica over-winter in Malaysia (Medway 1974). In the Hespenheide's (1975) study, an increase in the food size niche breadths of two swifts and a swallow during the wet season was interpreted as being a response to a worse situation where higher incidence of rain curtailed feeding. However, food was likely to have been more abundant and, since changes in feeding stations were not assessed, it is not known if greater restriction in air-space would have occurred as compensation for increase in range of prey taken.

In the present study lower air-space niche breadths and subsequent decreased overlaps in air-space were demonstrated, but again no compensation by expansion in other niche dimensions could be shown. Indeed it has already been suggested that no expansion in prey size niche breadths would be possible without greatly increased overlap, and the single comparative example shows the ranges of prey sizes taken by H. rustica in breeding and wintering areas to be almost the same. This could imply that the resident species breeding in the wet season may not feed their nestlings larger prey items than taken for self-maintenance, and/or in the dry season, because this would involve expansion of these niche breadths (Root 1967, this study).

The connotation of the above discussion is that although a demonstrable rise in the food supply occurs during the "winter" for the Palearctic species, this increase may not be sufficient to sustain simultaneous wintering and resident breeding populations. A similar view has been expressed by Miller (1963) with respect to migrants in Colombia, but elsewhere (Willis 1966, Moreau 1972) support has been for the opposite view; that "migrants are usually sub-ordinate to resident species and feed at peripheral or poorer foraging sites whenever residents are present" (Karr 1976a). Certainly, Sinclair (1978) has suggested that wherever residents and related migrants occur in East Africa, they do so in a non-competitive situation where the rains have stimulated surplus insect food. In this instance there are other factors which could affect breeding in the wet season such as flooding of ground nests of H. griseopyga and flood damage to bank nesting R. paludicola.

The situation pertaining to these aerial feeding birds is perhaps unique on a historical basis in that the four major Palearctic species have not only naturally increased their ranges from the end of the last earth-cooling period, but must have had their populations boosted by nesting in association with man. Therefore, there are presumably more wintering in Africa at this time than ever before and considerable changes may have already befallen the aerial feeding community. As Benson et al (1971) point out, many of the native species in Zambia are rare and localised in distribution and they suggest that these may have been more widespread in a cooler, moister epoch. At such a time the numbers of Palearctics wintering in Africa may have been

That the Palearctic species in Africa are far more numerous than native species is well-documented (Taylor 1949, Broekhuyson 1964, Moreau 1966, 1972), and is supported by observations in this study. Even. D. urbica, where it has been sighted, has been in large numbers. R. riparia winters more to the north of the equator (Moreau 1972), is less common than the other Palearctics in Zambia and Malawi for instance, and therefore will have less impact on the aerial feeding community examined in this study. It seems unlikely that such larger numbers of these species can be relegated to marginal feeding areas by the smaller populations of native species, the better areas in this case seemingly close to vegetation. However, Klopfer and MacArthur (1960, 1961) have indicated that for ecologically comparative bird communities smaller niche sizes are maintained in the tropics and more species are tolerated by this lowering of exclusivity of resource use.

The effects of diffuse competition must be taken into account since this will increase demands on the food spectrum. Although the insect size range has been shown to increase at the larger end in tropical ecosystems (Schoener and Janzen 1968), these larger insects are accounted for by the evolution of many more large-billed birds (Schoener 1971b) and the Hirundinidae as a family show no increase of this character in the tropics. However increases are witnessed in Africa by a wide diversity of Bee-eaters (see Fry 1972), insectivorous Falconidae, Shrikes (Lanidae), Pratincoles (Glareolidae) and others. Together with many flycatchers, the effect of these families as diffuse competitors with Hirundinidae and Apodidae is inestimable and limits to the definition of the aerial feeding guild are therefore indistinct.

Does this competitive situation account for a significant proportion of the annual mortality in the Palearctic species? Verheyen (1952) was of the opinion that 50% of *H. rustica* would die on the two annual migratory journeys, and weights of these birds migrating across the Sahara have certainly been shown to be low (Ash 1975). Mead (1970) estimated a 50% mortality between autumn in Britain and mid-February in South Africa. A realistic comparative estimate of migration mortality and wintering mortality is not feasible, but the latter could be high in a competitive situation. It must be remembered that increased temperatures will substantially reduce maintenance needs (Moreau 1972), although in this context Ricklefs (1971) suggested that overheating may have been an important factor in limiting the amount of foraging time in Mangrove Swallows *Tachycineta albilinea*. In addition, extensive moulting throughout the season (Broekhuysen and Brown 1963, Dowsett 1966, Mendelsohn 1973) may affect catching ability, particularly for *H. rustica*, and may increase protein demand.

6.5 Predation strategies in aerial feeding birds: integration of concepts

In order to survive, all organisms must be adapted to exploit or withstand environmental conditions in their favoured habitat, and adaptation of organisms will entail conformity to many different aspects of their environment. Changes that occur in the physical nature or patchiness of the environment or, for example, in intra- and inter-specific competition or predation pressures, may lead to conflicting demands and hence selection pressures for individuals which result in compromise adaptations. It is considered that natural selection should shape compromise adaptations so that the average animal in a persistent population is optimally adapted to its environment. The ultimate result of optimal adaptation should be a maximisation of the contribution of genotypes to subsequent generations.

In the present study, consideration has been given to foraging as a major activity, amongst all others, for which average behaviours and morphology should approximate to the optimal phenotype within each species (Sibly and McFarland 1976, McFarland 1976).

Within the aerial feeding guild in Britain the relationship of other activities to foraging, and hence to interactions between the species, can be given initial perspective by comparing the respective breeding systems. All four species are monogamous, as are the majority of birds (Lack 1968a), but vary as to how many pairs may nest in close proximity. The Sand Martin is almost invariably colonial, the House Martin is generally colonial but single pairs may be found with moderate frequency, small numbers of Swift nests may be grouped in a way that appears to be independent of nest-site availability, and the Swallow is in essence a solitary nester but pairs may be grouped as a function of the clumped distribution of suitable nesting sites (primarily farmsteads). The present studies of single nesting Swallows and colonial Sand Martins render these two species suitable for comparison.

Coloniality in Sand Martins was considered in this study to have evolved to reduce time spent minimising the risk of predation (cf. Hoogland and Sherman 1976), hence leaving more time for locating patchy food supplies. Loss of foraging time from having to defend the nest from competing conspecifics was less in the centre of the colony early in the season and, partly as a consequence of this, early breeders may have been able to produce more off-spring surviving to independence (as in tits for example, Perrins 1970, Dunn 1976). Net gain in foraging time could enhance the fitnesses of all colonial individuals above those of single nesting conspecifics, elevation of individual fitness being an essential pre-requisite for the maintenance of coloniality (Hamilton 1971, Alexander 1974). In contrast, Swallows may nest singly because no gain in foraging success could be achieved from a group situation. In support of this Snapp (1973) found no increase in reproductive output from pairs within larger groupings of nests (called colonies by Snapp). The present study has shown how the time spent by Swallows in deterring a potential predator resulted in fewer feeds being delivered to the brood, thus indicating a possible disadvantage of solitary nesting. However, since Swallows vigorously defend their nest-sites from conspecifics (Hosking and Newberry 1946, pers. obs.), nesting in close proximity could involve comparable time losses in inter-specific interactions.

The type of breeding system among aerial feeding birds will be associated with the characteristics of their insect prey, the distribution of those prey types in the air-space, and what flock sizes are most suitable for exploiting concentrations of insect food. Thus, breeding Swallows usually feed close to the nest-site, mostly in singles or pairs. This species was found to prey on larger insect types at a low level, the more even distribution and nearby availability of these prey types probably not requiring that Swallows should gain information from conspecifics on location of insect concentrations and hence coloniality would not serve this purpose. The other three aerial feeding species range further from the nest sites to collect food (Koskimies 1950, Lack and Owen 1955, Lack 1956, Bryant upbl., pers. obs.) and all from large feeding flocks. As has been suggested for the Sand Martin, the development of coloniality has resulted in individuals being able to exploit food concentrations more rapidly. Exposure to other feeding birds in a colonial situation may similarly benefit House Martins and Swifts since they both feed on insect prey types at aerial stations where prey concentrations are often sparse. Again, whether genuine social facilitation of foraging or parasitism of food finding abilities of others (Alexander 1974) is involved has not been determined. It is tempting to suggest that the white rump of the House Martin has evolved as a social signal, but this could equally be an adaptation to flock feeding in the wintering areas and is of no advantage during the breeding season. It may be mentioned that the Swift has other strategies relating to an unpredictable food supply, notably that of torpor in the nestlings reducing energy demand in bad weather (Koskimies 1950). Similarly, Bryant (1978a) has suggested that asynchronous hatching of House Martin nestlings results in spreading the peak of energy demand by the brood as a strategy to cope with an unpredictable food supply.

From the above discussion it is apparent that colonial or single nesting may result in differences in allocation of time to foraging, and related differences in utilization of the aerial insect food supply. Since the variety of resources used by a species is central to the theory of how many species can stably coexist in a habitat, it is of interest in the present study to examine the effect of (optimal) use of resources by each species on the other members of the community. Werner (1977) demonstrated that the optimal diet of two sunfish species resulted in overlap which was less than the theoretical limit (MacArthur and Levins 1967, May and MacArthur 1972), which would permit coexistence with an intermediate sunfish species, and that this intermediate species in fact segregated by habitat. In the present study species packing has been shown to be too close for co-existence along the prey size axis of the niche alone, and therefore spatial segregation assumes an importance in this respect. This explained why on good feeding days each aerial feeding species concentrated foraging into fewer patches and consequently showed decreased niche breadth, whereas this broadened when more patches were used for foraging on bad days. Spatial segregation may follow from optimal choice of feeding patches but if so, what are the effects on optimal prey choice?

Most models of optimal foraging to date (e.g. Emlen 1966, Schoener 1971, Werner and Hall 1974, Charnov 1976), have dealt with prey and patch choices in isolation, and have emphasised the effects of prey depletion on the latter (Charnov, Orians and Hyatt 1976). Hence, a conventional optimal foraging viewpoint would hold that each aerial feeder in this study should incorporate an increasingly higher proportion of large items into the diet as the abundance of larger insects increased, irrespective of the density of smaller insects. The effect of this in decreasing niche breadth can be shown in diagrammatic form (Figure 6.5.1). It may be noted that the extremes of a species utilization curve along the prey size continuum will be related to constraints imposed by particular morphological and behavioural adaptations. This conventional optimal diet model may be re-examined with respect to foraging by aerial feeding birds and their patch choices, the aggregation of aerial insects and foraging in situations with insignificant depletion effects as is suggested pertain to aerial feeding birds (Davies 1977b, Krebs and Cowie 1976). It appears that on good days when insect abundance is high, an aerial feeding bird may more effectively maximise its net energy gain by restricting forag-

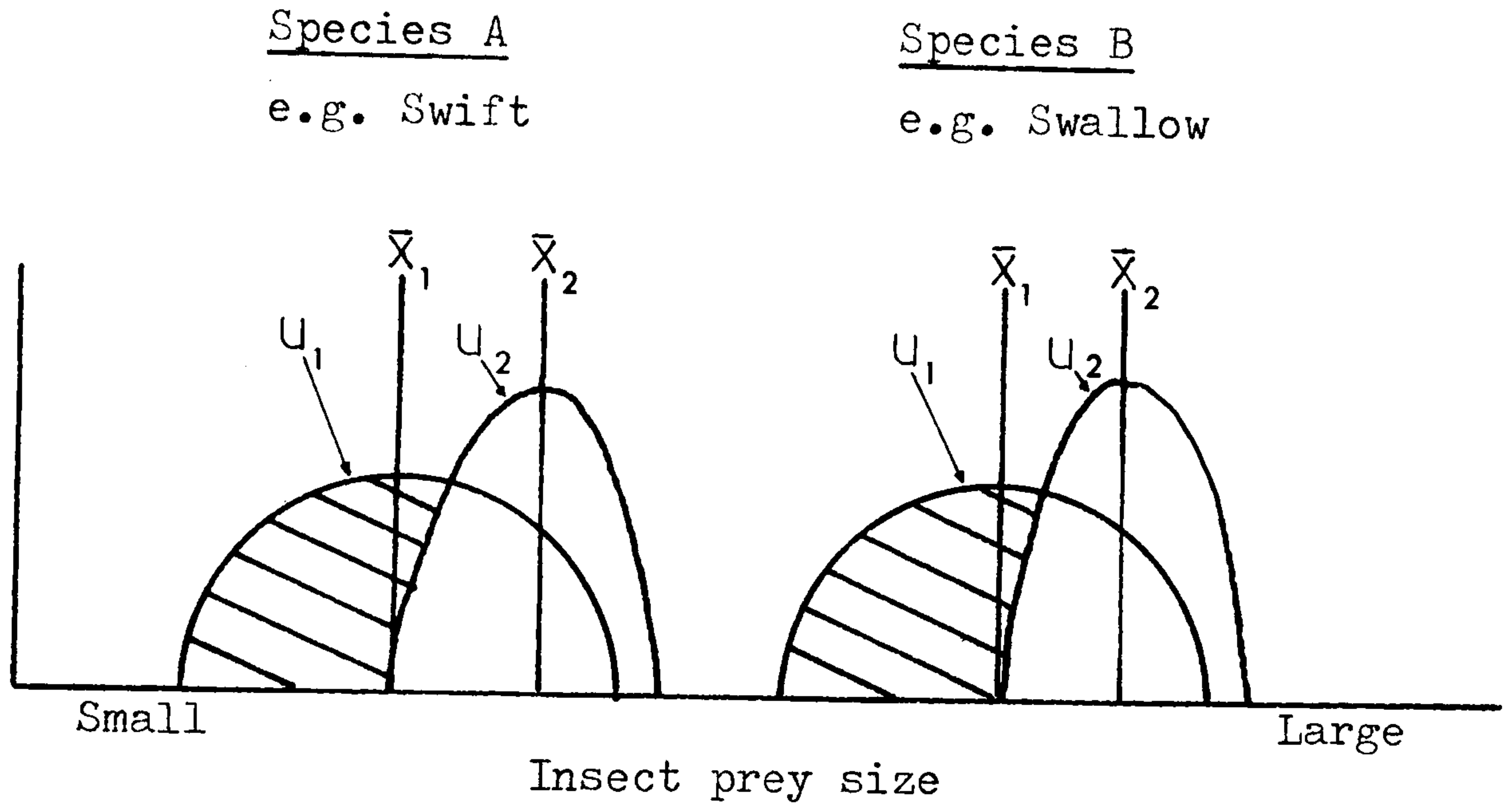


Figure 6.5.1. Prey choice in two coexisting species. For each species, u_1 is the distribution of prey sizes and $\bar{x}_1$ the mean prey size taken when the abundance of large insects is low. When the abundance of large insects is high u_1 and $\bar{x}_1$ respectively become u_2 and $\bar{x}_2$ in the diet of each species. Niche breadth of u_1 contracts to that of u_2. The distributions are not overlapped for clarity. See text for an explanation of why this may not occur.

ing to few patches in which insect prey are aggregated, hence minimising travel time between patches. These prey will be preferred types for the predator, in terms of its morphology and economy of energy expenditure in flight. Increased density of large insects will usually be parallelled by an increased abundance of smaller, swarming types of which the prey aggregations will be largely composed (see Chapter 2). Thus an optimal foraging strategy for an aerial feeding bird might entail selection of few patches from which a wide range of prey sizes are incorporated into the diet. This could be a favoured alternative strategy if maximisation of net energy intake could not be achieved by foraging in more patches from which only larger insects were selected. As shown in Figure 6.5.1 the result would be manifested as inclusion in the diet of prey sizes within the hatched areas (U_1). Indeed, the inclusion of smaller, aggregated prey types in the diet of the Sand Martin was proposed to account for observed smaller mean prey sizes and accompanying increased niche breadth under good feeding conditions.

However, this may not be the case with the Swallow since this species preys on larger, more mobile insects than do the other species. Some results in this study showed that the proportion of large items in the diet of Swallows became greater with an increase in abundance of large insects, and consequently a decrease in niche breadth may have been expected. In conflict with this, a separate analysis showed that prey size niche breadth in fact broadened on similarly good days. It is possible that in including progressively more large items in the diet on good days, the niche breadth could be simply expanded, but only to include yet larger insects, to a size greater than the original niche breadth. Limited variation in prey size niche breadths on the days sampled could have produced such a result. Change in mean prey size provides no solution as there is no correlation between this and either available insect data or environmental conditions. As has been previously intimated, Swallows might travel further from the nest, and hence through more patches, on days with reduced prey availability.

Most data in the present study emerge from analysis of a spectrum of environmental conditions ranging between very good and moderately poor. Only on one extremely bad day did analysis of prey size and patch use reveal that decreased niche breadth in both occurred simultaneously under these conditions. A threshold effect may be indicated here, whereby moderate reduction in aerial insect abundance accounts for the observed pattern of foraging throughout an increased range of patches, but further reduction results in elimination of insects from most patches and subsequent concentration of birds into those few that still provide food. The simultaneous contraction of the prey size niche breadths, arising from more powerful selection of items, may evidence the effects of (increased) competition in this situation.

To conclude, there may be an inverse relationship between specialisation in patch choice and specialisation in prey choice. Hence, an aerial feeding species selecting insect prey types which occur mainly in aggregations, such as the Swift, would specialise in patch choice and would have a rather generalised diet. The converse would operate for an aerial feeding species, such as the Swallow, selecting prey types (in a manner which broadly conforms to the predictions of optimal diet theories) with more regular spatial feeding distributions. A similar division could also apply within a species, depending on environmental conditions and how these might affect aggregation or spacing of insect prey. Hence, within a species the optimal phenotype would be that which could maximise net energy intake by switching at the optimal cross-over point from mainly patch specialisation to mainly diet specialisation.

SUMMARY AND CONCLUSIONS

1. The abundance of aerial insects increased sharply during April to reach a plateau in May which was maintained until the gradual September decline. Aerial insect density was higher nearer the ground, the spring rise in abundance occurred sooner, a greater proportion of larger insects were available, and smaller fluctuations in insect numbers indicated a more predictable food supply than at higher levels.

On a diurnal basis, biomass of aerial insects near the ground (0.2 - 3.0m) was lowest in early morning and peaked in mid-afternoon. There was a marked diurnal fluctuation in total insect numbers, but the density of large insects (>5 mm body length) was consistently low in early morning and increased throughout the day. The density of larger insects was higher later in the breeding season.

Differences in body plan of various insect types were shown to confer different flight speeds or mobilities on insects of a given size (expressed as wing span × body length mm^2).

2. The major pre-breeding influxes of the four species of aerial feeding birds into Britain (Swallow, Sand Martin, House Martin and Swift) are staggered and this was linked to their preferred prey and feeding station, insect quantity and quality at different heights and the spring rise in absolute insect abundance.

Throughout the breeding season the four species of bird were ecologically segregated with respect to size and mobility of their insect prey and with feeding station in the air-space. They were too closely packed along the prey size axis of the niche to coexist by prey size segregation alone.

Morphological adaptation to prey size was manifested in bill shape and not simply bill length or body weight. Potentially more important adaptation related to wing span and tail length influencing flight speed and manoeuvrability of the predators. Of various morphological and behavioural characters measured, only differences in the "functional bill shape" and "tail manoeuvrability index" appeared to be useful for predicting amounts of overlap in prey size and air-space respectively. Differences in wing and tail morphology were related to differences in mode of flight with the Swift and House Martin minimising flight energy expenditure by gliding much more than Sand Martin and Swallow.

Both Sand Martin and Swallow increased the ranges of prey sizes and mobilities taken in favourable feeding conditions, whilst the mean size of Sand Martin prey decreased, indicating selection for smaller, swarming insect types on good days. However, for all species the major effect of adverse feeding conditions on feeding station was to increase the number of patches in which feeding took place and consequently to increase niche breadth along this axis of the niche. Hence, it is postulated that both within species and within the aerial feeding guild there may be a propensity for switching between patch specialisation and prey specialisation; the crossover point between the two strategies will vary primarily with environmental conditions. Current theories of optimal patch and prey choice are discussed against the above perspective.

The total foraging niche size was smallest in the Swallow, but very similar for the other three species, and the Swallow consequently showed the lowest mean diffuse overlap. Diffuse overlap in air-space for each species was higher on bad days, but the lower pair-wise overlaps for air-space use in all conditions demonstrated how segregation in this niche dimension is more effective than segregation in characteristics of the prey.

Under very adverse conditions prey size overlaps between the hirundines were small; an increase in air-space overlap between Sand Martin and Swallow probably led to the decreased overlap in sizes of prey taken. Thus, it is concluded that with shortage of food resources in adverse conditions, competition between the aerial feeding species is evident.

Adult Sand Martins and Swallows select smaller prey for self-maintenance when broods have hatched. Mean prey sizes and mobilities in the predator diets were all larger than mean insect sizes and mobilities available to them.

3. Swallows brought back more food to larger broods, this being a function of number of meals delivered per unit time. Second broods received more meals but the same amount of food per brood, and therefore the average meal size was smaller.

More meals delivered to both the second broods and the larger first broods were due to an increase in the feeding rate of the male. The females only increased feeding rates for larger second broods.

Prey items of a smaller mean weight were delivered to second broods.

Mean foraging excursion times showed little diurnal variation but were slightly longer in the early morning which slightly depressed foraging efficiency. Foraging efficiency increased as a result of increased mean insect size in the chosen foraging patch and the larger mean size of prey caught there. However, potentially productive patches too distant from the nest were rejected. Of the major prey types, selection of an optimal size for fast-flying taxa was considered to be influenced by time and energy costs of pursuit.

Although apparently larger than normal broods can be raised it is postulated that extra feeding visits involve a reproductive cost e.g. increased risk of predation, diversion from other essential activities, etc. This cost will be borne primarily by the male and is non-adaptive in a monogamous breeding system requiring equal parental investment.

4. In colonial nesting Sand Martins, one pair with a centrally placed burrow were more able to minimise time spent deterring predators than a pair at the edge. Visits to the nest additional to those with food were considered to follow from conspecific nest-site competition. This was most severe at mid-season, in the centre of they colony. Earlier nesters caught larger prey items and delivered larger meals to their broods. The greater difference in prey type composition between the diets of edge and centre birds late in the season indicated they were less able to locate food concentrations than those nesting earlier.

Thus, there is an advantage in nesting early, with more birds feeding communally to aid location of food concentrations. The early nesting birds in the colony centre have more time for locating other feeding birds because they suffer less time loss through predator deterrence and competition at the nest-site. They consequently may collect more food per unit time and raise more off-spring. This interpretation depends on the few sample nests being representative of [illegible] the colony.

5. For swifts and hirundines of the West Palearctic, Nearctic and Ethiopian regions the faster a species flies the less manoeuvrable it will be. Functional bill shape was not positively correlated with tail manoeuvrability index and it is considered that selection for bill character is probably seconday to that for characters contributing to manoeuvrability and mode of flight.

Some indigenous African aerial feeders are breeding during the "winter" of the Palearctic species. For species not isolated geographically, there may be some nest-site segregation.

The Palearctic species maintained essentially the same feeding stations in winter quarters as in their breeding season but with fewer occurrences of Swifts and House Martins low down. However, the air-space niche breadths showed contraction and there was generally a reduction in overlap except between Swift and House Martin. The indigenous species showed differential air-space utilization, had small air-space niche breadths and where overlap was high the species involved apparently were not breeding during the "winter" of the Palearctic species. Thus, the aerial insect supply may be inadequate to sustain both wintering and breeding populations even though insect abundance is relatively high in the wet season.

Swallows, H. rustica, take many more Hymenoptera in Africa. The mean prey size and niche breadth of this species was very similar between Britain and Africa. With many more species utilizing the prey size axis of the niche there is likely to be compensation in another axis, probably air-space.

BIBLIOGRAPHY

ALEXANDER, R.D. 1971. The search for an evolutionary philosophy of man. R. Soc. Victoria Proc. 84: 99-120

ALEXANDER, R.D. 1974. The evolution of social behaviour. Ann. Rev. Ecol. Syst. 5: 325-383

ANDREWARTHA, H.G. and BIRCH, L.C. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago, 782 pp

ANTHONY, E.L.P. and KUNZ, T.H. 1977. Feeding strategies of the little brown bat, *Myotis lucifugus*, in southern New Hampshire. Ecology, 58: 775-786

ARMSTRONG, R.A. 1977. Weighting factors and scale effects in the calculation of competition coefficients. Am. Nat. 111: 810-812

ASH, J.S. 1969. Spring weights of trans-Saharan migrants in Morocco. Ibis 111: 1-10

ASHMOLE, N.P. and ASHMOLE, M.J. 1967. Comparative feeding ecology of sea-birds of a tropical oceanic island. Peabody Mus. Nat. Hist. Bull. 24: 1-131

ASHMOLE, N.P. 1968. Body size, prey size, and ecological segregation in five sympatric tropical terns (Aves: Laridae). Syst. Zool. 17: 292-304

BEAL, F.E.L. 1918. Food habits of the swallows, a family of valuable native birds. U.S. Dept. Agric. Bull. 619

BEHLE, W.H. 1944. The pelican colony at Gunnison Island, Great Salt Lake, in 1943. Condor. 46: 198-200

BENSON, S.W. 1953. A check-list of the birds of Nyasaland. Nyasaland Society and Publications Bureau, Blantyre and Lusaka.

BENSON, S.W., BROOKE, R.K., DOWSETT, R.J. and IRWIN, M.P.S. 1971. The birds of Zambia. Collins, London.

BLISS, C.I. 1967. Statistics in biology. Vol.I. McGraw-Hill.

den BOER, P.J. and GRADWELL, G.R. 1971 (eds.). Dynamics of populations. Proc. Adv. Stud. Int. 611 pp

BOYD, A.W. 1935. Report on the Swallow enquiry 1934. Brit. Birds, 24: 3-21

BOYD, A.W. 1936. Report on the Swallow enquiry 1935. Brit. Birds, 25: 98-115

BROEKHUYSEN, G.J. 1952. *Hirundo rustica* feeding on Amphipoda. Ostrich 23: 134-135

BROEKHUYSEN, G.J. 1964. The status and movements of the European Swallow, Hirundo rustica, in the southern part of Africa. Ardea 52: 140-165

BROEKHUYSEN, G.J. and BROWN, A.R. 1963. The moulting pattern of European Swallows, Hirundo rustica, wintering in the surroundings of Cape Town, South Africa. Ardea. 51: 25-43

BROOKE, R.K. 1956. Food of the European Swallow, Hirundo rustica. Ostrich 27: 88

BROWN, R.H. 1940. On incubation and feeding frequency of swallows and martins. Brit. Birds 32: 254

BROWN, W.L. and WILSON, E.O. 1956. Character displacement. Syst. Zool. 5: 49-64

BRYANT, D.M. 1972. The breeding biology of the House Martin, Delichon urbica, in relation to aerial insect abundance. unpubl. Ph.D. Thesis, University of London.

BRYANT, D.M. 1973. The factors influencing the selection of food by the House Martin, Delichon urbica L. J. Anim. Ecol. 42: 539-564

BRYANT, D.M. 1975a. Breeding biology of the House Martin, Delichon urbica, in relation to aerial insect abundance. Ibis 117: 180-215

BRYANT, D.M. 1975b. Changes in incubation patch and weight in nesting House Martins. Ring. Mig. 1: 33-36

BRYANT, D.M. 1978a. The establishment of weight hierarchies in the broods of House Martins, Delichon urbica. Ibis. 120: 16-26

BRYANT, D.M. 1978b. Environmental influences on growth and survival of nestling House Martins, Delichon urbica. Ibis. 120: 271-283

BRYANT, D.M. and HAILS, C.J. 1975. Mechanisms of heat conservation in the litters of mice. Comp. Biochem. Physiol. 50: 99-104

BURGER, J. 1974. Breeding adaptations of Franklin's Gull, Larus pipixcan to a marsh habitat. Anim. Behav. 22: 521-567

CACCAMISE, D.F. 1974. Competitive relationships of the Common and Lesser Nighthawks. Condor 76: 1-20

CHARNOV, E.L. 1973. Optimal foraging - some theoretical explorations. unpubl. Ph.D. Thesis. University of Washington.

CHARNOV, E.L. 1976. Optimal foraging: attack strategy of a mantid. Am. Nat. 110: 141-151

CHARNOV, E.L. and KREBS, J.R. 1974. On clutch size and fitness. Ibis 116: 217-220

CHARNOV, E.L., ORIANS, G.H. and HYATT, K. 1976. Ecological implications of resource depression. Am. Nat. 110: 247-259

CODY, M.L. 1968. On the methods of resource division in grassland bird communities. Am. Nat. 102: 107-147

CODY, M.L. 1974. Competition and the structure of bird communities. Monogr. in Pop. Biol. 7. Princeton University Press.

CUMMINS, K.W. and WUYCHECK, J.C. 1967. Caloric equivalents for investigations in ecological energetics. Int. Ver. Theor. Angew. Limnol. 18: 1-158

DAVIES, N.B. 1976a. Food, flocking and territorial behaviour of the Pied Wagtail, *Motacilla alba yarrellii* Gould, in winter. J. Anim. Ecol. 45: 235-253

DAVIES, N.B. 1976b. Parental care and the transition to independent feeding in the young Spotted Flycatcher, *Muscicapa striata*. Behav. 59: 280-295

DAVIES, N.B. 1977a. Prey selection and social behaviour in wagtails (Aves: Motacillidae). J. Anim. Ecol. 46: 37-57

DAVIES, N.B. 1977b. Prey selection and the search strategy of the

DAWKINS, M. 1971. Perceptual changes in chicks: Another look at the "search image" concept. Anim. Behav. 19: 566-574

Zambia. Puku. 4: 91-100

DUNN, E.K. 1976. Laying dates of four species of tits in Wytham Wood, Oxfordshire. Brit. Birds 69: 45-50

EMLEN, J.M. 1966. The role of time and energy in food preference. Am. Nat. 100: 611-617

EMLEN, J.M. 1968. Optimal choice in animals. Am. Nat. 102: 385-389

EMLEN, J.T. 1952. Social behaviour in nesting Cliff Swallows. Condor 54: 177-199

EMLEN, S.T. 1971. Adaptive aspects of coloniality in the Bank Swallow. Abstr. Am. Zool. 11: 47

EMLEN, J.M. and EMLEN, M.G.R. 1975. Optimal choice in diet: test of a hypothesis. Am. Nat. 109: 427-435

EMLEN, S.T. and DEMONG, N.J. 1974. Adaptive significance of synchronized breeding in the Bank Swallow. Abstr. A.O.U. Meetings 92: 8

EMLEN, S.T. and DEMONG, N.J. 1975. Adaptive significance of synchrozied breeding in a colonial bird: A new hypothesis. Science 188: 1029-1031

EWING, H.E. 1938. The speed of insect flight. Science 87: 414-415

FEINSINGER, P. 1976. Organisation of a tropical guild of nectarivorous birds. Ecol. Mono. 46: 257-291

FEINSINGER, P. and CHAPLIN, S.B. 1975. On the relationship between wing disc loading and foraging strategy in hummingbirds. Am. Nat. 109: 217-224

FOGDEN, M.P.L. 1972. The seasonality and population dynamics of equatorial forestbirds in Sarawak. Ibis 114: 307-343

FREEMAN, J.A. 1945. Studies in the distribution of insects by aerial currents. The insect population of the air from ground level to 300 feet. J. Anim. Ecol. 4: 128-154

FRY, C.H. 1972. The biology of African bee-eaters. Living Bird, 11: 75-112

GADGIL, M. 1972. The function of communal roosts: Relevance of mixed roosts. Ibis 114: 531-533

GASTON, A.J. 1974. Adaptation in the genus Phylloscopus. Ibis 116: 432-450

GIBB, J.A. 1958. Predation by tits and squirrels on the eucosmid Ernarmonia conicolona (Heyl.). J. Anim. Ecol. 27: 375-396

GIBB, J.A. 1962. L. Tinbergen's hypothesis of the role of specific search images. Ibis 104: 106-111

GIBB, J.A. and BETTS, M.M. 1963. Food and food supply of nestling tits (Paridae) in Breckland pine. J. Anim. Ecol. 32: 489-533

GILL, F.B. and WOLF, L.L. 1975. Foraging strategies and energetics of East African sunbirds at mistletoe flowers. Am. Nat. 109: 491-510

GLICK, P.A. 1939. The distribution of insects, spiders and mites in the air. Tech. Bull. U.S. Dept. Agric. No. 673: 1-150

GOSS-CUSTARD, J.D. 1977. Optimal foraging and size selection of worms by Redshank, Tringa totanus, in the field. Anim. Behav. 25: 10-29

GRANT, C. 1945. Drone bees selected by birds. Condor 47: 261-63

GRANT, P.R. 1972. Convergent and divergent character displacement. Biol. J. Linn. Soc. 4: 39-68

GRIFFITHS, D. 1975. Prey availability and the food of predators. Ecology 56: 1209-1214

GRUSON, E.S. 1976. A checklist of birds of the world. Collins, London. 212 pp von GUNTEN, K. 1961. Zur Ernährungsbiologie der Mehlschwalbe, Delichon urbica: Die qualitative Zusammensetzung der Nahrung. Orn. Beob. 58: 13-34

von GUNTEN, K. and SCHWARZENBACH, F.H. 1962. Zur Ernährungsbiologie der Mehlschwalbe, Delichon urbica: Quantitative Untersuchungen am Nestlingsfutter. Orn. Beob. 59: 1-22

HAILS, C.J. 1977. Energy expenditure in free-flying House Martins, Delichon urbica, during the breeding season. unpubl. Ph.D. Thesis, University of Stirling.

HALL, B.P. and MOREAU, R.E. 1970. An atlas of speciation in African passerine birds. Brit. Mus. Nat. Hist. London.

HAMILTON, W.D. 1971. Geometry for the selfish herd. J. Theor. Biol. 31: 295-311

HARDIN, G. 1960. The competitive exclusion principle. Science 131: 1292-1297

HARTLEY, P.H.T. 1948. The assessment of the food of birds. Ibis 90: 361-381

HERTZ, P.E., REMSEN, J.V. Jnr. and ZONES, S.I. 1977. Ecological complementarity of three sympatric parids in a California oak woodland. Condor 78: 307-316

HESPENHEIDE, H.A. 1966. The selection of seed size by finches. Wils. Bull. 78: 191-197

HESPENHEIDE, H.A. 1971. Food preference and the extent of overlap in some insectivorous birds, with special reference to the Tyrannidae. Ibis 113: 59-72

HESPENHEIDE, H.A. 1973. Ecological inferences from morphological data. Ann. Rev. Ecol. Syst. 4: 213-229

HESPENHEIDE, H.A. 1975. Selective predative by two swifts and a swallow in Central America. Ibis 117: 82-99

HOLLING, C.S. 1959a. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. Can. Entomol. 91: 293-332

HOLLING, C.S. 1959b. Some characteristics of simple types of predation. Can. Entomol. 91: 385-398

HOLLING, C.S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. Mem. Entomol. Soc. Can. 45: 1-60

HOLLING, C.S. 1966. The functional response of invertebrate predators to prey density. Mem. Entomol. Soc. Can. 48: 1-86

HOLMES, R.T. and PITELKA, F.A. 1968. Food overlap among coexisting sandpipers on northern Alaskan tundra. Syst. Zool. 17: 305-318

HOOGLAND, J.L. and SHERMAN, P.W. 1976. Advantages and disadvantages of Bank Swallow, Riparia riparia coloniality. Ecol. Mono. 46: 33-58

HORN, H.S. 1966. Measurement of overlap in comparative ecological studies. Am. Nat. 100: 419-424

HORN, H.S. 1968. The adaptive significance of colonial nesting in the Brewer's Blackbird, Euphagus cyanocephalus. Ecology 49: 682-894

HOSKING, E. and NEWBURY, C. 1946. The Swallow. Collins. London.

HUBBARD, S.F. and COOK, R.M. 1978. Optimal foraging by parasitoid wasps. J. Anim. Ecol. 47: 593-604

HUTCHINSON, G.E. 1957. Concluding remarks. Cold. Spring. Harbour. Symp. Quant. Biol. 22: 415-427

HUTCHINSON, G.E. 1959. Homage to Santa Rosalia, or Why are there so many kinds of animals? Am. Nat. 93: 145-159

JANZEN, D.H. 1973. Sweep samples of tropical foliage insects; effects of seasons, vegetation types, elevation, time of day, and insularity. Ecology, 54: 96-110

JANZEN, D.H. and SCHOENER, T.W. 1968. Differences in insect density and diversity between wetter and drier sites during a tropical dry season. Ecology 49: 96-110

JOHNSON, C.G. 1950a. A suction trap for small airborne insects which automatically segregates the catch into successively hourly samples. Ann. appl. Biol. 37: 80-91

JOHNSON, C.G. 1950b. The comparison of suction trap, sticky trap and tow-net for the quantitative sampling of small airborne insects. Ann. appl. Biol. 37: 268-285

JOHNSON, C.G. 1969. The migration and dispersal of insects by flight. Methuen, London.

JOHNSON, N.K. 1966. Bill size and the question of competition in allopatric and sympatric populations of Dusky and Gray Flycatchers. Syst. Zool. 15: 70-87

JOHNSON, R.F. 1967. Seasonal variation in the food of the Purple Martin, Progne subis, in Kansas. Ibis. 109: 8-13

KARR, J.R. 1976a. On the relative abundance of migrants from the north temperate zone in tropical habitats. Wils. Bull. 88: 433-458

KARR, J.R. 1976b. Seasonality, resource availability, and community diversity in tropical bird communities. Am. Nat. 110: 973-994

KATZ, P.L. 1974. A long term approach to foraging optimization. Am. Nat. 108: 758-782

KEAR, J. 1962. Food selection in finches with specific reference to interspecific differences. Proc. Zool. Soc. London. 138: 163-204

KLOPFER, P.H. and MACARTHUR, R.H. 1960. Niche size and faunal diversity. Am. Nat. 94: 293-300

KLOPFER, P.H. and MACARTHUR, R.H. 1961. On the causes of tropical species diversity: niche overlap. Am. Nat. 95: 223-226

KOSKIMIES, J. 1950. The life of the Swift, Micropus apus (L), in relation to weather. Ann. Acad. Sci. Fenn (A) (IV Biol.) 15: 1-151

KREBS, J.R. 1973. Behavioural aspects of predation. In Bateson and Klopfer (eds.), Perspectives in Ethology. Plenum Press

KREBS, J.R. 1974. Colonial nesting and social feeding as strategies for exploiting food resources in the Great Blue Heron, Ardea herodias. Behav. 51: 99-131

KREBS, J.R. and COWIE, R.J. 1976. Foraging strageties in birds. Ardea 64: 98-116

KREBS, J.R., ERICHSEN, J.T., WEBBER, M.I. and CHARNOV, E.L. 1977. Optimal prey selection in the Great Tit, Parus major. Anim. Behav. 25: 30-38

KREBS, J.R., KACELNIK, A. and TAYLOR, P. 1978. Test of optimal sampling by foraging Great Tits. Nature 275: 27-31

KREBS, J.R., RYAN, J.C. and CHARNOV, E.L. 1974. Hunting by expectation or optimal foraging? A study of patch use by chickadees. Anim. Behav. 22: 953-964

KRUUK, H. 1964. Predators and anti-predator behaviour of the Black-headed Gull, Larus ridibundus L. Behav. Suppl. 17 vii + 129 pp

KUZNIAK, S. 1967. Observations on the breeding biology of the Swallow, Hirundo rustica. (Polish). Acta. Orn. 10: 177-211

LACEY, E. 1910. Swifts eating drones of the hive bee. Brit. Birds. 3: 263

LACK, D. 1954. The natural regulation of animal numbers. Oxford University Press, Oxford. 343 pp.

LACK, D. 1956a. Swifts in a tower. Chapman and Hall. London.

LACK, D. 1956b. Further notes on the breeding biology of the Swift, Apus apus. Ibis 98: 606-619

LACK, D. 1966. Population studies of birds. Oxford University Press, Oxford 341 pp

LACK, D. 1968a. Ecological adaptation for breeding in birds. Methuen, London, 409 pp

LACK, D. 1968b. Bird migration and natural selection. Oikos 19: 1-9

LACK, D. 1971. Ecological isolation in birds. Blackwells, Oxford.

LACK, D. and LACK, E. 1951. The breeding biology of the Swift, Apus apus. Ibis 93: 501-546

LACK, D. and OWEN, D.F. 1955. The food of the Swift. J. Anim. Ecol. 24: 120-136

LAWTON, J.H. 1973. The energy cost of "food-gathering". In Benjamin, Cox and Peel (eds.), Resources and Population. Academic Press.

LEVINS, R. 1968. Evolution in changing environments. Princeton University Press, Princeton, New Jersey.

LEWIS, T. 1965. The effects of an artificial windbreak on the aerial distribution of flying insects. Ann. appl. Biol. 55: 503-512

LEWIS, T. 1966. An analysis of the components of wind affecting the accumulation of flying insects near artificial windbreaks. Ann. appl. Biol. 58: 365-370

LEWIS, T. and STEPHENSON, J.W. 1966. The permeability of artificial windbreaks and the distribution of flying insects in the leeward sheltered zone. Amn. appl. Biol, 58: 355-363

LEWIS, T. and TAYLOR, L.R. 1965. Diurnal periodicity of flight by insects. Trans. R. ent. Soc. Lond. 116: 393-476

LEWIS, T. and TAYLOR, L.R. 1967. Introduction to experimental ecology. Academic Press, London.

LIND, E.A. 1962. Verhalten der Mehlschwalbe, Delichon u. urbica (L.) zu ihren feinden. Ann. Zool. Soc. 'Vanamo'. 23: 1-38

LÖHRL, H.V. and GUTSCHER, H. 1973. Zur Brutökologie der Rauchschwalbe, Hirundo rustica, in einem südwestdeutschen Dorf. J. Ornith. 114: 399-416

LUNK, W.A. 1962. The Rough-winged Swallow, a study based on its breeding biology in Michigan. Publ. Nuttall Orn. Club, No.4

LYULEEVA, D.S. 1970. Energy of flight in swallows and swifts (Russian). Doklady. Akad. Nauk. SSSR, 190: 1467-1469

MACARTHUR, R.H. 1968. The theory of the niche, pp.159-176. In Lewontin, R.C. (ed.), Population biology and evolution. Syracuse University Press, Syracuse, New York, 205 pp

MACARTHUR, R.H. 1971. Patterns of terrestrial bird communities, pp.189-221. In Farner and King (eds.), Avian Biology Vol.I Academic Press. New York and London. 586 pp

MACARTHUR, R.H. 1972. Geographical ecology. Harper and Row. New York.

MACARTHUR, R.H. and LEVINS, R. 1964. Competition, habitat selection and character displacement in a patchy environment. Proc. Nat. Acad. Sci. 51: 1207-1210

MACARTHUR, R.H. and LEVINS, R. 1967. The limiting similarity, convergence and divergence of coexisting species. Am. Nat. 101: 377-385

MACARTHUR, R.H. and PIANKA, E.R. 1966. On optimal use of a patchy environment. Am. Nat. 100: 603-609

MACARTHUR, R.H. and WILSON, E.O. 1967. The theory of island biogeography. Princeton University Press. Princeton, New Jersey

MACKWORTH-PRAED, C.W. and GRANT, C.B.H. 1963. Birds of the southern third of Africa. Vols. I and II. Longmans. London.

MAY, R.M. 1973. Stability and complexity in model ecosystems. Princeton University Press, Princeton, New Jersey. 263 pp

MAY, R.M. 1975. Some notes on estimating the competition matrix, α . Ecology, 56: 737-741

MAY, R.M. and MACARTHUR, R.H. 1972. Niche overlap as a function of environmental variability. Proc. Nat. Acad. Sci. U.S.A. 69: 1109-1113

McFARLAND, D.J. 1976. Form and function in the temporal organisation of behaviour. In Bateson and Hinde (eds.), Growing points in ethology. Cambridge University Press. London.

McFARLAND, D.J. 1977. Decision making in animals. Nature, 269: 15-21

McLACHLAN, G.R. and LIVERSIDGE, R. 1970. Roberts birds of South Africa. 3rd ed. Trustees of the John Voelcker bird book fund. Cape Town.

MEAD, C.J. 1970. The winter quarters of British Swallows. Bird Study 17: 229-240

MEAD, C.J. and PEPLER, G.R.M. 1975. Birds and other animals at Sand Martin colonies. Brit. Birds 68: 89-99

MEDWAY, LORD 1974. A ringing study of migratory Barn Swallows in West Malaysia. Ibis 115: 60-86

MENDELSOHN, J.M. 1973. Some observations on age ratio, weight and moult of the European Swallow, <u>Hirundo rustica</u>, in the Central Transvaal. Ann. Trans. Mus. 28: 79-88

MERTENS, J.A.L. 1969. Influence of brood size on the energy metabolism and water loss of nestling Great Tits, *Parus major major*. Ibis 111: 11-16

MILLER, A.H. 1963. Seasonal activity and ecology of the avifauna of an equatorial cloud forst. Univ. Calif. Publ. Zool. 66: 1-78

MØLLER, A.P. 1974. Bestandstaethed og ungeproduktion hos en bestand af Landsvale, *Hirundo rustica*, 1971-73. Dansk. Orn. Foren. Tidsskr. 68: 81-86

MOREAU, R.E. 1939. Numerical data of African birds' behaviour at the nest: *Hirundo s. smithii*, the Wire-tailed Swallow. Proc. Zool. Soc. Lond. 109: 109-125

MOREAU, R.E. 1940. Numerical data on African bird's behaviour at the nest, II: *Psalidoprocne holomelaena massaica*, the Rough-wing Bank Martin. Ibis 82: 234-248

MOREAU, R.E. 1942. The breeding biology of *Micropus caffer streubelii*, Hartlaub., The White-rumped Swift. Ibis 84: 27-49

MOREAU, R.E. 1948. Ecological isolation in a rich tropical avifauna. J. Anim. Ecol. 17: 113-126

MOREAU, R.E. 1972. The Palearctic-African bird migration systems. Academic Press. London.

MOREAU, R.E. and MOREAU, W.M. 1939. Observations on Swallows and House Martins at the nest. Brit. Birds, 33: 146-157

MORIOKA, H. 1974. Jaw musculature of Swifts (Aves; Apodidae). Bull. Nat. Sci. Mus. Tokyo, 17: 1-16

MORSE, D.H. 1974. Niche breadth as a function of social dominance. Am. Nat. 108: 818-830

NEWTON, I. 1967. The adaptive radiation and feeding ecology of some British finches. Ibis 109: 33-98

ORIANS, G.H. 1961. The ecology of blackbird (*Agelaius*) social systems. Ecol. Mono. 31: 285-312

PARTRIDGE, L. 1976. Some aspects of the morphology of Blue Tits, *Parus caeruleus*, and *Coal Tits*, P. ater, in relation to their behaviour. J. Zool. Lond. 179: 121-134

PENNYCUICK, C.J. 1969. The mechanisms of bird migration. Ibis 111: 525-556

PENNYCUICK, C.J. 1972. Animal flight. Inst. Biol. No.33, London. 69 pp

PERRINS, C.M. 1970. The timing of bird's breeding seasons. Ibis 112: 242-255

PETERSEN, A.J. 1955. The breeding cycle in the Bank Swallow. Wils. Bull. 67: 235-286

PIANKA, E.R. 1966. Latitudinal gradients in species diversity: a review of concepts. Am. Nat. 100: 33-46

PIANKA, E.R. 1969. Sympatry of desert lizards, (Ctenotus), in Western Australia. Ecology 50: 1012-1030

PIANKA, E.R. 1975. Niche relations of desert lizards. In Cody and Diamond (eds.), Ecology and evolution of communities. Harvard University Press. Cambridge, Mass.

PULLIAM, H.R. 1974. On the theory of optimal diets. Am. Nat. 108: 59-74

PURCHON, R.D. 1947. The nesting activities of the Swallow. Proc. Zool. Soc. Lond. 118: 146-170

PYKE, G.H., PULLIAM, H.R. and CHARNOV, E.L. 1977. Optimal foraging: a selective review of theory and tests. Quart. Rev. Biol. 52: 137-154

RAPPORT, D.J. 1971. An optimization model of food selection. Am. Nat. 105: 575-587

RICKLEFS, R.E. 1967. Relative growth, body constituents, and energy content of nestling Barn Swallows and Red-winged Blackbirds. Auk. 84: 560-570

RICKLEFS, R.E. 1971. Foraging behaviour of Mangrove Swallows at Barro Colorado Island. Auk. 88: 635-651

RICKLEFS, R.E. and COX, G.W. 1977. Morphological similarity and ecological overlap among passerine birds on St. Kitts, British West Indies. Oikos 29: 60-66

ROOT, R.B. 1967. The niche exploitation pattern of the Blue-gray Gnatcatcher. Ecol. Mono. 37: 317-350

ROUGHGARDEN, J. 1972. Evolution of niche width. Am. Nat. 106: 683-718

ROYAMA, T. 1966. Factors governing feeding rate, food requirement and brood size of nestling Great Tits, Parus major. Ibis 108: 313-347

ROYAMA, T. 1970. Factors governing the hunting behaviour and selection of food by the Great Tit, Parus major (L.) J. Anim. Ecol. 39: 619-668

SAVILE, D.B.O. 1950. The flight mechanism of swifts and hummingbirds. Auk. 67: 499-504

SCHOENER, T.W. 1965. The evolution of bill size differences among sympatric congeneric species of birds. Evolution 19: 189-213

SCHOENER, T.W. 1968. Sizes of feeding territories among birds. Ecology 49: 123-141

SCHOENER, T.W. 1969. Models of optimum size for solitary predators. Am. Nat. 103: 277-313

SCHOENER, T.W. 1971a. Theory of feeding strategies. Ann. Rev. Ecol. Syst. 2: 369-404

SCHOENER, T.W. 1971b. Large-billed insectivorous birds: a precipitous diversity gradient. Condor 73: 154-161

SCHOENER, T.W. 1974. Some methods for calculating competition coefficients from resource utilization spectra. Am. Nat. 108: 322-340

SCHOENER, T.W. and JANZEN, D. 1968. Notes on environmental determinants of tropical versus temperate insect size patterns. Am. Nat. 102: 207-224

SIBLY, R. and McFARLAND, D.J. 1976. On the fitness of behaviour sequences. Am. Nat. 110: 601-617

SIMONS, S. and ALCOCK, J. 1971. Learning and the foraging persistence of White-crowned Sparrows, *Zonotrichia leucophrys*. Ibis 113: 477-482

SINCLAIR, A.R.E. 1978. Factors affecting the food supply and breeding season of resident birds and movements of Palearctic migrants in a tropical African savannah. Ibis 120: 480-497

SMITH, J.M. and GRAVES, H.B. 1973. Mobbing behaviour of Barn Swallows, *Hirundo rustica erythrogaster*. Abstr. Bull. Ecol. Soc. Am. 54: 43

SMITH, J.N.M. and DAWKINS, R. 1971. The hunting behaviour of individual Great Tits in relation to spatial variations in their food density. Anim. Behav. 19: 695-706

SMITH, J.N.M. and SWEATMAN, H.P.A. 1974. Food searching behaviour of titmice in patchy environments. Ecology 55: 1216-1232

SMYTHE, N. 1974. Biological monitoring data - insects. pp.70-115. In Rubinoff, R.W. (ed.), 1973 environmental monitoring and baseline data. Smithson Inst. Environ. Sci. Prog. Washington, D.C.

SNAPP, B.D. 1973. The occurrence of colonial breeding in the Barn Swallow, *Hirundo rustica*, and its adaptive significance. unpubl. Ph.D. Thesis. Cornell University, Ithaca, N.Y.

SOUTHWOOD, T.R.E. 1966. Ecological methods. Methuen, London.

STEARNS, S.C. 1976. Life-history tactics: a review of the ideas. Quart. Rev. Biol. 51: 3-47

STEMMLER-MORATH, C. 1933. Fangt der Mauersegler auch Bienen? Orn. Beob. 30: 103-104

STONER, D. 1935. Temperature and growth studies on the Barn Swallow. Auk. 52, 399-406

STONER, D. 1936. Studies on the Bank Swallow, *Riparia r. riparia,* in the Oneida Lake Region. Roosevelt Wildlife Ann. 4: 126-233

STORER, R.W. 1966. Sexual dimorphism and food habits in three North American accipiters. Auk. 83: 423-436

TAYLOR, J.S. 1949. Notes on the martins, swallows and swifts: Fort Beaufort C.P. Ostrich 20: 26-28

TAYLOR, L.R. 1955. The standardization of air-flow in insect suction traps. Ann. appl. Biol. 43: 390-408

TAYLOR, L.R. 1962. The absolute efficiency of insect suction traps. Amn. appl. Biol. 50: 405-421

TAYLOR, L.R. and PALMER, M.P. 1972. Aerial sampling. pp.189-234. In van Emden, H.F., Aphid Technology. Academic Press. London.

THOMAS, J.F. 1933-39. The food of nestling swallows. Brit. Birds. 27: 231-232; 28: 171-172; 29: 244-245; 30: 293-294; 31: 293-294; 31: 234-235; 32: 233-236; 33: 335-336

TINBERGEN, J.M. 1976. How Starlings, *Sturnus vulgaris* (L.), apportion their foraging time in a virtual single-prey situation on a meadow. Ardea. 64: 155-170

TINBERGEN, L. 1960. The natural control of insects in pinewoods, I. Factors influencing the intensity of predation by songbirds. Arch. Neerl. Zool. 13: 265-336

TINBERGEN, N. 1952. On the significance of territory in the Herring Gull. Ibis 94: 158-159

TRIVERS, R.L. 1971. The evolution of reciprocal altruism. Quart. Rev. Biol. 46: 35-37

TRIVERS, R.L. 1972. Parental investment and sexual selection. pp. -36-179. In Campbell, B. (ed.), sexual selection and the descent of man, 1871-1971. Aldine Publ. Co., Chicago.

ULFSTRAND, S. 1977. Foraging niche dynamics and overlap in a guild of passerine birds in a south Swedish coniferous woodland. Oecologia 27: 23-45

UTTER, J.M. 1971. Daily energy expenditures of free-living Purple Martins and Mockingbirds. unpubl. Ph.D. Thesis, Rutgers University, New Jersey.

van VALEN, L. 1965. Morphological variation and width of ecological niche. Am. Nat. 99: 377-389

von VIETINGHOFF-RIESCH, A.F. 1955. Die Rauchschwalbe. Dunker und Humblot, Berlin.

VERHEYEN, R. 1952. Nos hirondelles dans leurs quartiers d'hiver.

VOOUS, K.H. 1960. Atlas of European birds. Nelson. London.

VOOUS, K.H. 1977. List of recent Holarctic bird species. B.O.U. Academic Press. London.

WALSH, H. 1978. Food of nestling Purple Martins. Wils. Bull. 90: 248-260

WARD, P. 1965. Feeding ecology of the Black-faced Dioch, Quelea quelea. Ibis 107: 173-214

WARD, P. 1969. The continuous recording of birds nesting visits using radioactive tagging. Ibis 111: 93-95

WARD, P. and ZAHAVI, A. 1973. The importance of certain assemblages of birds as "information centres" for food finding. Ibis 115: 517-534

WERNER, E.E. 1977. Species packing and niche complementarity in three sunfishes. Am. Nat. 111: 553-578

WERNER, E.E. and HALL, D.J. 1974. Optimal foraging and the size selection of prey by the Bluegill Sunfish, Lepomis macrochirus. Ecology 55: 1042-1052

WILLIAMS, G.C. 1966. Natural selection, the costs of reproduction and a refinement of Lack's principle. Am. Nat. 100: 687-690

WILLIS, E.O. 1966. The role of migrant birds at swarms of army ants. Living Bird 5: 187-231

WILLSON, M.F., KARR, J.R. and ROTH, R.R. 1975. Ecological aspects of avian bill size variation. Wils. Bull. 87: 32-44

WILSON, D.S. 1975. The adequacy of body size as a niche difference. Am. Nat. 109: 769-784

WITHERBY, H.F., JOURDAIN, F.C.R., TICEHURST, N.F. and TUCKER, B.W. 1938-41. The handbook of British birds. London.

WYNNE-EDWARDS, V.C. 1962. Animal dispersion in relation to social behaviour. Oliver and Boyd, Edinburgh. 653 pp.

ZAHAVI, A. 1971. The function of pre-roost gatherings and communal roosts. Ibis 113: 106-109

ZARET, T.M. and RAND, A.S. 1971. Competition in tropical stream fishes: support for the competitive exclusion principle. Ecology 52: 336-342

APPENDIX I

1. Wing length to body length ratios for different insect taxa.

Body length				
Very short	Short	Equal	Long	Very long
Psocoptera	Plecoptera	Scatopsidae	Tabanidae	Tipulidae
Aphidoidea	Neuroptera	Brachycera*	Stratiomyidae	Culicidae
Psyllidae	Heteroptera	Empididae	Dolichopodidae	Chironomidae
Formicoidea	Homoptera	Phoridae	Brachycera*	Bibonidae
	Lepidoptera	(Acalypterate) (Schizophora†)	Syrphidae	Ichneumonidae
	Trichoptera	Opomyzidae	Sepsidae	Apidae
	Simuliidae	Borboridae	Muscidae	Vespidae
	Psychodidae	Agromyzidae	Cordilurinae	Bombus sp.
	Cecidomyidae	Chloropidae		
	Lonchopteridae	Chalcidoidea		
	Cynipidae	Pteromalidae		
	Coleoptera	Proctotrupoidea		

* ≃ 50% in each category

† most sub-taxa

2. Statistics of transformation of available insect and prey size class data

	Log mm^2					Log mm	mm	
Species	Mean	S.D.	g_1	g_2	χ^2	χ^2	χ^2	N
Swift	1.4660	0.3320	0.525	0.747	51.94			796
House Martin	1.5003	0.2265						
Sand Martin	1.5677	0.3073	0.158	0.631	62.25			2,623
Swallow	1.7640	0.3345	0.150	0.465	21.87	22.0	4,677.8	1,691
<u>Height (m)</u>								
12.2	1.3040	0.3270	0.257	-0.370	100.25			4,071
1.8	1.2350	0.3410	1.110	2.503	2,798.25			5,003
Ground level	1.2640	0.3650	1.388	3.682	5,316.25	5,312.5	355,811.0	6,090

g_1 = skewness g_2 = kurtosis

$$\chi^2 = \frac{g_1^2}{V(g_1)} + \frac{g_2^2}{V(g_2)} \quad \text{with 2 D.F.}$$

3. Statistics of observations of feeding heights (m)

	Mean	S.D.	Range	N
High level				
Swift	66.2	64.1	17.6 - 352.9	47
House Martin	54.2	51.7	12.5 - 235.3	56
Sand Martin	29.3	17.6	12.5 - 147.1	108
Swallow	32.9	39.7	12.5 - 132.4	16
All species	43.4	44.4	12.5 - 352.9	227
Mid-level				
Swift	13.7	3.0	5.9 - 20.6	79
House Martin	12.4	3.3	4.4 - 19.1	113
Sand Martin	13.5	3.6	4.4 - 19.1	110
Swallow	8.9	3.0	3.7 - 14.7	55
All species	12.5	3.6	3.7 - 20.6	357
Low level				
Swift	3.2	0.8	1.5 - 5.1	20
House Martin	2.4	0.7	1.5 - 5.1	42
Sand Martin	2.6	1.3	0.7 - 5.1	110
Swallow	1.4	0.8	0.3 - 5.1	81
All species	2.2	1.2	0.3 - 5.1	253
All levels				
All species	17.7	28.3	0.3 - 352.9	837

4. Correlation matrix of subjective weather categories and 24 hour insect abundance samples ($\log_{10} n + 1$)

	12.2m	1.8m	Ground level
Wind speed	- 0.208***	- 0.272***	- 0.219 ***
Air temperature	0.386***	0.429***	0.400***
Sunshine	- 0.040 N.S.	0.050 N.S.	- 0.007 N.S.
Cloud Cover	- 0.018 N.S.	- 0.139 *	- 0.078 N.S.
Rainfall	- 0.194***	- 0.254***	- 0.155***

$n = 220$

*** $P \leq 0.001$

* $P < 0.05$

5. Factors influencing the feeding distributions of the four aerial feeding species.
Symbols and layout as in Figure 2.8.12 * = variables significantly correlated (< 0.05, r in first column)

SWIFT

1	r		β
T	0.53		0.514
I	0.28		0.208
II	0.15	*	-0.189
C	-0.14	*	0.179
R	-0.16	*	-0.116
III	0.27		0.103
S	0.26		0.063

4			
S	0.38		0.401
R	-0.30		-0.211
T	0.31		0.192
W	-0.14	*	-0.188
C	-0.26		0.239

7			
R	0.22		0.22

2W			
T	-0.22		-0.148
S	-0.22		-0.147

2L			
T	-0.21		-0.166
W	0.14	*	0.147
S	-0.18	*	-0.101

5			
T	-0.36		-0.298
III	-0.22		-0.137
S	-0.21		-0.054
I	-0.17	*	0.074
II	-0.18	*	-0.059

8			
T	-0.40		-0.380
R	0.36		0.332
III	-0.28		-0.199
S	-0.19	*	0.127
II	-0.20		0.079
C	0.20	*	0.016
I	-0.24		-0.013

10W			
T	-0.48		-0.426
R	0.19	*	0.131
I	-0.25		-0.305
S	-0.33		-0.166
C	0.21		-0.157
III	-0.16	*	0.039

10L			
T	-0.46		-0.41
W	0.20		0.25
I	-0.29		-0.32
III	-0.14	*	0.22
R	0.20		0.10
C	0.26		-0.21
S	-0.30		-0.20

3W			
W	0.19	*	0.190

3L			
W	0.19	*	0.190

6			
II	-0.17	*	-0.145
W	0.17	*	0.129
R	0.14	*	0.074
C	0.16	*	0.077

9			
T	-0.38		-0.374
R	0.35		0.317
S	-0.18	*	0.131
I	-0.22		-0.084
C	0.20		0.027
II	-0.17	*	0.029
III	-0.19	*	-0.022

11W			
T	-0.23		-0.193
S	-0.16	*	-0.064

11L			
T	-0.24		-0.2
W	0.21		0.22

HOUSE MARTIN

1	r		β
T	0.45		0.349
S	0.35		0.226
R	-0.21		-0.108
C	-0.23		0.024

4			
T	0.37		0.297
W	-0.20		-0.215
III	0.21		0.127
C	-0.26		-0.071
I	0.23		0.120
II	0.21		-0.089
S	0.23		0.034

7			
I	-0.24		-0.249
T	0.14	*	0.214
II	-0.21		-0.185
S	0.15	*	0.032

2W			
II	0.21		0.192
R	-0.14	*	-0.125
W	-0.12	*	-0.093
III	0.14	*	0.016
I	0.13	*	-0.014

2L			
W	0.20		0.200

5			
W	-0.20		-0.190
T	-0.12	*	-0.111

8			
III	-0.32		-0.333
R	0.16	*	0.136
T	-0.20		-0.104
II	-0.17		0.197
III	-0.24		-0.140

10W			
T	-0.21		-0.183
S	-0.15	*	-0.061

10L			
W	0.28		0.301
T	-0.24		-0.182
R	0.17		0.120
II	-0.17		-0.048
S	-0.18		-0.139
C	0.18		-0.114
I	-0.13	*	-0.048

3W			
W	0.14	*	0.146
T	-0.12	*	-0.108
II	-0.12	*	-0.015

3L			
W	0.25		0.248
T	-0.13	*	-0.124
R	0.13	*	0.089

6			
C	0.16	*	0.138
III	0.16	*	0.152
W	0.13	*	0.096

9			
T	-0.34		-0.237
R	0.28		0.183
III	-0.28		-0.283
I	-0.14	*	0.103
C	0.22		0.063
S	-0.22		0.006

11W			
W	0.23		0.215
T	-0.19		-0.151
C	0.22		0.091
S	-0.17		-0.028

11L			
W	0.30		0.283
T	-0.26		-0.227
C	0.29		0.136
R	0.14	*	0.030
S	-0.20		0.022

SAND MARTIN

1	r		β
T	0.45		0.458
I	0.11	*	-0.192
R	-0.22		-0.109
S	0.34		0.160
C	-0.25		0.109

4			
T	0.53		0.538
W	-0.19		-0.137
R	-0.25		-0.114
II	0.27		0.344
III	0.15		-0.346
C	-0.25		0.205
S	0.32		0.105

7			
III	0.26		0.378
T	0.24		0.171
II	0.14		-0.234

2W			
W	-0.30		-0.255
R	-0.20		-0.113
I	0.15		0.092
C	-0.21		-0.137
S	0.14		-0.048
III	0.11	*	0.071
II	0.12	*	-0.063

2L			
W	0.27		0.279
T	-0.23		-0.306
R	-0.13	*	-0.232
I	-0.11	*	0.102
II	-0.10	*	-0.077
S	-0.10	*	0.015

5			
III	-0.37		-0.394
W	-0.21		-0.217
R	0.10	*	0.097
II	-0.25		0.148
I	-0.31		-0.102
T	-0.18		-0.020

8			
II	0.23		0.209
III	0.19		0.024
I	0.16		

10W			
W	-0.30		-0.249
III	0.18		0.237
C	-0.24		-0.237
I	0.17		-0.107
S	0.14		-0.058
II	0.19		0.041
R	-0.11	*	0.004

10L			
W	0.26		0.248
T	-0.17		-0.135
S	-0.13	*	-0.022

3W			
T	-0.21		-0.186
R	0.09	*	0.041
S	-0.13		-0.060
C	0.10	*	-0.051

3L			
W	0.45		0.419
T	-0.19		-0.276
III	0.14		0.270
R	0.18		0.102
S	-0.17		0.160
C	0.24		0.082

6			
T	-0.26		-0.155
III	-0.19		-0.168
S	-0.18		-0.057
C	0.18		0.057
I	-0.18		0.075
R	0.12	*	0.030
II	0.17		-0.029

9			
R	0.20		0.176
III	0.15		0.221
T	-0.12		-0.153
S	-0.18		-0.013
C	0.16		0.003

11W			
T	-0.16		-0.141

11L			
W	0.40		0.339
T	-0.21		-0.285
R	0.17		0.080
S	-0.18		0.112
C	0.23		0.0[illegible]2

SWALLOW

<table>
<tr><td colspan="2">1
r β
W 0.11 * 0.114</td><td colspan="2">4
T 0.22 0.223</td><td colspan="2">7
S 0.20 0.171
T 0.17 0.050
C -0.13 * 0.025</td></tr>
<tr><td>2W</td><td>2L
II -0.14 * -0.116
W 0.12 * 0.084
III-0.12 * -0.007</td><td>5
C -0.30 -0.232
W -0.24 -0.157
R -0.20 -0.057
I 0.11 * 0.050</td><td>8
W -0.16 -0.194
III-0.11 * -0.154</td><td>10W</td><td>10L</td></tr>
<tr><td>3W
T -0.16 * -0.155</td><td>3L
W 0.28 0.269
T -0.12 * -0.091</td><td>6
III 0.46 0.285
T 0.42 0.261
I 0.41 0.091
W -0.13 * -0.026
S 0.13 * 0.011
II 0.43 0.013</td><td>9
III-0.42 -0.590
C 0.28 0.334
II -0.31 0.341
T -0.36 -0.154
R 0.13 * -0.085
I -0.35 -0.094
S -0.19 0.052
W 0.12 * -0.003</td><td>11W
III-0.28 -0.184
C 0.13 * 0.079
T -0.21 -0.064
I -0.26 -0.082
R 0.14* 0.033</td><td>11L
W 0.35 0.265
T -0.34 -0.247
R 0.30 0.160
III-0.30 -0.144
II -0.29 0.155
I -0.30 -0.130
S -0.14 * 0.081
C 0.21 0.046</td></tr>
</table>

6. Gliding/active flight ratios data

Patch	Swallow			Sand Martin			House Martin			Swift		
	Gliding Mean time (s)	Active Mean time (s)	G/ratio σ	G $\bar{x}$(s)	A $\bar{x}$(s)	G/A σ	G $\bar{x}$(s)	A $\bar{x}$(s)	G/A σ	G $\bar{x}$(s)	A $\bar{x}$(s)	G/A σ
1	24.6	23.0	0.247	39.8	19.8	0.364	45.4	8.8	1.486	53.6	1.7	19.549
2W	3.8	27.1	0.052	4.6	25.6	0.065	14.2	9.1	0.500	24.4	10.0	1.100
2L	2.8	31.1	0.060	11.0	22.5	0.254	12.0	11.1	0.536	24.0	12.8	0.322
3W	4.6	46.0	0.022	3.0	23.1	0.052	9.4	12.9	0.411	12.8	17.1	0.268
3L	4.4	62.9	0.009	3.6	30.0	0.063	9.8	15.6	0.367	19.8	19.0	0.335
4	42.4	37.5	0.129	24.0	19.1	0.819	53.1	8.5	1.360	48.2	3.2	3.290
5	19.4	57.1	0.094	12.2	26.0	0.114	46.4	25.5	0.164	45.8	10.6	1.932
6	4.0	33.3	0.070	4.8	22.8	0.055	27.0	21.3	0.302	16.0	12.9	0.668
7	41.0	25.8	0.416	46.8	24.1	0.254	43.0	7.1	1.776	40.4	4.4	3.106
8	16.4	40.0	0.028	22.8	43.0	0.142	25.8	9.8	0.957	28.4	5.0	3.336
9	3.6	45.0	0.041	7.6	44.7	0.045	13.8	24.2	0.191	16.0	16.7	0.504
10W	5.8	44.6	0.037	6.4	32.0	0.070	23.0	15.8	0.491	23.4	10.0	1.105
10L	3.0	33.3	0.043	6.0	40.0	0.052	18.2	16.9	0.338	23.8	8.1	1.862
11W	4.0	36.4	0.057	2.2	18.3	0.064	12.0	24.0	0.228	16.0	14.8	0.290
11L	3.6	40.0	0.048	2.4	30.0	0.022	8.2	21.0	0.153	17.0	14.1	0.674

For Swallow patch 6 and Sand Martin patch 5, n = 10: all other patches, n = 5.

7. Comparison of the variances (F) in prey size between the four predators.

	House Martin	Sand Martin	Swallow
Swift	2.13	1.16	1.02
House Martin		1.84	2.18
Sand Martin			1.19

8. Overlap in prey type between aerial feeding birds.

<u>Diffuse</u>

Swift	0.818	House Martin	0.844
Swallow	0.734	Sand Martin	0.982

<u>Pairwise</u>

	Swift	House Martin	Sand Martin
Swallow	0.624	0.658	0.858
Sand Martin	0.864	0.874	
House Martin	0.834		

APPENDIX II

1. Available aerial insects: diurnal variation data

	Early season (June/July)					Late season (August/September)		
Active Daytime 90 minute period		Number insects >5mm at all stations		Mean insect dry weight (mg) all stations			Number >5mm	$\bar{x}$ mg
	n	$\bar{x}$	σ	$\bar{x}$	σ	n	$\bar{x}$	$\bar{x}$
2	6	0.667	0.606	0.251	0.159			
3						1	4.000	0.752
4	6	1.167	0.649	0.201	0.021	2	2.625	0.879
5	6	1.778	1.088	0.517	0.310	3	4.806	0.981
6	6	2.222	0.878	0.557	0.388	1	5.200	0.708
7	3	1.890		0.650		3	8.440	1.145
8	3	2.833		0.504		2	10.600	0.888
9	6	2.305	0.764	0.595	0.912	2	2.875	1.377
10	6	2.752	1.233	0.485	0.103	2	2.250	1.054

2. Food delivery to nestling Swallows: diurnal variation data

		First broods						Second broods						
Active Daytime 90 min period		Kcal/min/ $g^{0.67} \times 10^3$		Mean item dry weight (mg)		No. items/min $g^{0.67}$			Kcal/min $g^{0.67} \times 10^3$		$\bar{x}$ mg		No. items/min $g^{0.67}$	
	n	$\bar{x}$	σ	$\bar{x}$	σ	$\bar{x}$	σ	n	$\bar{x}$	σ	$\bar{x}$	σ	$\bar{x}$	σ
2	6	1.080	0.371	6.900	3.929	0.040	0.031							
3								2	1.470		6.850		0.040	
4	6	1.491	0.798	11.733	6.632	0.048	0.072	4	1.685	0.835	8.063	4.767	0.049	0.032
5	6	1.379	0.604	15.517	9.948	0.021	0.013	5	1.660	1.179	6.980	2.144	0.045	0.022
6	6	1.410	1.262	24.783	17.162	0.013	0.011	7	1.676	0.743	9.873	2.311	0.034	0.017
7	3	2.071		20.967		0.021		6	1.059	0.628	10.253	5.268	0.022	0.011
8	3	2.237		16.433		0.027		6	1.177	0.718	9.743	5.971	0.025	0.011
9	6	1.385	0.783	20.117	8.356	0.014	0.009	4	1.594	1.190	6.088	4.366	0.056	0.030
10	6	1.635	0.676	11.950	5.606	0.033	0.021	4	1.197	0.397	4.403	2.017	0.063	0.035

3. Data on rates of feeding of nestling Swallows from automatic recording of visits

Active Daytime 90 minute period	Number of visits by both sexes									
	Normal sized broods						Enlarged broods			
	Firsts: 5 nestlings			Seconds: 4 nestlings			Firsts: 7 nestlings		Seconds: 6 nestlings	
	n	$\bar{x}$	σ	n	$\bar{x}$	σ	n	$\bar{x}$	n	$\bar{x}$
2	4	37.8	8.6							
3	4	46.3	6.3	3	50.7		2	49.5		
4	4	43.8	14.9	3	55.0		2	67.0	1	98.0
5	5	55.6	14.7		51.7		2	64.0	3	66.3
6	5	54.6	12.9	4	61.0	16.4	2	72.5	3	72.7
7	5	45.6	12.3	4	64.5	4.9	2	59.0	2	78.0
8	5	50.8	10.9	4	58.5	11.8	2	56.5	1	86.0
9	5	45.0	7.9	5	65.0	7.5	2	47.5	1	76.0
10	4	40.5	12.9	4	49.8	13.7	2	40.5	1	52.0
11	4	47.0	15.6	3	57.0		2	43.5	1	50.0.
12	3	27.0					3	41.0		

4. Data on rate of feeding of nestling swallows

Source		Brood age during observation (days)	Number in brood	Brood mass $g^{0.67}$	Feeds by ♂ and ♀ per hour
Moreau and Moreau	1939	11, 15	3	15.70	15.5
Brown	1940	15	4	20.14	27.0
Purchon	1947	9-15	4	18.43	37.2
Snapp	1973	8-13	1	7.07	11.8
		"	2	11.30	19.0
		"	3	14.72	26.8
		"	4	17.84	31.0
		"	5	20.78	29.3
		"	6	23.38	34.7
Present study		9-11, 14,15	5	21.98	29.9
		12-13	7	27.92	35.5
<u>Second broods</u>					
Snapp	1973	8-13	1	7.07	20.0
			3	14.72	23.0
			4	17.84	32.3
			5	20.78	31.6
			6	23.38	44.6
Present study		9-10,11	4	16.9	38.5
		11, 13	6	24.52	47.7

5. Single nestling weights (g) from growth curve data

Age in days	8	9	10	11	12	13	14	15	$\bar{x}$
A	14.5	17.4	18.9	19.7	20.9	21.2			18.8
B		15.5	17.3	18.9	20.6	21.5	21.8	22.6	19.7

A, Snapp 1973; B, Kuzniak 1967, present study